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Studies on Phenology and Intra-annual Tree Ring Growth along Altitudinal Gradients in the Werdenfelser Region

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Studies on Phenology and Intra-annual Tree Ring Growth along Altitudinal Gradients in the Werdenfelser Region

(Untersuchungen zu Phänologie und intra-annuellem Stammwachstum entlang von Höhengradienten im Werdenfelser Land)

Christina Schuster

I went to the woods because I wished to live deliberately,
I wanted to live deep and suck out all the marrow of life,
To put to rout all that was not life and not when I had come to die
Discover that I had not lived.

Henry David Thoreau

Abstract

Background and Objectives

In the thematic field of ecosystems and human environments, one topic recently became critical: climate change. In the last century global average air temperature increased by about 0.7 °C, mainly due to human emissions of atmospheric greenhouse gases since the Industrial Revolution. This has already led to (and will lead to) changes in weather patterns and serious consequences for ecosystems across the world. Mean temperatures rose by 1.1 °C in Southern Germany and even by about 1.5 °C in the European Alps. Thus, the Alps with their various microhabitats and specialized species are especially threatened by climate change. Some species only slowly adapt (left-behind) or have no retreating areas (nowhere-to-go). Moreover, future scenarios predict further temperature increases above the global average in this region.

Phenology, the science of recurring natural events, has developed to be an essential tool in the detection of how shifts in the abiotic environment influence processes and functioning of terrestrial ecosystems: Changing temperature shifts the onset dates of phenological phases. This circumstance has reinforced the interest in phenological research in recent years and therefore phenology is a main focus of this thesis. The second focus is the scientific field of dendroecology (tree ring growth) because numerous studies have reported increased tree growth in Central Europe due to recent global warming. In our study, the phenology of seven and the tree-ring growth of two tree species in the montane forest of the Werdenfelser Land (Southern Bavaria) were investigated along altitudinal gradients. Since air temperature is the most important environmental parameter changing with elevation and influencing plant phenology and growth, altitudinal gradients can serve as so-called space-for-time experiments: Temperature variations in time are replaced by temperature variations in space.

Summarizing, the objective of this thesis was to estimate impacts of climate change on alpine tree phenology and stem growth by investigations along natural gradients. Hereby, the following research questions were at the heart of our study:

a) What is the magnitude of tree phenological response to a wide range of elevation and thus temperature regimes?
b) Do inversion situations in alpine areas influence leaf senescence phenology?
c) Is the intra-annual course of tree ring growth and its differentiation phases related to leaf phenology, elevation and temperature?

Methods

In the study area Werdenfelser Land, four altitudinal gradients (700-1800 m a.s.l.) with 42 study sites separated by 100 m in elevation were installed including temperature and humidity loggers at each site and a fully equipped meteorological station on each gradient. At each site three adult and three juvenile trees were chosen from seven tree species (*Abies alba* MILL., *Acer pseudoplatanus* L.*,* *Fagus sylvatica* L., *Larix decidua* MILL., *Picea abies* L. (KARST), *Pinus mugo* TURRA and *Pinus sylvestris* L.). They were observed weekly from April to July and from September to October in the years 2010 and 2011. The most foreward phenological phase for each individual was noted according to species-specific observation keys. These keys based on the BBCH Code (Meier 1997) were adjusted to the tree species and photographs of detailed phenological phases were added. Onset dates for phenological phases were calculated by logistic regression of the observation data over time. Using linear regressions of onset dates against elevation, altitudinal response rates of the onset dates were determined. Based on the logger data from the gradients, temperature lapse rates could be determined and were combined with the altitudinal response rate. In this way, the responses of phenological onset dates to temperature were identified. In 2011, at eight sites on two of the gradients, separated by 200 m in elevation, microcores of two individuals of *P. abies* and two of *F. sylvatica* were taken using a Trephor tool. Sampling took place once a week in early spring and at longer intervals later on. Thin sections were cut and stained in Safranin-O-Astrablau to visualize different phases of xylem cell development. Ring width of phloem and xylem cells as well as growing, cell wall thickening and lignified cells were measured three times at each thin section. On these measurements Gompertz and Hadwiger curves were fitted, dependent on the phase. Tree-ring growth onset dates were calculated based on these models. The onset dates and altitudinal response rates were compared to temperature and leaf phenology.

Results and Conclusions
We were able to determine numerous species-specific and phase-specific phenological response rates for the seven tree species. Our phenological response rates displayed advanced phenological phases in spring and delayed phases in autumn with increasing temperature; magnitudes matched to values of prior studies. In total, we determined an extension of the vegetation period of about two weeks per degree. Moreover we found the relation between required chilling period and bud burst forcing temperatures to be very distinct for deciduous species, but less pronounced and highly variable for evergreen species. We additionally found a consistent pattern in temperature responses between different phases: Early spring and late autumn phases show higher response rates than late spring and early autumn phases. Comparing the species, *A. pseudoplatanus*, *L. decidua* and *P. abies* spring phenology turned out to be highly sensitive to elevation and temperature, followed closely by *F. sylvatica* and finally by *A. alba* and the *Pinus* species. We found leaf senescence in autumn as sensitive to temperature as leaf development in spring, especially in case of strongly increased temperatures like in the year 2011. These results were in contrast to other studies reporting responses in autumn to be smaller than in spring. Considering the magnitudes of spring and autumn phenological shifts, we conclude that it plays a major role in which season the temperature increases most.

Inversions, which extraordinarily frequently occurred in autumn 2011, influenced the altitudinal pattern of phenology as we could show for the first time in detail for phenological senescence phases. Trees in the valleys faced with cold temperatures responded with advanced senescence onset dates, whereas the signal was stronger in late phases and stronger for *A. pseudoplatanus* compared to *F. sylvatica*. It is still unclear if climate change influences the weather patterns favoring inversion situations. Thus, we consider this phenomenon as highly variable in space and time but common in alpine regions.

We used the new method of microsampling to determine onset dates of different phases in tree-ring development and their relation to phenology. Tree ring width and maximal extension of all differentiation phases were reduced with elevation. Growing season for *F. sylvatica* was drastically reduced, but remained almost unchanged for *P. abies*. This indicates that *F. sylvatica* stem growth might be highly adaptable to changes in temperature and likely benefits from the lengthened vegetation period. Start dates in wood formation were related to specific phenological phases, but end dates were independent from phenology. First phloem cells in *P. abies* occurred about seven weeks before xylogenesis and bud burst. *P. abies* differentiation phases in xylogenesis were not independent from each other and moreover might be linked to phenological temperature response (especially bud burst). For *F. sylvatica* we now could differentiate that first phloem cells occur with bud burst, first xylem cells with leaf unfolding and the maximum growth rate when young leaves are fully unfolded. *F. sylvatica* wood formation was more strongly controlled by exogenous parameters compared to *P. abies* and probably will show a stronger reaction to climate change. Thus, in higher elevations like our study area we expect an extended season for stem growth, especially for deciduous species. In lower elevations however, increasing temperatures could lead to reduced stem growth caused by drought stress.

Deutsche Kurzfassung

Hintergrund und Zielsetzung

In jüngster Zeit darf ein Schlagwort in der Diskussion über die natürliche und anthropogen geprägte Umwelt nicht fehlen: der Klimawandel. Im letzten Jahrhundert stieg die globale Jahresmitteltemperatur um etwa 0.7 °C an. Die Hauptursache dafür waren ansteigende anthropogene Emissionen von Treibhausgasen seit Beginn der Industriellen Revolution. Als Konsequenz sind heute schon Veränderungen in Witterungsmustern und Wetterlagen sowie gravierende Auswirkungen auf Ökosysteme auf dem ganzen Planeten bereits nachweisbar. Regional betrachtet stiegen die Temperaturen in Süddeutschland sogar um 1.2 °C und in den Europäischen Alpen um etwa 1.5 °C. Daher zählen die Alpen mit zahlreichen kleinstrukturierten Habitaten und hochangepassten Tier- und Pflanzenarten zu den Ökosystemen, die besonders durch den Klimawandel bedroht sind. Einige hier ansässige Arten können sich nur langsam anpassen oder finden keine Rückzugsräume. Darüber hinaus prognostizieren Zukunftsmodelle für diese Region weiterhin stark ansteigende Temperaturen über dem globalen Durchschnitt.

Die Phänologie, die Wissenschaft vom Eintrittszeitpunkt wiederkehrender Ereignisse, ist heute ein wichtiges Werkzeug, um den Einfluss von veränderten abiotischen Umweltfaktoren auf Prozesse und Funktionsweisen terrestrischer Ökosysteme festzustellen: Veränderte Temperaturen verschieben die Eintrittszeitpunkte von phänologischen Phasen. Dieser Umstand verstärkte in den letzten Jahren das Interesse an phänologischen Studien und macht daher die Phänologie auch zu einem Kernthema der vorliegenden Dissertation. Das zweite Kernthema ist das Wissenschaftsfeld der Dendroökologie, da mehrere Studien ein zunehmendes Baumwachstum in Mitteleuropa beobachteten und den steigenden Temperaturen des Klimawandels zuschrieben.

In unserer Studie wurden die Phänologie von sieben und das Ringwachstum von zwei Baumarten im montanen Bergwald im Werdenfelser Land entlang von Höhengradienten untersucht. Da die Temperatur der wichtigste Parameter ist, der mit der Höhe abnimmt und der sowohl die Phänologie und das Wachstum von Pflanzen maßgeblich beeinflusst, können Höhengradienten für sogenannte Raum-für-Zeit-Experimente herangezogen werden: Temperaturänderungen im zeitlichen Verlauf werden hierbei durch Temperaturänderungen im Raum ersetzt.

Zusammengefasst war das Ziel dieser Arbeit, den Einfluss des Klimawandels auf die Phänologie und das Stammwachstum einiger Baumarten im Alpenraum entlang von Höhengradienten zu untersuchen. Dabei standen folgende Forschungsfragen im Zentrum:

a) Wie groß ist die Reaktion der Phänologie der ausgewählten Baumarten auf eine breite Spannweite von Höhen und daher Temperatur-Regimen?
b) In welcher Weise beeinflussen Inversionslagen im Alpenraum die Herbst-Phänologie?
c) Ist das Stammwachstums im Jahresverlauf mit seinen verschiedenen Differenzierungs-Phasen mit der Phänologie, der Höhe und der Temperatur verknüpft?

Methoden

Im Untersuchungsgebiet Werdenfelser Land wurden vier Höhengradienten (700-1800 m ü.N.N.) mit Temperatur- und Luftfeuchte-Loggern an 42 Beobachtungsstandorten im Abstand von 100 Höhenmetern und mit je einer vollausgestatteten meteorologischen Station angelegt. Von sieben Baumarten (*Abies alba* MILL., *Acer pseudoplatanus* L., *Fagus sylvatica* L., *Larix decidua* MILL., *Picea abies* L. (KARST), *Pinus mugo* TURRA und *Pinus sylvestris* L.) wurden an jedem Standort drei adulte Bäume und drei Bäume aus der Verjüngung ausgewählt. Diese wurden von April bis Juli und von September bis Oktober in den Jahren 2010 und 2011 phänologisch beobachtet. Dafür wurde jeweils das am weitesten vorangeschrittene phänologische Stadium eines Individuums nach einem artspezifischen Beobachtungsschlüssel notiert. Diese Schlüssel, die mehrere Phasen beinhalten, basieren auf Meiers (1997) BBCH Code. Sie wurden an die jeweilige Art angepasst und durch Abbildungen der detaillierten Phasen ergänzt. Die Eintrittszeitpunkte der phänologischen Phasen wurden durch logistische Regression der Beobachtungen über die Zeit berechnet. Durch lineare Regression der Eintrittszeitpunkte über die Höhe konnten höhenabhängige phänologische Änderungsraten bestimmt werden. Mithilfe der Logger-Daten von den Gradienten wurden Temperatur-Änderungsraten mit der Höhe errechnet und mit den höhenabhängigen phänologischen Änderungsraten verknüpft. Somit konnten Reaktionen der Eintrittszeitpunkte auf die Temperatur ermittelt werden.

Im Jahr 2011 wurden an acht Standorten mit 200 m Höhenabstand an zweien der existierenden Gradienten sogenannte „Microcores“ von jeweils zwei Individuen von *Picea abies* und *Fagus sylvatica* mithilfe eines Trephors genommen. Die Probeentnahme erfolgte einmal wöchentlich im Frühjahr und später in größeren Abständen. Aus den Microcores wurden Dünnschnitte erstellt und mit Safranin-O-Astrablau eingefärbt, damit die verschiedenen Differenzierungsphasen sichtbar wurden. Die Ringweite von Xylem und Phloem sowie von Zellen im Wachstums-, Zellwandverdickungs- und Lignifizierungs-Stadium wurde an jedem Schnitt drei Mal gemessen. Auf diese Daten wurde je nach Stadium ein Gompertz oder ein Hadwiger Modell angepasst, aus dem Eintrittszeitpunkte des Baumring-Wachstums errechnet wurden. Die Eintrittszeitpunkte und deren höhenabhängige Veränderung wurden mit Temperatur und Blattphänologie verglichen.

Ergebnisse und Schlussfolgerungen

Wir konnten eine Vielzahl an art- und phasen-spezifischen phänologischen Reaktionsraten der sieben Baumarten bestimmen. Die phänologischen Reaktionen zeigten frühere Frühjahrs- und spätere Herbst-Phasen mit steigenden Temperaturen; die Größenordnungen stimmten mit früheren Studien überein. Insgesamt ergab sich eine Verlängerung der Vegetationsperiode von etwa zwei Wochen pro Grad Celsius. Der Zusammenhang zwischen längerer Ruhephase im Winter und geringeren Temperatursummen, die für den Knospenaufbruch im Frühjahr benötigt werden, war für Laubbäume sehr ausgeprägt. Nadelbäume zeigten hierfür eine geringere und stark art-abhängige Reaktion. Zusätzlich konnten wir zeigen, dass die phänologische Reaktion auf Temperaturänderungen stark von der beobachteten Phase abhängt: Frühe Phasen im Frühjahr und späte Phasen im Herbst reagierten stärker als späte Frühjahrs- und frühe Herbst-Phasen. Im Vergleich der Baumarten war festzustellen, dass *A. pseudoplatanus*, *L. decidua* und *P. abies* die stärkste phänologische Reaktion im Frühjahr aufwiesen, dicht gefolgt von *F. sylvatica*. Das Schlusslicht bildeten *A. alba* und die *Pinus*-Arten. Wir stellten fest, dass die Blattseneszenz im Herbst im gleichen Maße auf Temperaturänderungen reagieren kann wie Frühjahrsphasen, vor allem wenn die Temperaturen stark erhöht sind wie beispielsweise im Herbst 2011. Diese Feststellung steht im Widerspruch zu anderen Studien, die die Herbstreaktionen geringer einstuften als die Frühjahrsreaktionen. Wir schließen daraus, dass es eine große Rolle spielt, wann im Jahresverlauf intensive Temperaturerhöhungen auftreten, da dies die Verhältnisse der Verschiebungen von Frühjahrs und Herbst-Phänologie stark beeinflusst.

Inversionslagen, die im Herbst 2011 besonders häufig auftraten, beeinflussten das phänologische Muster entlang der Höhengradienten, was wir zum ersten Mal sehr detailliert für Blattseneszenz-Phasen zeigen konnten. Die Bäume in Tallage reagierten mit früheren Eintrittszeitpunkten der Blattseneszenz wenn sie längere Zeit kälteren Temperaturen ausgesetzt waren. Dieses Signal war für spätere Herbstphasen stärker ausgeprägt als für frühe Phasen und stärker für *A. pseudoplatanus* als für *F. sylvatica*. Es ist noch unklar, ob durch den Klimawandel Witterungsverhältnisse, die Inversionslagen begünstigen, zunehmen werden. Daher schlussfolgern wir, dass dieses Phänomen sehr variabel in Raum und Zeit, aber häufig im Alpenraum auftritt.

Mithilfe der kürzlich eingeführten Methode des „Microsampling“ ermittelten wir Reaktionsraten von Eintrittsterminen verschiedener Phasen des Baumring-Wachstums. Das absolute Stammwachstum sowie die maximale Ausdehnung der einzelnen Differenzierungs-Phasen nahmen mit der Höhe ab. Die Stammwachstums-Zeit von *F. sylvatica* nahm mit der Höhe ebenfalls stark ab, die von *P. abies* jedoch blieb beinahe unverändert. Die Ergebnisse implizieren, dass das Stammwachstum von *F. sylvatica* stark auf Temperaturänderungen reagiert und daher von der Verlängerung der Vegetationsperiode profitieren kann. Der Beginn des Stammwachstums war eng mit dem Auftreten spezieller phänologischer Phasen verknüpft, das Ende trat jedoch unabhängig von der Phänologie ein. Die ersten Phloemzellen erschienen etwa sieben Wochen vor Knospenaufbruch und Xylembildung. Die unterschiedlichen Differenzierungs-Phasen scheinen dabei für *P. abies* nicht unabhängig voneinander und zusätzlich stark mit der Phänologie (vor allem dem Knospenaufbruch) verknüpft zu sein. Bei *F. sylvatica* konnten wir eine enge Verbindung zwischen den Eintrittszeitpunkten von ersten Phloemzellen mit Knospenaufbruch, ersten Xylemzellen mit Blattentfaltung und der maximalen Wachstumsrate mit vollständig entfalteten jungen Blättern feststellen. Im Gesamten erscheint das Stammwachstum von *F. sylvatica* im Vergleich zu *P. abies* stärker durch äußere Umweltfaktoren beeinflusst zu sein und wird daher vermutlich eine stärkere Reaktion auf den Klimawandel zeigen. In höher gelegenen Regionen wie unserem Untersuchungsgebiet erwarten wir daher eine Verlängerung der Stammwachstums-Zeit, insbesondere für Laubbäume. In tieferen Lagen hingegen könnten steigende Temperaturen und Trockenstress ein reduziertes Stammwachstum zur Folge haben.

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List of Abbreviations

Units:

Metric units are used and indicated in standard abbreviations (e.g. m, mm...) which are not explained here in detail. For temperature, degree Celsius (°C) is used uniformly.

Geography:

N: north
E: east
m a.s.l.: meters above sea level
S: south
W: west
m ü.N.N: Meter über Normal Null

Gradients:

KRA: Kramer gradient, south aspect (KRA_S)
KRE: Kreuzeck gradient, north (KRE_N) and south (KRE_S) aspect
SCH: Schachen gradient, north aspect (SCH_N)

Phenology:

BBCH: This abbreviation indicates „Biologische Bundesanstalt, Bundessortenamt und CHemische Industrie“, which developed the BBCH Code primarily for agricultural plants.

Publication I (Chapter 5):

MD: montane deciduous species (*Acer pseudoplatanus* L., *Fagus sylvatica* L.)
ME: montane evergreen species (*Abies alba* MILL., *Picea abies* L. (KARST), *Pinus sylvestris* L.)
HE: species in high elevation (*Larix decidua* MILL., *Pinus mugo* TURRA)

Publication II (Chapter 6):

No abbreviations

Publication III (Chapter 7):

SD: growth start date
ED: growth end date
GP: growth period
MR: maximum growth rate
MD: date of maximum growth rate
MW: final (maximum) ring width

Further Abbreviations:

FPAR: Fraction of Photosynthetically Active Radiation absorbed by vegetation
LAI: Leaf Area Index
MODIS: Moderate Resolution Imaging Spectroradiometer
NDVI: Normalized Difference Vegetation Index
SLA: Specific Leaf Area

Institutes:

ASP: Bayerisches Amt für forstliche Saat- und Pflanzenzucht
BaySF: Bayerische Staatsforsten
DWD: Deutscher Wetter Dienst
HMGU: Helmholtz Zentrum München – German Research Center for Environmental Health
IMK-IFU: Institute of Meteorology and Climate Research - Atmospheric Environmental Research
IPG: International Phenological Garden
LfU: Bayerisches Landesamt für Umwelt
LMU: Ludwig-Maximilian-Universität München
LWD: Lawinenwarndienst Bayern
LWF: Bayerische Landesanstalt für Wald und Forstwirtschaft
TUM: Technische Universität München
UBA: Umweltbundesamt
UFS: Umweltforschungsstation Schneefernerhaus
UnivA: University of Augsburg
USA-NPN: USA-National Phenology Network

1 Outline of the Thesis

This thesis is composed of three peer-reviewed research papers, of which two are accepted and already published (Chapters 5 and 6) and one is submitted (Chapter 7). They contain the main results of the studies on phenology and tree ring growth along altitudinal gradients in the Werdenfelser Land. The scientific background is presented in the General Introduction (Chapter 2), followed by the chapters on Motivation and Aims (Chapter 3) and Materials and Methods (Chapter 4). Further results not yet published are presented briefly in Chapter 8. Results of all publications are discussed in the General Discussion (Chapter 9) and summarized in Summary and Conclusions (Chapter 10).

In the **General Introduction** (Chapter 2), natural and anthropogenic climate change and its global and regional consequences, especially in the European Alps, are described. Phenology as a branch of science and an indicator of climate change is introduced as well as the research area of dendroecology with the recently introduced method of microsampling. Moreover, the suitability of altitudinal gradients for investigations of temperature responses is presented.

Motivation and Aims (Chapter 3) contains a short description of the project KLIMAGRAD, in which this thesis was integrated, and the thesis' research objectives.

The regional setting of the study, installed infrastructure and observation sites are described in **Materials and Methods** (Chapter 4). The observation years are briefly characterized by presenting data from the meteorological stations. All methods of tree phenology observations and microsampling are presented in detail.

In the first publication (Chapter 5) **"Shifting and extension of phenological periods with increasing temperature along elevational transects in southern Bavaria"** (Schuster et al. 2013, *Plant Biology*, doi: 10.1111/plb.12071), the results of the phenological observations along the altitudinal gradients are presented. For the seven observed tree species, altitudinal response rates and phenological response rates were determined. Increasing temperatures led to advanced phenological phases in spring and delayed phases in autumn and therefore to an extension of the vegetation period. Moreover, differences in the required winter chilling time and spring forcing temperature between deciduous and evergreen species could be illustrated.

The second publication (Chapter 6) **"Frequency of inversions affects senescence phenology of *Acer pseudoplatanus* and *Fagus sylvatica*"** (Schuster et al. 2013, International Journal of Biometeorology, doi: 10.1007/s00484-013-0709-0) focuses on autumn leaf senescence phenology of two deciduous tree species and the impact of inversion situations in mountainous regions. In autumn 2011, inversions occurred especially frequently and resulted in advanced senescence phases within the cold air pools in the valleys. *A. pseudoplatanus* responded stronger and faster than *F. sylvatica* when faced with cold temperatures.

The third publication (Chapter 7) **"Intra-annual tree ring formation of Norway spruce and European beech in relation to elevation and phenology"** (Schuster et al., submitted to *OIKOS*, 25.09.2013.) deals with the intra-annual development of two widespread European tree species: *F. sylvatica* and *P. abies*. Ample results comprise the timing of different cell categories (phloem cells, xylem cells, growing cells, wall thickening cells and lignified cells) within the year and in relation to elevation, temperature and leaf phenology. Cambium reactivation started several weeks before bud burst for the evergreen *P. abies* and approximately with bud burst for the deciduous *F. sylvatica*. Increasing temperatures not only extended the vegetation period of the leaves, but also the tree ring growing season. This was very distinct for *F. sylvatica*, but only slightly visible for *P. abies*. Therefore, in the study area, *F. sylvatica* stem growth could profit more from rising temperatures.

In **Further Results in Alpine Phenology** (Chapter 8), some additional results, which are of interest for this thesis but not published yet, are briefly summarized. This includes the comparison of our data with remote sensing data, phenological responses of generative phases (flowering, seeds) and phenological variations of different classes (adult or juvenile tree, upper or lower part of the crown, north or south aspect).

The **General Discussion** (Chapter 9) integrates all important results of Chapters 5 to 8 and puts them in context with other scientific studies on tree phenology and dendroecology to draw a picture of future developments in alpine forest ecosystems. The importance and timeliness of the results of this thesis are highlighted.

Finally, the thesis is summarized in **Summary and Conclusions** (Chapter 10).

At the end of the manuscript, the combined **References** for all chapters and a **Publication List** with the author's **Individual Contributions** are integrated.

2 General Introduction

2.1 Climate Change

Natural Climate Variations

Climate is the mean state and the common course of meteorological parameters at a given location over a defined period (van Eimern & Häckel 1984). The minimum duration of this period is 30 years, thus the World Meteorological Organization (WMO) defined the period 1961-1990 as a reference period for current climate. Direct measurements of climatic parameters, primarily temperature, have been collected for the last 150 years. Some data series even go back to the 17th century. Using different proxy-data like from tree ring, geological layer or ice core parameters the history of the earth's climate can be reconstructed. Considering climate over a time period of geological eras it can be stated that change is the only constant in climate (Figure 2.1).

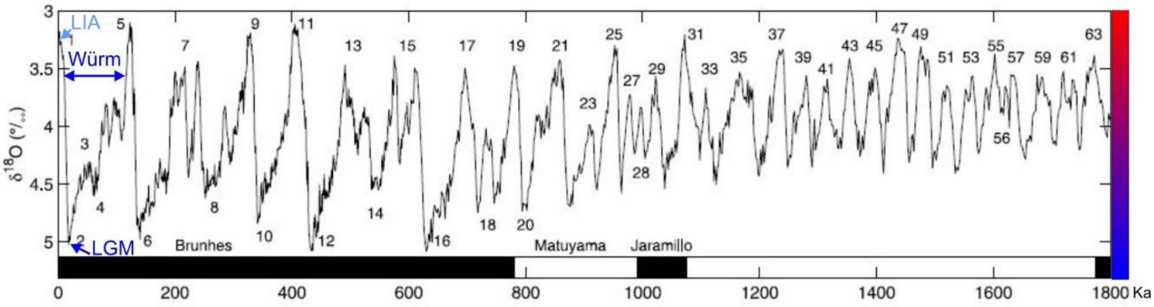

Figure 2.1 Variations of quaternary temperature (Lisiecki & Raymo 2005).

Human Impacts

Considering the climate of recent centuries, a strong increase in temperature (Figure 2.2) and CO_2 concentration of the atmosphere has been detected. The 100-year trend show that global air temperature has increased by 0.74 ± 0.18 °C (1906-2005, IPCC 2007a), especially in the last four decades (Luterbacher et al. 2004, Hansen et al. 2006, Hansen et al. 2010). Several years of the last two decades were among the warmest since the beginning of instrumental observations (IPCC 2007a, Hansen et al. 2010). This increase can be connected with anthropogenic activities since the Industrial Revolution in the 1850s. In particular, the combustion of fossil fuels has released large amounts of CO_2, which is considered as the most important greenhouse gas (Hofmann et al. 2006, IPCC 2007a). CO_2 concentration has increased from 280 ppm in preindustrial times to 379 ppm in 2005 and to 394 ppm in 2012 (IPCC 2007a, NOAA 2012) – compared to a natural variance between 180 to 300 ppm in the last 650 000 years (IPCC 2007a). In the same period, CH_4 concentration in the atmosphere varied between 320 and 790 ppb – but increased to 1774 ppb in 2005 (IPCC 2007a).

Other anthropogenic released gases and particles are also relevant for global warming, e.g. CH_4, N_2O, FCKWs, sulfates, aerosols, ground-level ozone and dust (IPCC 2007a). Prognoses for the future predict that global warming will continue. Based on different scenarios including human societal development, CO_2 concentrations and radiative forcing, an increase of global air temperature by 2.0-6.1 °C are possible until a stable level will be reached (IPCC 2007c). Even if the concentration of greenhouse gases in the atmosphere remains constant, climate feedback processes and delayed reactions will lead to rising temperatures (IPCC 2007a, Solomon et al. 2009).

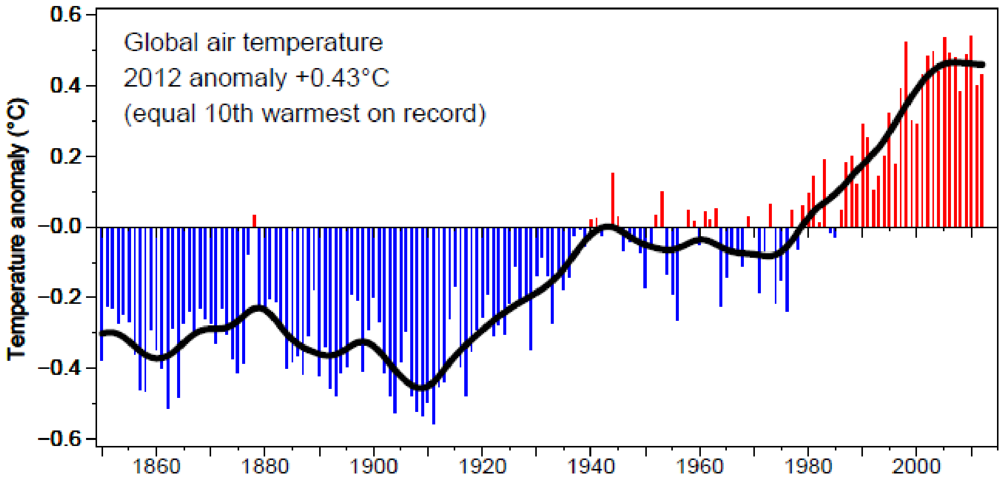

Figure 2.2 Global air temperature anomalies from 1850-2012 in relation to the 1961-1990 period average (Morice et al. 2012).

Global and Regional Consequences

Climate change has already affected all continents and most oceans. In particular the increase in global mean temperature is influencing biological and physical systems (IPCC 2007a, IPCC7b, Walther et al. 2002, Zhang et al. 2007, Rosenzweig et al. 2008). Moreover, shifts in precipitation patterns and amounts have been observed. Extreme weather events, (storms, drought, heat waves or heavy rainfall) are reported to occur more frequently (IPCC 2007a). The cryosphere is known to respond sensitive to global warming. Consequently, snow and ice cover and duration have reduced all over the world (IPCC 2007a). Permafrost, sea ice and glaciers, which are important freshwater reserves, are melting rapidly and are retreating. The global average sea level has been raised, mainly due to thermal expansion (IPCC 2007a).

Plants and animals show different responses to changes in their environment, whereas changes are highly heterogenos in space (Walther et al. 2002). A multitude of such responses have been discovered in recent time. Species distributions are shifting polewards or to higher elevations and species composition is changing (Penuelas & Boada 2003, Walther 2004, Parmesan 2006, Erschbamer et al. 2009). Where snow and glaciers retreat, the vegetation is on successive advance (Nagl & Erschbamer 2010, Röhrlich 2013). Exposure to new pests and diseases or just increased concurrence situations due to invasive species can lead to extinction of vulnerable species. Population density can increase and morphological adaptation is possible (reproduction, genetics). Adaptations of different magnitudes or in different directions can result in disturbances of biotic interactions or between trophic levels (mismatches e.g. in pollination or predator-prey relationships; Stenseth & Mysterud 2002, Parmesan 2006). Migrant birds return earlier in spring, don't leave their summer habitat or even decline due to uneven changes in their summer and winter habitats (Huppop & Huppop 2003, Jenni & Kery 2003, Sparks et al. 2005, Jones & Cresswell 2010). Plant phenological onset dates like leaf unfolding, flowering and senescence have been shown to shift with higher temperatures: spring phases are advanced and autumn phases are delayed (e.g. Menzel & Fabian 1999, Menzel et al. 2001, Walther et al. 2002, Sparks & Menzel 2002, Estrella et al. 2006, Parmesan 2007, Vitasse et al. 2011).

European Alps

Impacts of global change have been observed all over the world, but at different magnitudes: The Alps are especially threatened by climate change since alpine species are highly specialized and adapted to the harsh living conditions or habitats with less concurrence (Körner 2003). Since the end of the 19th century they have been faced with increased temperatures of almost double (1.5 °C) the global average (0.7 °C; e.g. Theurillat & Guisan 2001, Schröter et al. 2005, Nogués-Bravo et al. 2007).

Although the trend in snow amount has been within the range of background interannual variation since the mid-1980s in the Swiss Alps (Beniston 2006), prognoses predict strong temperature increases for the Alps: The 2071-2100 period is expected to be 4 °C warmer in winter and up to 6 °C warmer in summer compared to the 1961-1990 reference period (A2 scenario, IPCC 2007c). Thus, summer rainfall will be significantly curtailed (Beniston 2006) and precipitation in winter will more frequently occur in the form of rain rather than snow (Beniston et al. 2003, Laghari et al. 2012). This is displacing the zero-degree isotherm and with it the snow line at higher elevations. As a consequence, the date of snowmelt at a given location will advance in spring and snow cover duration will be shortened.

Alpine glaciers have lost 30-40 % of their surface and about 50 % of their volume since 1900 and models indicate that 30-50 % of the mountain glaciers will disappear by 2050 (Haeberli & Beniston 1998). Since these mountain climate parameters influence the alpine water resource we also have to expect a change in soil moisture, groundwater recharge, evaporation and runoff. Runoff by 2100 is predicted to change by seasonality and amount, so that water will be available at different times and in different quantities compared to the present situation (Beniston 2010). Besides, increased water usage by man could cause or strengthen changes in water availability for the vegetation.

Including various environmental parameters, habitat conditions are changing drastically and species distributions (including forest boundaries) are shifting in higher elevations (e.g. Stützer 1999, Walther et al. 2005, Gehrig-Fasel et al. 2007, Lenoir et al. 2008, Erschbamer et al. 2009, Erdle et al. 2013). Not all species respond in the same way, some can only adapt really slowly (left-behind) and suddenly are faced with new concurrence situations. This means that initially species richness will increase but will result in a loss of biodiversity in longer time scales (Klanderud & Birks 2003, Parmesan 2006, Lenoir et al. 2008, Erschbamer et al. 2009). In high elevations, refuges are missing (nowhere-to-go), which is leading to a high probability for extinction (Beniston et al. 1997, Williams et al. 2003, Schröter et al. 2005, Pounds et al. 2006, Parmesan 2006). Habitat fragmentation is also a factor not to be overlooked in alpine regions, where habitats are already small due to small-scale changes in topography.

2.2 Phenology

Definition

Phenology is the study of the timing of recurring natural events (Schnelle 1955, Lieth 1974). This includes animal and plant life cycles, the biotic and abiotic factors influencing their timing as well as the interrelation among phases of the same or different species. In the meanwhile, seasonal abiotic processes like ice duration on lakes or rivers are also considered. The name "phenology" is based on the Greek word "phainestai", which means to show or to appear.

Phenological Observations as Climate Change Indicators

The observation of natural life-cycles has a long non-scientific tradition: In historic times knowledge about plant development phases was essential for survival, for example about the timing of fruit ripening (Defila & Jeanneret 2007, Demarée & Rutishauser 2009). Thus, a long time ago humans started to record plant phenological events. A popular example for a long-term data series is cherry flowering in Japan, which has been recorded since 705 AD at the imperial residence in Kyoto (Aono & Kazui 2008). In modern times the science of phenology has gained significant importance (Sparks et al. 2000, Sparks & Menzel 2002). Since the timing of phenological phases is strongly coupled with meteorological parameters, they can act as a proxy for example (or in particular) for air temperature (Chmielewski & Rötzer 2001, Fitter & Fitter 2002, Sparks & Menzel 2002, Menzel 2005, Menzel et al. 2006, Možný et al. 2012). Therefore, they are suitable as climate change indicators (Parmesan 2007, Inouye 2008) and long-term phenological observation series can serve for climate variability reconstructions (Chuine et al. 2004, Menzel 2005, Možný et al. 2012).

Knowledge about responses of organisms to climate variability helps us to predict impacts of future climate change on the biosphere (Sparks & Carey 1995). For comparable long-term data series on a European scale, F. Schnelle and E. Volkert founded the network of the International Phenological Gardens (IPG) in the 1960s. Vegetatively reproduced plants were established at all sites (89 across Europe, state 2010), which are equipped with climate stations. In Germany, the German Meteorological Service (DWD) has run a phenological observation network since 1951 based on volunteer participants. In recent times there has been a great effort to launch more phenological networks such as the newly founded USA-National Phenology Network (USA-NPN, www.usanpn.org) or the new, in the framework of the project KLIMAGRAD established, phenological network of arctic and alpine botanical gardens (Menzel et al. 2013).

The observation programs often provide instructions for phenological observations to standardize the recorded data. Observation keys are inevitable to avoid subjective estimations. Usually these observation keys are composed of detailed descriptions of the phenological phases, respective photographs and reference numbers. A well-known key is the BBCH Code, which was developed for agricultural plants (Meier 1997). To determine phenological phase onset dates from observational raw data, a conversion is often necessary. Different methods to determine onset dates from BBCH observations were described by Cornelius et al. (2011).

In recent times, automatically performed observations by remote sensing (digital cameras or satellites) have gained importance. Images are analyzed e.g. for the Normalized Difference Vegetation Index (NDVI) or the amount of green channel reflection from the vegetation. Using satellite images, no differentiation between species is possible but vegetation dynamics on a large scale can be determined (Myneni et al. 1997, Chen & Pan 2002, Zhang et al. 2003, Stöckli et al. 2008, Reed et al. 2009, White et al. 2009). Digital cameras, on the other hand, can be used for similar analysis of tree canopy or single tree images (e.g. Graham et al. 2010, Alberton et al. 2012, Sonnentag et al. 2012). Remote sensing observations represent important indicators of environmental effects of climate change (Reed et al. 2009).

Influencing Parameters and Detected Shifts

Besides reported shifts in plant distribution (e.g. Parmesan & Yohe 2003, Root et al. 2005, Lavergne et al. 2006, Kelly & Goulden 2008, Lenoir at el 2008, Erschbamer et al. 2009), numerous studies have provided evidence of phenological shifts of plant and animal life cycles (e.g. Hughes 2000, Sparks & Menzel 2002, Walther et al. 2002, Walther 2004, Linderholm 2006, Parmesan 2006, Vitasse et al. 2011). Many simple to highly complex models have been developed to predict the onset of phenological phases from meteorological parameters (Hänninen 1990, Hunter & Lechowicz 1992, Chuine & Cour 1999, Rötzer et al. 2004, Migliavacca et al. 2008, Thuiller et al. 2008, Olsson et al. 2013). Dominant triggers for spring phenology are spring forcing temperatures (Hickin & Vittum 1976, Castonguay et al. 1984, Hunter & Lechowicz 1992) and sufficient winter chilling (Perry 1971, Chuine & Cour 1999). Additionally, date of snowmelt, water availability, CO_2 concentrations or life traits are important parameters.

An example of trait effects is that flowering of wind-pollinated plants advanced more strongly than insect-pollinated species (Ziello et al. 2012b). CO_2 impacts on phenology turned out to be highly variable between species and are not well understood since they often are confounded with other conditions, such as light, water or nutrient availability. Flowering of wild species showed advanced, delayed or no response to increased CO_2 (Asshoff et al. 2006, Springer & Ward 2007, Rosenzweig et al. 2008). Determined phenological responses to drought were also not consistent: either an extension (Llorens & Penuelas 2005, Jentsch et al. 2009) or a shortening (Llorens & Penuelas 2005) of the flowering duration was reported. In alpine areas, the beginning of the growing season was influenced by the timing, depth and duration of snow cover (Inouye & Wielgolaski 2003). In general, longer snow cover delayed (Weaver & Collins 1977, Inouye 2008, Torp et al. 2010, Cooper et al. 2011), and shortening of snow cover advanced the timing of phenological phases (e.g. Price & Waser 1998, Inouye et al. 2003, Wipf et al. 2009, Lambert et al. 2010, Wipf 2010, Chen et al. 2011). For example, flowering time was advanced by up to 11 days for every two weeks earlier snowmelt, whereas early species showed stronger responses (Dunne et al. 2003, Wipf 2010).

Based on regional and global analyses on plants, spring phases were proved to advance about 2.3-2.5 days per decade (Parmesan & Yohe 2003, Root et al. 2003, Menzel et al. 2006). Advanced flushing of 1.9 to 6.6 days $°C^{-1}$ was reported for spring phases in Europe (Menzel et al. 2006, Vitasse et al. 2009b, Pellerin et al. 2012). Temperature response rates were stronger for warmer countries and earlier phenological phases and declined through the year (Fitter & Fitter 2002, Menzel et al. 2006, Jeong et al. 2011). Early species were highly adapted to strong temperature variability in spring and consequently react more sensitively (Menzel et al. 2006).

Autumn leaf senescence of deciduous trees was delayed by higher temperatures in smaller or similar magnitudes compared to spring phases (Menzel & Fabian 1999, Estrella & Menzel 2006, Vitasse et al. 2009b, Röthlisberger 2010). For example, Menzel et al. (2006) showed advanced spring phases of about 4.6 days $°C^{-1}$, whereas autumn phases were delayed by 2.4 days $°C^{-1}$. Temperature and photoperiod are considered the most important abiotic drivers of senescence (Thomas & Stoddart 1980, Larcher 2003, Estrella & Menzel 2006, Migliavacca et al. 2008, Delpierre et al. 2009, Körner & Basler 2010, Caffarra & Donnelly 2011, Vitasse & Basler 2013). Moreover, the variation of leaf senescence was shown to be correlated with the variation of precipitation (Archetti et al. 2013). However, not all climate factors influencing leaf coloring have been found yet (Estrella & Menzel 2006). Interpretation of autumn changes is often difficult since autumn phases are hard to define clearly, extreme weather conditions (e.g. snow, storms) can bring abrupt changes and data are not as intensively collected compared to spring events (Sparks & Menzel 2002).

As a result of shifted phenological phases the whole vegetation period, which is often defined as the time span between leaf unfolding and leaf coloring, was lengthened by increasing temperatures (Menzel & Fabian 1999, Defila & Clot 2001, Stöckli & Vidale 2004, Linderholm 2006, Vitasse et al. 2009b, Montgomery et al. 2012). In Europe, the vegetation period was prolonged by 10.8 days since the beginning of the 1960s (Menzel & Fabian 1999). Similar values were reported by Myneni et al. (1997, 12 days for northern latitudes) and Defila & Clot (2005, 13.3 days within 50 years in Switzerland). Montgomery et al. (2012) determined a lengthening of 10-20 days under experimental warming of +1.8 to +3.6 °C. Advanced spring phases contributed about 55 % and delayed autumn phases contributed about 45 % to the lengthening of the vegetation period (Davi et al. 2006).

2.3 Dendroecology and Microsampling

Dendroclimatology and Dendroecology

As perennial organisms, trees are exposed to the environmental elements of their location over decades or centuries. Their growth is influenced by regional site characteristics including soil conditions, photoperiod, neighboring vegetation, the annual course of temperature, water availability, air gases (e.g. CO_2, pollutants) and extreme events. The regular restoration of functional phloem and xylem by cambial activity guarantees the perennial life of trees (Plomion et al. 2001) and keeps a record of their activities, strains and successes year after year. In seasonal climates, the repetitive annual cycle results in obvious tree-rings. Hence, tree-rings are able to conserve the climate of the past – a circumstance, researchers make use of.

Calibrated with recent climate, chronologies of tree ring width and density allow the reconstruction of climatic conditions prior the instrumental measurements (e.g. Hughes et al. 1984, Briffa et al. 1990, Frank & Esper 2005, Dzenis et al. 2013). This approach is termed dendroclimatology and is a sub-discipline of paleoclimatology. The subject of dendroecology, mostly used in forest ecology, deals with the prediction of tree growth in recent and future times based on their response to climatic conditions known from the past. Dendroecological studies are reliable tools for the characterization of local and regional weather and climate variation. The ability to study connections between tree ring formation and climate depends on several factors like tree species, elevation, site characteristics, measured tree-ring parametersand the standardization method used (Fritts 1976, Schweingruber 1996).

Microsampling – Reducing the Scale

In recent time, a new focus was added to the field of dendroecology: Investigations on the tree-ring formation at the cellular level and its relations to environmental conditions (Rossi et al. 2007, Deslauriers et al. 2008, Gričar et al. 2008, Gryc et al. 2012). The time scale of interest is reduced from several decades to one single or few years. The size of sampled wood cores also reduced drastically. Several techniques, tools and methods were tested (Eckstein 1983, Petersen & Eckstein 1988, Rossi et al. 2006a), until a specialized tool for small woody samples (1.6 cm length and 2 mm in diameter) was developed (the Trephor tool, Rossi et al., 2006a). "Microsampling" as a term for this technique (Deslauriers et al. 2003, Mäkinen et al. 2003) and "microcore" as a term for the small wood core (Rossi et al. 2006a) are now commonly used. Contrary to classic dendroclimatology, the intra-annual course of wood growth requires a repeated microsampling within a year (Gričar et al. 2006, Deslauriers et al. 2003, Rossi et al. 2006a, Moser et al. 2010), thus the scale of sampling intervals is also reduced.

Usually, thin sections are cut from the microcores using a microtome and stained to make the different cell development phases visible. With the short sampling intervals, timing of cambium reactivation in spring can be determined, which begins with cell division of the cambial layer followed by differentiation in phloem and xylem (Denne & Dodd 1981, Kozlowski & Pallardy 1997, Larcher 2003). Within the course of the year, the proportions of cells in various differentiation phases (e.g. expansion, cell wall deposition and lignification; Plomion et al. 2001, Gryc et al. 2012) can be identified for each sampling date and compared with the course of environmental parameters within the year.

Tree Ring Growth Responses to Environmental Parameters

Plant and therefore tree-ring growth is controlled by the most limiting environmental factor (Fritts 1976). Hence, series of tree-rings are suitable to detect a species' reaction to these parameters (Spiecker 2002, Dobbertin 2005). The natural distribution area of trees is generally described by amplitudes of annual mean temperature and annual precipitation sum (Fang & Lechowicz 2006, Kölling 2007, Thuiller et al. 2008), whereas limits vary between species. However, a minimum air temperature threshold of about 5-6 °C for stem and shoot growth and about 4 °C soil temperature for root growth must be exceeded (Loris 1981, Körner 1999, Röhrlich 2013.).

Near the distribution edges, the response of tree growth to climatic influences is increased: Trees at high elevations or high latitudes are very sensitive to temperature and show strong climatic signals (Jacoby & D'Arrigo 1989, Cook 1990, Briffa et al. 2002, Frank & Esper 2005, Yang et al. 2013). At lower elevations and latitudes, trees are most sensitive to precipitation and may be directly threatened by increased temperatures and droughts due to global warming (Jump et al. 2006, Luckman 2006, Yang et al. 2013). In general, cold temperatures and drought periods result in a decline of wood formation (Fritts 1971, Bigler et al. 2006, Eilmann et al. 2006, Klemmt et al. 2009, Wagner et al. 2013). Since the 1990s numerous studies have reported increased wood growth in Central Europe probably due to recent global warming (Pretzsch 1992, Spiecker et al. 1996, Dobbertin & Giuggiola 2006). However, rising CO_2 concentrations are also considered to stimulate tree growth leading to larger stem increment, in particular for young trees (Hättenschwiler et al. 1997, Dawes et al. 2013).

An apparent reaction of tree ring growth at the cellular level to varying environmental factors within a year is the production of earlywood with thin cell walls and large lumen in spring and early summer followed by latewood with compact lumen and more flattened cells (Fritts 1976) that results in visible tree rings. Most gymnosperms and dicotyledonous angiosperms in seasonal climates produce one tree ring per year. For cambium reactivation in spring, temperatures of about 4.4-8.6 °C (Wilcox 1962, Loris 1981, Horáček et al. 1999, Rossi et al. 2007, Deslauriers et al. 2008) and sufficient soil water content (Abe et al. 2003, Schweinguber 2007) are required. The beginning of xylogenesis is advanced by higher temperatures (Deslauriers et al. 2008). With increasing elevation or latitude, tree-ring width decreases (Burger 1941, Larcher 2001, Kozlowski et al. 1991, Dobbertin & Giuggiola 2006), a pattern which is considered to be closely linked to the reduced growing season length with elevation (White et al. 1999).

2.4 Natural Gradient Studies

To detect changes in the phenological timing of wildlife (plants and animals), long-term data series are required, most optimally over several decades (temporal gradient studies, Fitter et al. 1995, Sparks & Carey 1995, Crick & Sparks 1999, Inouye et al. 2000, Dunne et al. 2004, Menzel et al. 2006). Site resampling studies (e.g. Grabherr et al. 1994) also can show changes for example in plant associations. As described above, lots of these long-term series are recorded in phenological networks due to the importance of phenological records for climate change research and agrometeorology (e.g. Menzel 2000, Chmielewski & Rötzer 2001, Menzel et al. 2006). In Phenological Garden networks, often plant clones with the same genetic information are observed under relatively controlled circumstances (e.g. the same soil substrate) to minimize other than climate influences on phenology. The advantage of networks is that they provide consistent records over larger regions. Observations made by individual persons (e.g. Sparks & Carey 1995, Inouye et al. 2000, Fitter & Fitter 2002) mostly cover only a small spatial area (e.g. their own garden).

However, the required extensive long-term studies that are necessary for conclusions on the phenological response to a changing environment often cannot be conducted to satisfy the multitude of scientific unanswered questions. Therefore, spatial gradients like altitudinal (Defila & Clot 2005, Dittmar & Elling 2006, Ziello et al. 2009, Vitasse et al. 2011, Cornelius et al. 2012), latitudinal (Parmesan & Yohe 2003, Badeck et al. 2004, Parmesan 2007) or urbanization gradients (Ziska et al. 2003, Zhang et al. 2004, Mimet et al. 2009, Jochner et al. 2012a) are often used. Thereby, temperature declines from lower to higher elevations, from lower to higher latitudes and from city centers to countryside. Temperature is likely to be the most important factor changing along natural gradients and controlling phenological growth phases (Hickin & Vittum 1976, Castonguay et al. 1984, Hunter & Lechowicz 1992, Larcher 2003, Estrella & Menzel 2006, Körner 2007, Migliavacca et al. 2008, Caffarra & Donnelly 2011). Observations along spatial gradients are so called “space-for-time warming experiments” (Körner 2003, 2007): the temperature variation in time is replaced by the temperature variation in space. Spatial gradients consequently simulate climate change across space, whereas temporal gradients detect real climate change over time.

This thesis focuses on temperature and phenological variations along altitudinal gradients in an alpine region (Werdenfelser Land, Southern Bavaria). Altitudinal gradients allow the study of phenological responses to a wide range of temperature in a relatively short time (Dittmar & Elling 2006, Vitasse et al. 2009b). The variation of air temperature along altitudinal transects in different parts of the European Alps is described by Machalek (1974) and Kaiser (1992). An average value for temperature decrease with elevation in the European Alps is about -0.54 to -0.58 °C 100 m^{-1} (Rolland 2003). In our study area, daily mean lapse rates varied between -0.32°C 100 m^{-1} in December and -0.62 °C 100 m^{-1} in late spring (April/May) and in summer (June, Kirchner et al. 2012). It must kept in mind that phenological response to temperature is linear in elevation but becomes non-linear with increased warming in time (Pope et al. 2013, Jochner et al. 2013b). However, differences in phenological patterns linked to different temperature regimes can serve as first approximations to future changes under a global warming scenario. It can be expected that with a warming of one degree Celsius, the general pattern of phenological timing is shifted by about 200 m upwards in elevation.

Note: In this thesis the terms “altitude” and “elevation” are both used. The same applies for the terms “gradient” and “transect”. Both are represented in the scientific literature and preferences as to usage differ between journals and between referees.

3 Motivation and Aims

3.1 Motivation: the Project KLIMAGRAD

The present thesis “Studies on Phenology and Intra-annual Tree Ring Growth along Altitudinal Gradients in the Werdenfelser Region” (Untersuchungen zu Phänologie und intra-annuellem Stammwachstum entlang von Höhengradienten im Werdenfelser Land) was prepared within the framework of the joint research project KLIMAGRAD (Climate Change Impact Monitoring at Altitudinal Gradients / Auswirkungen des Klimawandels in den Alpen - Erfassung mittels Höhengradienten).

Main task of KLIMAGRAD was research on the interaction between atmosphere and biosphere, in which the vegetation is an important biophysical (albedo, leaf area index) and biochemical (gas and particle exchange) parameter. Facing anthropogenic enforced global warming, this system will experience severe changes: As mentioned above, the Alps are especially affected by climate change. Prognoses forecast above-average temperature increases and intensification of changes in distribution of precipitation and extreme weather phenomena.
The impact of increased temperatures was proved a. o. in the alpine species composition at mountain tops. Comparison of old and new vegetation mappings show species and vegetation zones rising to higher elevations. Regions in high elevations with strong abiotic changes (decrease in snow load and snow cover duration, decrease in glacier volume and area, permafrost thawing…) are particularly suitable for this kind of observations. In short time scales, this leads to an increased species-diversity. However, since alpine species are faced with increased competitive pressure, missing retreating areas (nowhere-to-go) and often are only slowly adaptive (left-behind), a long-scale loss in biodiversity is expected. Endemic species in the Alps are especially vulnerable. Moreover, extended vegetation periods and shifting of phenological phases – for example earlier bud burst or flowering – are reported in several studies. Therefore, a special focus of the KLIMAGRAD project was on the alpine vegetation in the montane to sub-alpine zones of the study area.

The Werdenfelser Land around Mount Zugspitze, southern Bavaria, provides excellent options for ecological research on interactions between vegetation and climate/weather because…

… it is Germanys highest differences in elevation in the Northern Calcareous from the sub-nival zone (Zugspitze 2962 m a.s.l.) to the valley floors (around 700 m a.s.l.).
… the strong regional and local differentiation of the vegetation mirrors the different elevational levels, aspect, microsites and microclimates.
… typical mixed forest covers the mountain slopes (European Spruce, European Beech and European Silver Fir; European Larch and Swiss Stone Pine in higher elevations). Additionally, we can find all typical types of vegetation up to the sub-nival zone.
… the infrastructure offers good accessibility (cable cars, forest roads).
… already existing meteorological measurements from different institutes (UFS, DWD, UBA, IMK-IFU, LWD) are available.
… chronicles and recordings of other alpine institutes (e.g. Alpine Botanical Garden Schachen, UFS, LWF Forest Reserves, former and other actual projects of TUM, LfU Alpine Mapping, BayFORKLIM…) provide a well-founded data base.
… the extensive facilities of the UFS Schneefernerhaus (2650 m a.s.l.) constitute a unique platform for researches of processes in atmosphere, hydrosphere, geosphere and biosphere. It is member of the GAW (Global Atmosphere Watch) and VAO (Virtual Alpine Observatory).

The Werdenfelser Land is an area with numerous non-climatic factors exerting pressure on the environment (land use change, pollution, fragmentation, tourism…). This is particularly of interest since alpine ecosystems provide a variety of functions like drinking water supply, avalanche protection, erosion protection and recreation area. Today, these functions are already threatened and will be questioned in the future.

Therefore, KLIMAGRAD includes several interdisciplinary subprojects in the area of Garmisch-Partenkirchen and the Zugspitze occupying different objectives:

1: Infrastructure: new meteorological stations and gradients in the study area (TUM)

2: Phenological and phytosociogical observations in the montane to subalpine zone alongside altitudinal gradients in the Wetterstein mountains and at Schachen (TUM, LMU, Botanical Garden Munich)

3: Altitudinal dependent plant sociological and habitat observations in the subalpine to subnival zone at the Zugspitzplatt (UnivA)

4: Emission / Deposition of volatile organic compounds (VOC) and nitrogen compounds (TUM, HMGU)

This thesis includes the author’s work in subprojects 1 and 2.

KLIMAGRAD was financed by the Bavarian State Ministry of the Environment and Public Health in the framework of the “Klimaprogramm Bayern 2020” attended by Prof. Dr. Tanja Gschlößl. The duration of the project was three years until end of January 2013. Interim reports were handed to the Bavarian State Ministry of the Environment and Public Health in October 2010 and 2011, the final report in January 2013. Main originator and organizer of KLIMAGRAD was the Chair of Ecoclimatology, Technische Universität München (Prof. Dr. Annette Menzel, Prof. Dr. Michael Leuchner, Dipl. Geoökol. Christina Schuster). Project partners were: Systematische Botanik, Ludwig-Maximilians-Universität München (Prof. Dr. Susanne Renner); Botanischer Garten München-Nymphenburg (Dr. Andreas Gröger); Lehrstuhl für Physische Geographie und Quantitative Methoden, Arbeitsgruppe Biogeographie, Universität Augsburg (Prof. Dr. Arne Friedmann, Dipl. Geogr. Oliver Korch); Cooperation Group „Comprehensive Molecular Analytics“ (CMA), Helmholtz Zentrum München (Dr. Manfred Kirchner, Dr. Gert Jakobi).
Moreover, KLIMAGRAD should enrich and intensify the investigations embedded in the exploratory focus “Biosphere and Geosphere” (Chair: Prof. Dr. Annette Menzel) of the Environmental Research Station Schneefernerhaus (UFS), located at Zugspitze (2650 m a.s.l.).

KLIMAGRAD

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3.2 Aims of the Thesis

In Chapter 2 (General Introduction), the current state of science in the fields of phenology and dendroecology was briefly described. However, there remain a lot of questions unanswered, of which some of them are investigated in this thesis. Since altitudinal gradients serve as “space-for-time warming experiments” (Körner 2003, 2007) we designed our study along four transects (700 m to 1800 m a.s.l.) with observation sites located every 100 m in elevation. At the gradients, we selected seven common tree species of the montane forest for phenological observations (see Chapter 4, Materials and Methods). The three pillars this thesis is based on are the following key questions:

a) What is the magnitude of tree phenological response to a wide range of elevation and thus temperature regimes?

b) Do inversion situations in alpine areas influence leaf senescence phenology?

c) Is the intra-annual course of tree ring growth and its differentiation phases related to leaf phenology, elevation and temperature?

In the following, detailed research questions and their respective backgrounds are discussed.

Tree Phenology

Increasing temperatures due to global warming have caused an extension of the growing period in recent decades (e.g. Menzel & Fabian 1999, Linderholm 2006). This trend is mainly due to advanced spring events (e.g. Ahas et al. 2002, Cleland et al. 2007) but also delayed leaf senescence is reported (Menzel et al. 2006, Estrella & Menzel 2006, Vitasse et al. 2009a). Existing studies mostly focus on one or a few species, and response to climate change is considered highly variable between species. Therefore we wanted to

- identify specific response rates of seven common alpine tree species to elevation and temperature

and moreover to

- determine phenological differences between groups (montane deciduous, montane evergreen and high elevation species).

Since a high number of studies are restricted to observations of a few phenological phases like bud burst or beginning of leaf coloring, in our study we

- determine responses from a high number of phenological phases and quantify differences between them.

Including these numerous phenological phases, we are able to

- determine a lengthening of the vegetation period with increasing temperature and moreover to compare the magnitude of relations of phenological periods (spring and autumn events).

Phenological phases in spring predominantly are triggered by winter chilling (Chuine & Cour 1999) and spring warming (Hickin & Vittum 1976, Castonguay et al. 1984). For our seven tree species we therefore aimed to

- determine the influence of chilling and forcing temperatures on the timing of phenological phases.

Leaf senescence was observed during the two observation years included in this study. In 2011, an extraordinary high frequency of inversion situations in the alpine study area occurred. Under the influence of these inversions, trees at lower elevations faced colder temperatures than normal. Phenological shifts due to inversions have been observed in some studies (Baumgartner 1962, Sauberer & Dirmhirn 1954, Bastian & Steinhardt 2002, Wegener 2006), but have never been described in detail. Therefore, we analyzed our senescence data with the questions

- whether a high occurrence of inversion days is related to an advanced shift of leaf senescence at lower elevations due to reduced temperature sums.

and

- whether inversion-induced cold temperature responses differ systematically between species and phenological phases.

Tree Ring Growth

In the research field of dendroecology, temperature is considered to be the most important factor controlling intra-annual tree growth. Since temperature is also one of the most important variables changing with elevation and latitude (Körner 2007), it has been widely reported that tree ring growth is reduced with increasing elevation and latitude (e.g. Burger 1941, Larcher 2001, Kozlowski et al. 1991, Dobbertin & Giuggiola 2006). However, the microsampling technique and the focus on intra-annual tree ring growth are relatively new.

Our study aims to

- describe the course of the tree ring growth within a year at different elevations

and

- find connections between the timing of different cell categories (phloem cells, xylem cells, growing cells, wall thickening cells and lignified cells).

Similar to leaf phenology, phenological phases in wood formation differ between life traits and species. For our tree ring study, we focused on two widely distributed tree species which are also commonly used in the timber industry: *F. sylvatica* and *P. abies*. Including sampling sites at two gradients, our aims were to

- identify differences in tree ring growth timing between a deciduous and a evergreen species and between northern and southern aspects.

Timing of secondary stem growth in some studies was related to the timing of observed leaf phenology (Čufar et al. 2008, Moser et al. 2010, Michelot et al. 2012). However, there are still gaps in the knowledge of how intra-annual environmental conditions, phenology and wood formation are related to each other. In particular, how these interactions differ between species and with elevation has not been satisfactorily investigated (Moser et al. 2010).

Thus, we wanted to find out

- how the timing of different phases in tree ring growth is influenced by leaf phenology, elevation and temperature.

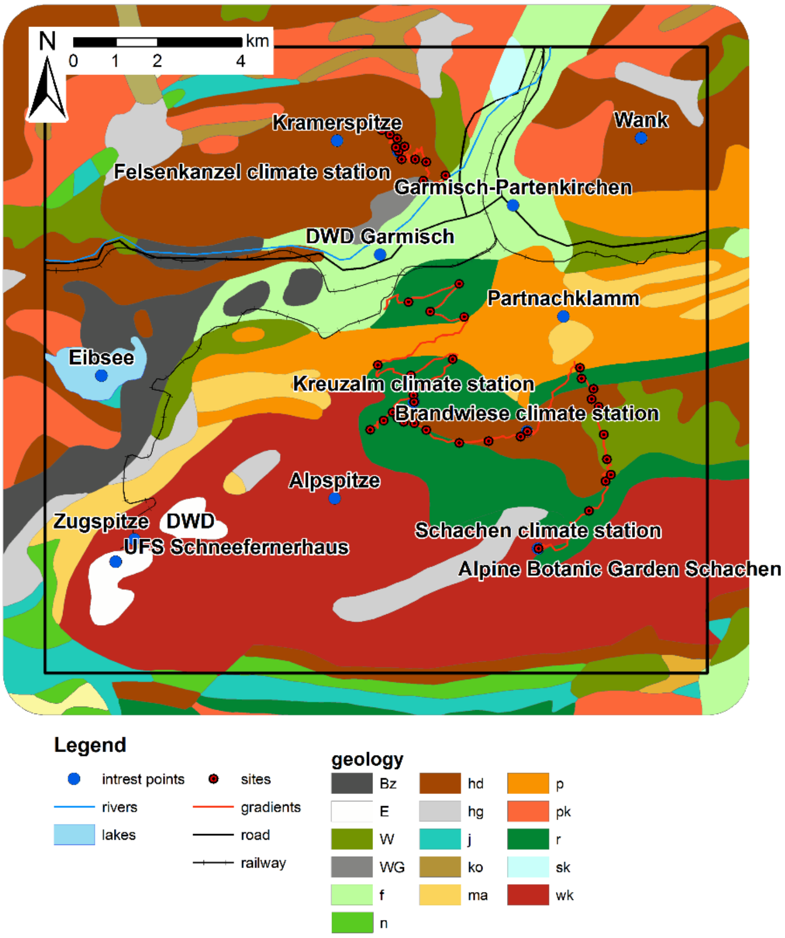
The beginning of xylogenesis is advanced by higher temperatures in spring (Deslauriers et al. 2008) and the tree ring width is considered to be closely linked to the growing season length (Burger 1941, Kozlowski et al. 1991, White et al. 1999, Larcher 2001, Dobbertin & Giuggiola 2006). Since global warming extends the vegetation period (Menzel & Fabian 1999, Linderholm 2006), we wanted

- to estimate how the two species, which are the main tree species in wide parts of Europe, would likely react to recent climate change by lengthening of the growing period.

4 Materials and Methods

4.1 Regional Setting and Climate

Formation of the Alps began 140 million years ago in the recent alpine area. Tectonic plates were folded, broken and mounted up and formed the small-scale changes in the region’s geology and the alternation of layers with different hardiness. Landscape as we know today was formed in these mountains by weather, erosion and sedimentation, mainly during the ice ages when valleys, moraines, lakes and main streams were formed. Hilly areas in front of the German Alps are wide in the Allgäu and practically not present in the area of Berchtesgaden, where the Calcareous Alps rise steeply. In between, the Werdenfelser Land is located in southern Bavaria and includes the area around Garmisch-Partenkirchen (47°30’ N, 11°6’ O, 708 m a.s.l.) and Mittenwald (47 27’ N, 11°16’ O, 923 m a.s.l.). It is limited by the Wetterstein Mountains in the south and the Karwendel in the east and includes Germany’s highest mountain: Zugspitze (47°25’16’’ N, 10°59’11’’ O, 2962 m a.s.l.). The dominant geological layers out of the Trias period are the dolomia principle formation (Kramer, Wank) and Wetterstein limestone (Wettersteingebirge, Zugspitze). Also Plattenkalk and alpine Muschelkalk appear (Figure 4.1). A special characteristic is the more acidic Raibler layer, because here acidic indicator plants occur in the calcareous dominated region. Besides, there are quaternary deposits of hillside rocks and moraines of the Würm Ice Age (Bayerisches Geologisches Landesamt 2004).



Geology abbreviations:

Bz: rockslide material
E: firn, glacier
W: upper moraine (Würm)
WG: hillside rocks (Würm)
f: floodplain material
n: Schrambach/ Roßfeld/ Tannheimer layers
hd: dolomia principle formation
hg: weathered hillside rock
j: Lias base limestone
ko: Oberrät limestone
ma: alpine Muschelkalk
p: Partnach layers
pk: Plattenkalk
r: Raibler/ Cardita layers
sk: debris cone
wk: Wetterstein limestone

Figure 4.1 Geological map of the study area (Bayerisches Geologisches Landesamt 2004, created with ESRI ArcGIS).

Dominant tree species in the mountainous mixed forests in the study area are European spruce (*Picea abies* L. (KARST)) and European beech (*Fagus sylvatica* L.) with an admixture of Sycamore (*Acer pseudoplatanus* L.) and Silver fir (*Abies alba* MILL.). On dry southern slopes, Scots pine (*Pinus sylvestris* L.) is distributed. Fir, beech and spruce are replaced at higher elevations by European Larch (*Larix decidua* MILL.), Mountain pine (*Pinus mugo* TURRA) and Swiss stone pine (*Pinus cembra* L.). In the study area, the latter is only present close to tree line at Schachen. Less frequently, ash and alder species occur, for example *Sorbus aucuparia* L., *Sorbus aria* (L.) CRANTZ and *Alnus viridis* (CHAIX) DC. At lower elevations, some precious hardwood can be found.
The tree line is located between 1750 m a.s.l. (southern aspects) and 1850 m a.s.l. (northern aspects). Large areas, especially around Schachen and Kramer, are forest nature reserves and a lot of forests at high elevations are currently not used by the timber industry.

Climate characteristics can be described by the long-term data from Garmisch (719 m a.s.l.) and Zugspitze (2960 m a.s.l.), since they represent the lowest and the highest location in the study area. Climate diagrams based on long-term data (1961-1990) show warm summer and cold winter seasons and a precipitation maxima in summer (Figure 4.2). At Zugspitze, precipitation is high almost throughout the year. Annual mean temperatures are 6.5 °C for Garmisch and -4.8 °C for Zugspitze and annual sums of precipitation are 1363 mm and 2003 mm, respectively. (www.dwd.de).

Due to the alpine surrounding, extreme and sudden weather changes are common. Frosts and snowfall often occur late in spring, as well as early in autumn. Typically in summer, thunderstorms and heavy rainfalls bring large amounts of water into the watersheds and sometimes cause landslides and floods.

In mountainous areas, elevation is an important factor influencing climate conditions (air pressure and density, vapor pressure, radiation, wind velocity, and of course temperature). Topography (e.g. slope, aspect and dimension) also affects climate parameters (Barry 2008). Consequently, in the Alps we can find a variety of macro and microclimates not always following the elevational trend of environmental parameters, but often reflected by the vegetation composition (Körner et al. 2007).

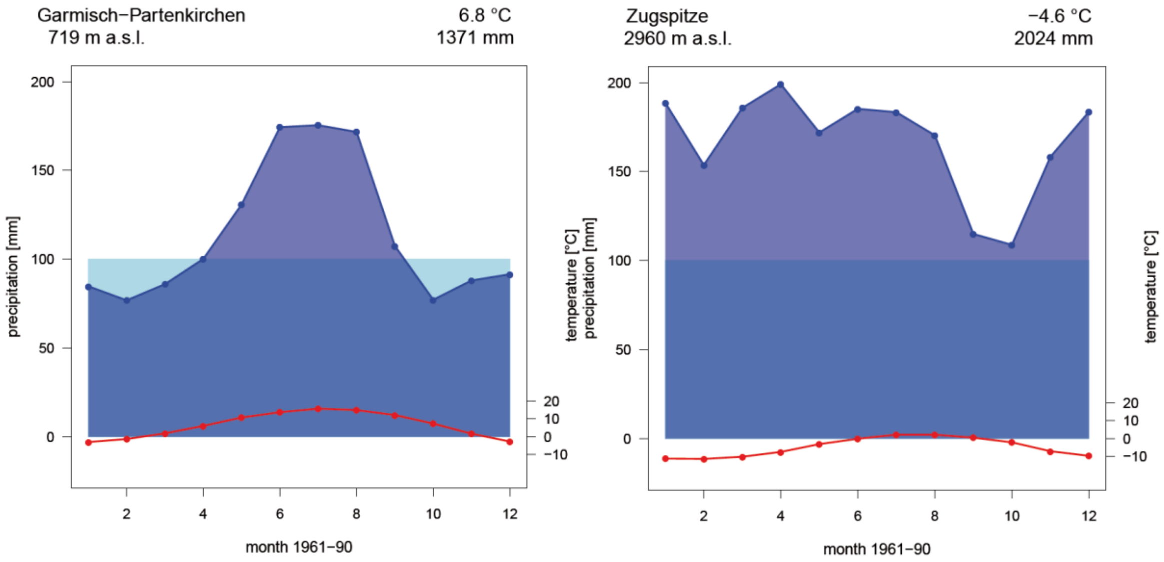


Figure 4.2 Climate diagrams for Garmisch-Partenkirchen (719 m a.s.l.) and Zugspitze (2960 m a.s.l.) based on long-term data in the reference period 1961-1990.

4.2 Meteorological Stations

Meteorological Stations in Southern Bavaria

The meteorological stations in Garmisch (719 m a.s.l., since 1936) and at the top of Zugspitze (2960 m a.s.l., since 1949) are operated by the German Meteorological Service (DWD), which runs a dense network within Germany (Figure 4.3). Climate and weather information is recorded and archived for several decades, sometimes even back to the 18th century. Daily, monthly and yearly data from Germany as well as worldwide and satellite data is freely available online. The DWD also provides long-term mean data as for example the 1961-1990 reference period. For more information see the webpage: www.dwd.de. Additionally, the German Avalanche Warning Service (LWD) provides meteorological data from mid to high elevations of the alpine region (Figure 4.3).

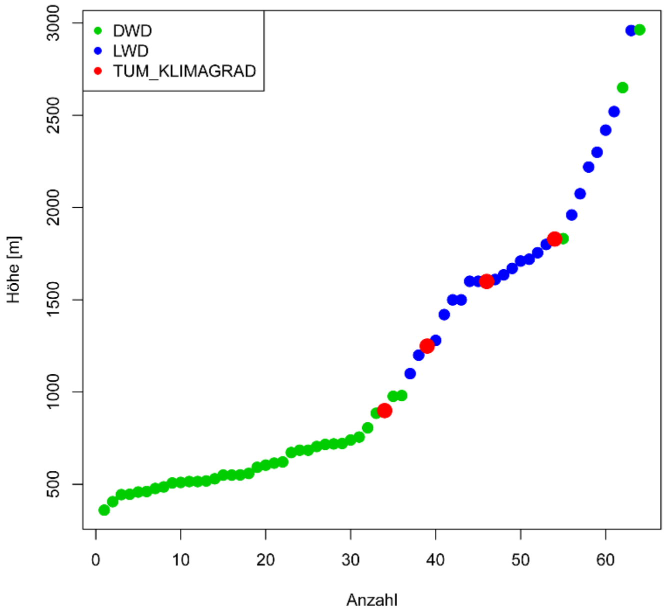
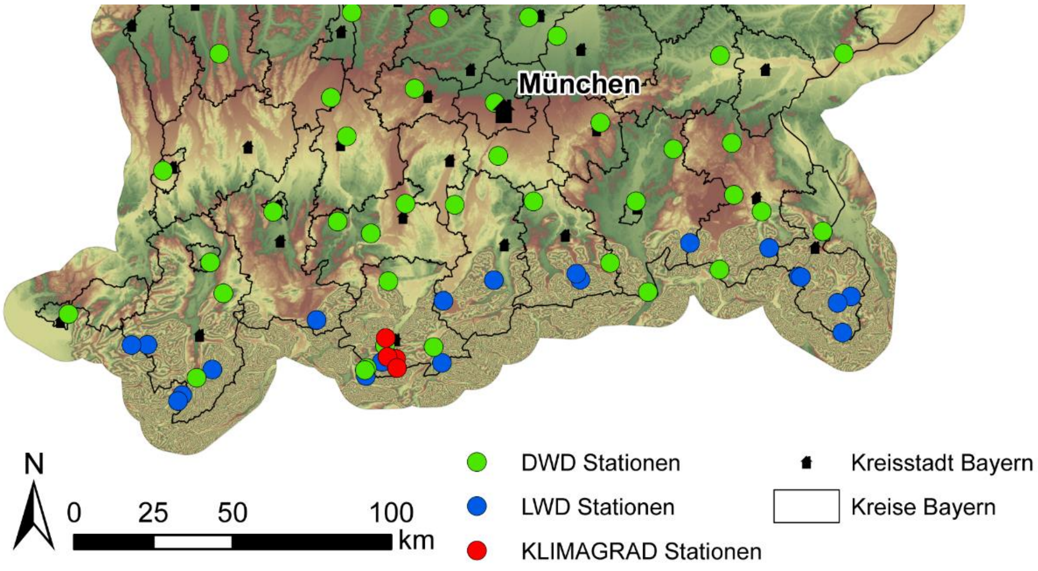


Figure 4.3 Distribution of meteorological stations in southern Bavaria in elevation (left) and space (below). In addition to DWD (green) and LWD (blue) stations, four stations were installed within the KLIMAGRAD project.



KLIMAGRAD Meteorological Stations
Within the KLIMAGRAD project, four new meteorological stations in the Werdenfelser Land were installed. Contracts were signed with the Bavarian State Ministry of the Environment and Public Health, the government of Upper Bavaria, the District Office of Garmisch-Partenkirchen and the Bavarian State Forest Enterprise. Equipment and instruments for the meteorological stations were ordered at Sommer Mess-Systemtechnik (Austria), as they provide robust stations for harsh alpine conditions and easy online data management on a web server. This is an advantage due to several users of the datasets. Since other institutions (especially the Avalanche Warning Service LWD) use the same stations, comparability between datasets is ensured. Set up and technical work at the sites (transportation, fundamentals) was done by members of the Chair of Ecoclimatology (TUM) and Gartenbau Hansjörg Köhler (Garmisch-Partenkirchen).

Sites, Dates and Instruments
For the four meteorological climate stations, the locations at Brandwiese in the Reintal valley (900 m a.s.l.), Felsenkanzel at Kramer (1250 m a.s.l.), Kreuzalm at Kreuzeck (1600 m a.sl.) and the Botanical Garden at Schachen (1830 m a.sl.) were chosen after exploration of the surroundings of Garmisch-Partenkirchen (Figure 4.4). They provide various fundamental meteorological data from different elevation levels (Table 4.1). All stations are run by solar panel and battery, as no external electricity can be used in this mountainous location. 10 minutes measurement means are logged and sent by a GPRS modem to the web server provided by Sommer (http://mds.sommer.at). There, data can be plotted and downloaded. A login is necessary given by the administrator of the Chair of Ecoclimatology.

Figure 4.4 The meteorological stations at Brandwiese (900 m a.s.l., top), Felsenkanzel (1250 m a.s.l., left), Kreuzeck (1600 m a.s.l., bottom) and Schachen (1830 m a.s.l., right).

Table 4.1 Geographical location, elevation and meteorological parameters at the four KLIMAGRAD meteorological stations.

station	**Felsenkanzel**	**Kreuzalm**	**Brandwiese**	**Schachen**
location	47.51°N 11.07°E	47.45°N 11.07°E	47.45°N 11.11°E	47.42°N 11.11°E
elevation [m a.s.l.]	1250	1600	900	1830
mast height [m]	4	6	6	6
date established	07.04.2010	30.03.2010	31.03.2010	19.11.2009
solar radiation [W/m^2]	✓	✓	✓	✓
air temperature [°C]	✓	✓	✓	✓
air humidity [%]	✓	✓	✓	✓
soil temperature 5 cm [°C]	✓	✓	✓	✓
soil temperature 25 cm [°C]	✓	✓	✓	✓
soil surface temperature [°C]	✓	✓	✓	✓
wind direction [°]	*	✓	✓	✓
wind speed [m/s]	*	✓	✓	✓
precipitation [mm]	✓	*	*	✓
lightning protection	✓	✓	✓	✓
solar panel	✓	✓	✓	✓
battery	✓	✓	✓	✓
antenna	✓	✓	✓	✓
GPRS modem	✓	✓	✓	✓
data recorded on server	✓	✓	✓	✓

* added in September 2012

Annual Means 2010-2012

Several problems with the meteorological stations occurred, but were handled as fast as possible in the alpine surrounding. Since the traditional Johanni fire is held once a year (24th June) at a fireplace close to the Felsenkanzel-Station, the mast and instruments have to be removed and then reassembled each year. Therefore, data were interrupted on 23.-26.6.2010, 23.-25.6.2011 and 22.-25.6.2012. For the yearly average values presented in Table 4.2, it is important to know that the stations of Brandwiese, Felsenkanzel and Kreuzalm were established only in spring 2010, thus the months January to March are missing in the calculation. At Kreuzalm in summer 2012 a data backup mistake occurred and led to data loss for several days. In December 2012, less sunshine for the solar panel caused problems in charging the battery at Brandwiese station. Therefore data of several hours was lost. Because of this, these values also have to be handled with caution. Instruments installed in September 2012 were not integrated into the yearly average calculation.

In the annual means (Table 4.2), the altitudinal differences are reflected: Mean temperature decrease with elevation. However, the valley of Brandwiese (900 m a.s.l.) is influenced by cold air drainage from the Zugspitzplatt and Kreuzeck, which leads to a reduction of mean air temperatures. On the other hand, Felsenkanzel station is located at a very sun-exposed place of southern aspect, thus proportionally is subjected to higher temperatures. The year 2011 was the warmest of the observation years. Precipitation was high in all years (about 1200-2000 mm) as expected in an alpine region. Wind velocities were higher in the more exposed upper elevations.

Table 4.2 Yearly averages for the meteorological parameters at the four stations in the years 2010-2012 based on daily mean values.

year	parameter	Brandwiese 900 m a.s.l.	Felsenkanzel 1250 m a.s.l.	Kreuzeck 1600 m a.s.l.	Schachen 1830 m a.s.l.
2010	mean air temperature [°C]	7.9	7.7	5.5	2.2
2010	maximum air temperature [°C]	15.1	16.6	14.4	10.7
2010	minimal air temperature [°C]	0.8	-0.4	-2.8	-6.8
2010	mean relative humidity [%]	87.0	78.6	80.0	73.2
2010	solar radiation [W/m^2]	118	136	139	119
2010	soil temperature 25 cm [°C]	10.2	10.3	6.6	4.0
2010	soil temperature 5 cm [°C]	10.8	10.1	6.5	4.0
2010	soil surface temperature [°C]	2.1	5.7	-5.8	-5.6
2010	precipitation sum [mm]	no device	1866	no device	1197
2010	mean wind velocity [m/s]	0.3	no device	1.6	0.8
2010	mean wind direction [°]	204	no device	230	161
2010	maximum wind velocity [m/s]	8.9	no device	18.3	17.3
2011	mean air temperature [°C]	6.9	7.7	5.8	4.9
2011	maximum air temperature [°C]	13.3	15.4	13.6	12.6
2011	minimal air temperature [°C]	0.0	-0.4	-2.5	-3.6
2011	mean relative humidity [%]	83.4	69.4	71.6	64.6
2011	solar radiation [W/m^2]	123	142	145	138
2011	soil temperature 25 cm [°C]	8.5	9.6	6.6	4.5
2011	soil temperature 5 cm [°C]	8.9	9.5	6.5	4.6
2011	soil surface temperature [°C]	2.4	7.4	2.7	-3.4
2011	precipitation sum [mm]	no device	1961	no device	1306
2011	mean wind velocity [m/s]	0.3	no device	1.4	0.8
2011	mean wind direction [°]	198	no device	222	159
2011	maximum wind velocity [m/s]	9.5	no device	19.8	15.6
2012	mean air temperature [°C]	6.3	6.5	4.5	3.6
2012	maximum air temperature [°C]	13.1	16.2	14.0	13.0
2012	minimal air temperature [°C]	-1.6	-2.9	-4.8	-6.5
2012	mean relative humidity [%]	86.3	73.3	75.6	69.0
2012	solar radiation [W/m^2]	117	131	134	129
2012	soil temperature 25 cm [°C]	8.3	9.5	5.9	4.0
2012	soil temperature 5 cm [°C]	8.7	9.6	5.7	4.2
2012	soil surface temperature [°C]	2.4	4.6	2.0	-4.4
2012	precipitation sum [mm]	no device	1920	no device	1870
2012	mean wind velocity [m/s]	0.3	no device	1.5	0.9
2012	mean wind direction [°]	204	no device	219	160
2012	maximum wind velocity [m/s]	9.3	no device	18.7	17.2

Air Temperature

For air temperature, the daily variation, warm phases and cold snaps are visible in Figure 4.5 as well as the yearly temperature course with cold winters and warm summers. The amplitude is larger at higher elevation (e.g. at the Schachen station). Cold snaps within higher temperature phases, for example, are visible in spring 2011. All years have a positive anomaly to the long-term mean (1961-1990) except for few months (May and September 2010, July 2011, February 2012) and therefore were clearly warmer than the climate normal period. The largest positive anomaly was November 2011 when temperature and sunshine records were especially high in mountainous regions (DWD 2011). This month was also the driest November in Germany since the beginning of climate records (2012). Moreover, in autumn 2012, inversions situations frequently occurred. The largest negative anomaly to the long-term mean was February 2012 with an extremely cold phase of about -20°C, which is also noticeable in Figure 4.5.

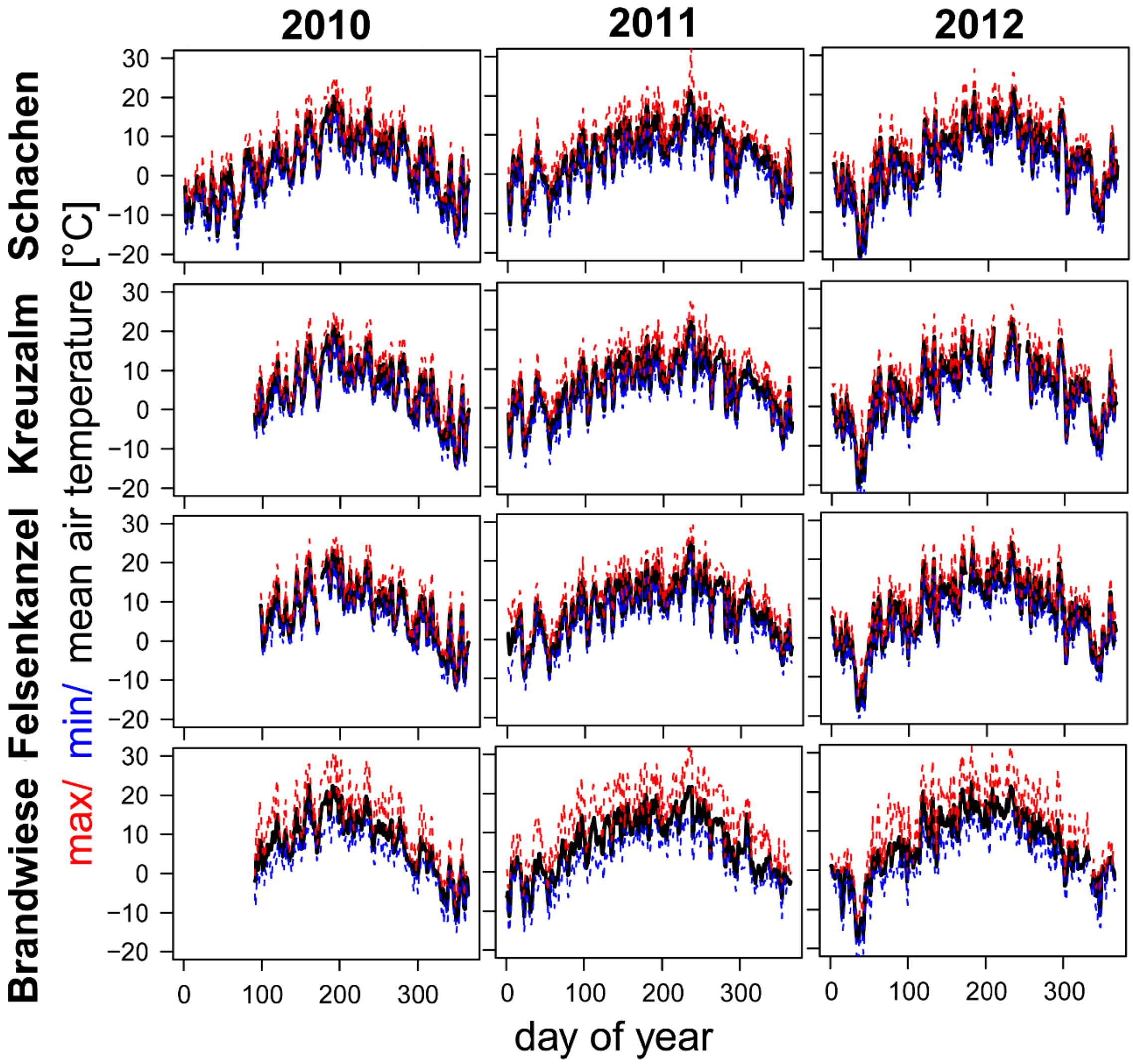


Figure 4.5 Daily mean (black), maximum (red) and minimum (blue) air temperature at the four stations in the years 2010-2012.

Soil Temperature

The soil temperature at 25 cm depth (black line in Figure 4.6) is colder than at 5 cm depth (brown line) and shows a smaller amplitude. In both curves, the beginning and end of snow cover can be estimated. The warm spring in 2011 led to an earlier snow melt compared to 2010, particularly at the exposed south-aspect station at Felsenkanzel (Figure 4.6). At the highest station at Schachen, snow cover in 2012 lasted long into early summer (Figure 4.6). At Felsenkanzel, the sensor at 25 cm depth was damaged in August 2011 probably due to heavy rain and could only be replaced in summer 2012. The soil surface temperature (green line in Figure 4.6) was measured by an infra-red sensor, resulting in low values in winter due to snow reflection. The surface temperature is extremely dependent on solar radiation and rises rapidly with high insolation. The influence of the sun also influences the temperature amplitudes at 5 cm depth: During days, it is heated more and during nights cooled more compared to deeper soil.

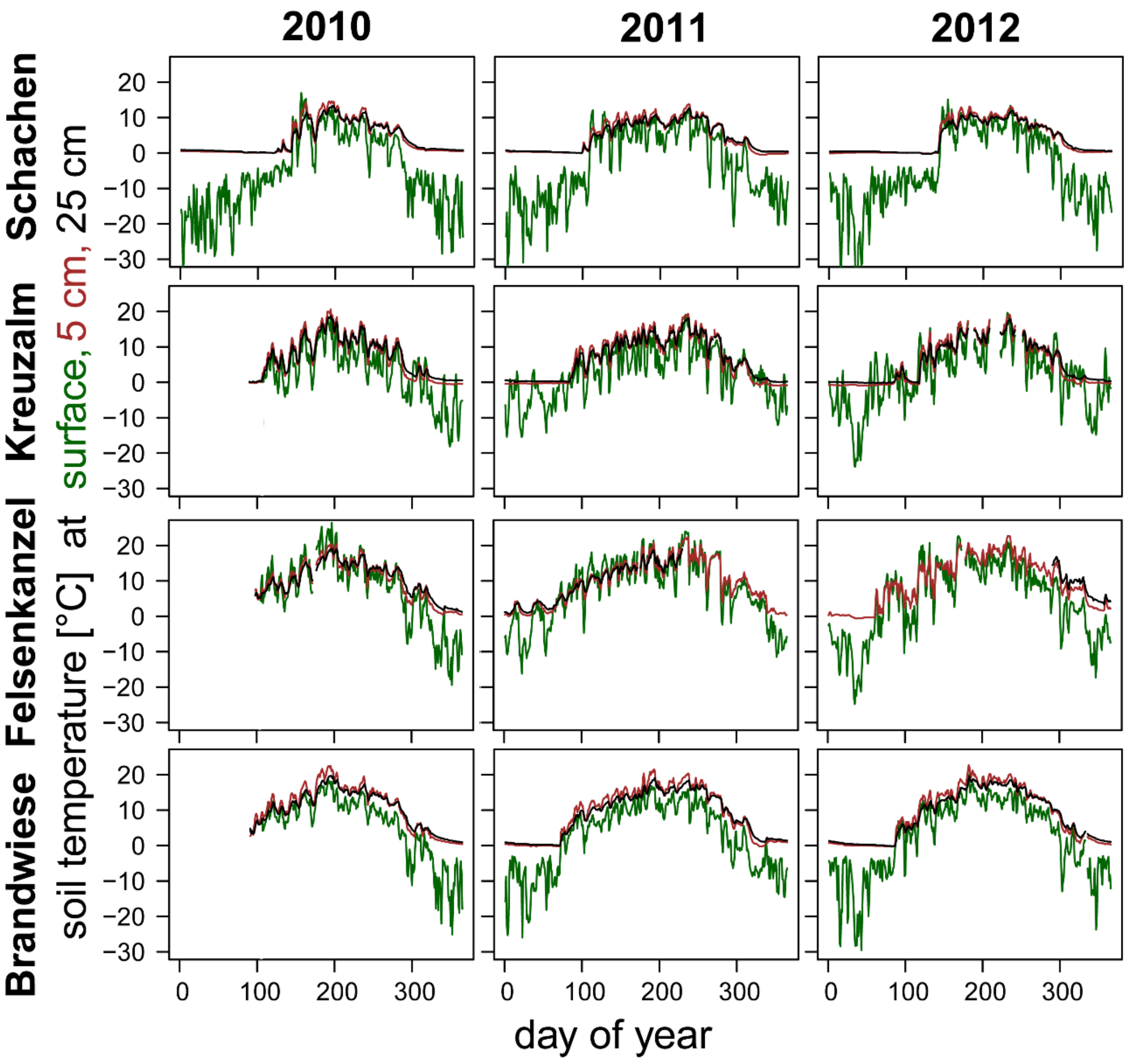


Figure 4.6 Daily mean soil temperature at the surface (dark green), at 5 cm (brown) and 25 cm depth (black) at the four stations in the years 2010-2012.

Relative Humidity and Precipitation

Relative air humidity varies strongly from day to day since it is dependent on air temperature (Figure 4.7). It increases in the cold nights and decreases during days with increasing temperatures. In the narrow valley where the Brandwiese station is located, air humidity is almost constantly high. In particular the warm and dry November 2011 is extraordinary with the lowest air humidity in all three years and no rain in the whole month (Figure 4.7). At the stations Brandwiese and Kreuzalm there was no precipitation gauge installed until autumn 2012 (the data for the winter months of 2012 are not included).

August 2010 was the wettest August in Germany since the beginning of climate records (DWD 2010), which can be seen in the Felsenkanzel data in Figure 4.7. However, in mountainous regions, summer thunderstorms with heavy rain are especially common. Thus, other months also show very high precipitation sums.

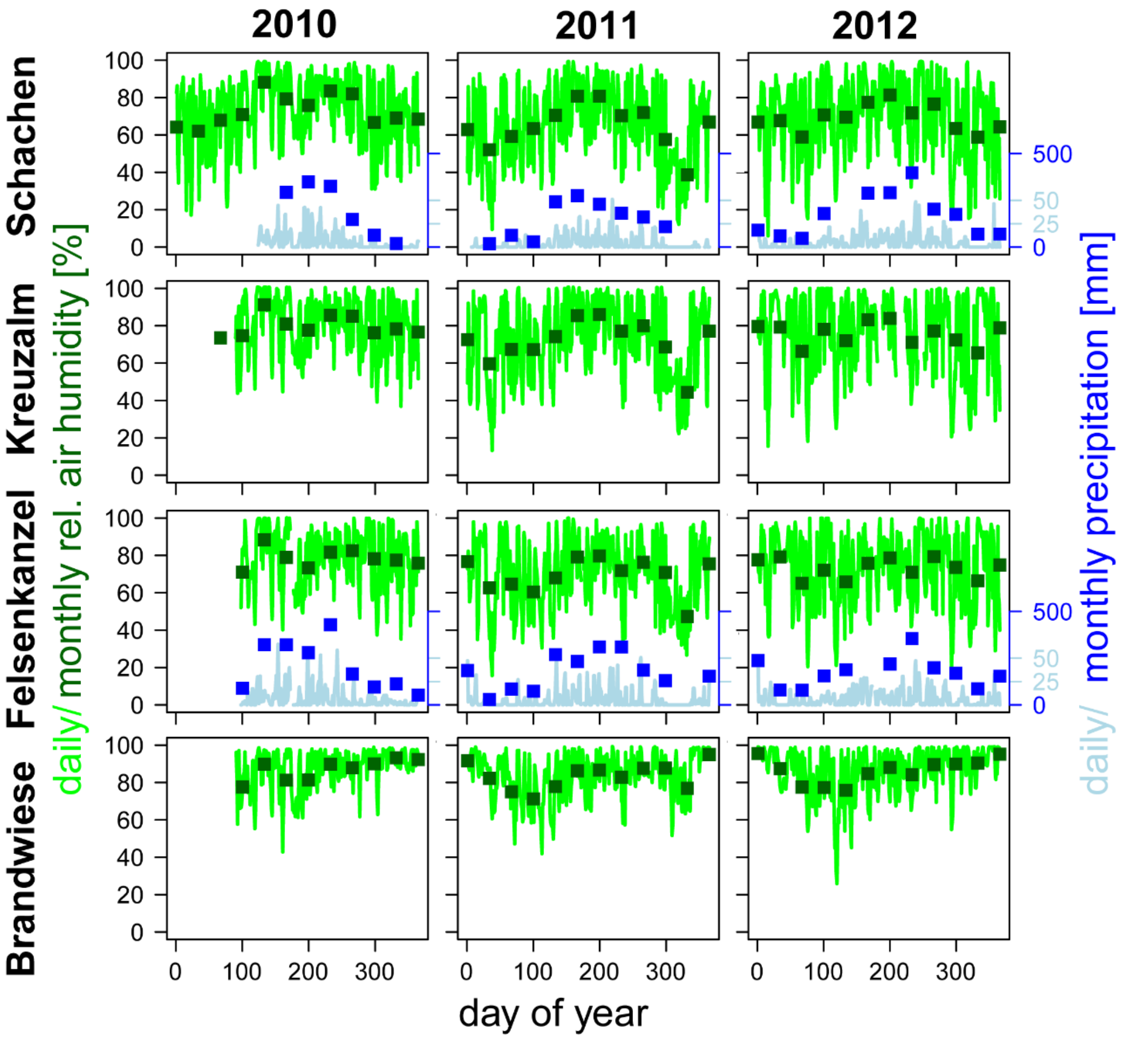


Figure 4.7 Daily (green) and monthly mean (dark green) relative air humidity and daily (light blue) and monthly (blue) precipitation sums at the four stations in the years 2010-2012.

Wind Speed and Wind Direction

With higher elevation, the frequency of strong winds increases. In the valleys like at Brandwiese it hardly exceeds 1 m/s, whereas at Kreuzalm, which is situated on a mountain saddle, maximum wind velocity reached almost 8 m/s in 2012 (Figure 4.8). Wind directions in the alpine area strongly depend on the relief. At Brandwiese and Kreuzalm, the wind direction is most frequently S-W, which means the wind is coming down the alpine ridge along the Reintal valley. At Schachen with a mainly S and S-E wind direction, the wind is descending the Wetterstein mountain chain. However, at the saddle at Kreuzalm, strong winds from the Loisach valley (N-E direction) also occur.

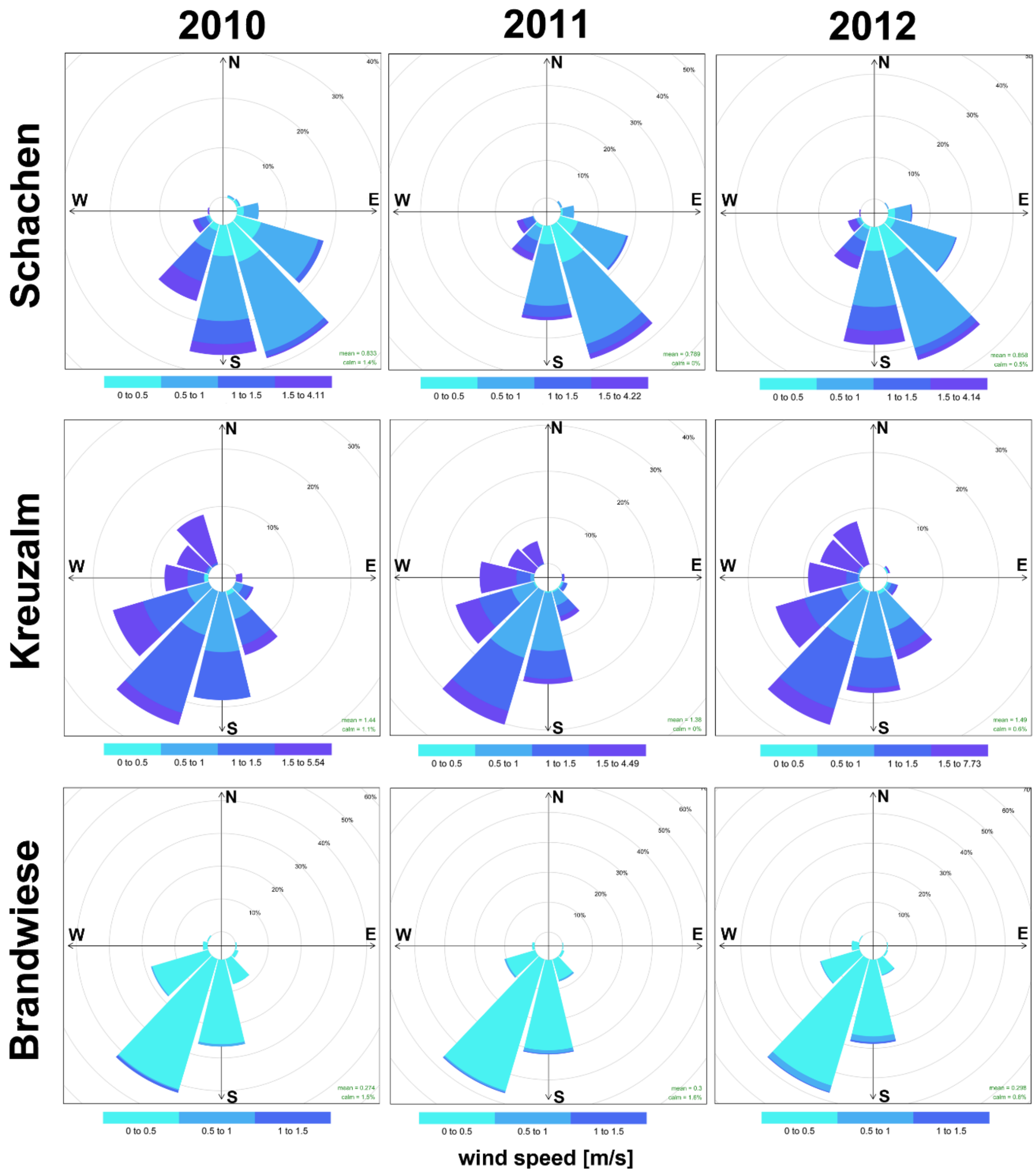


Figure 4.8 Wind directions and wind speeds at three stations in the years 2010-2012.

Solar Radiation

Solar radiation strongly influences air temperature (and therefore relative air humidity), surface and soil temperature in their daily course. The amplitude of daily means is from almost zero to about 400 W/m^2 (Figure 4.9). On clear days, records of solar radiation show a perfect parabolic curve and reach maxima of about 400 W/m^2 (winter) or 1200 W/m^2 (summer). When insolation decreases in autumn and winter, the daily amplitudes of air and soil temperature are flattened or even disappear.

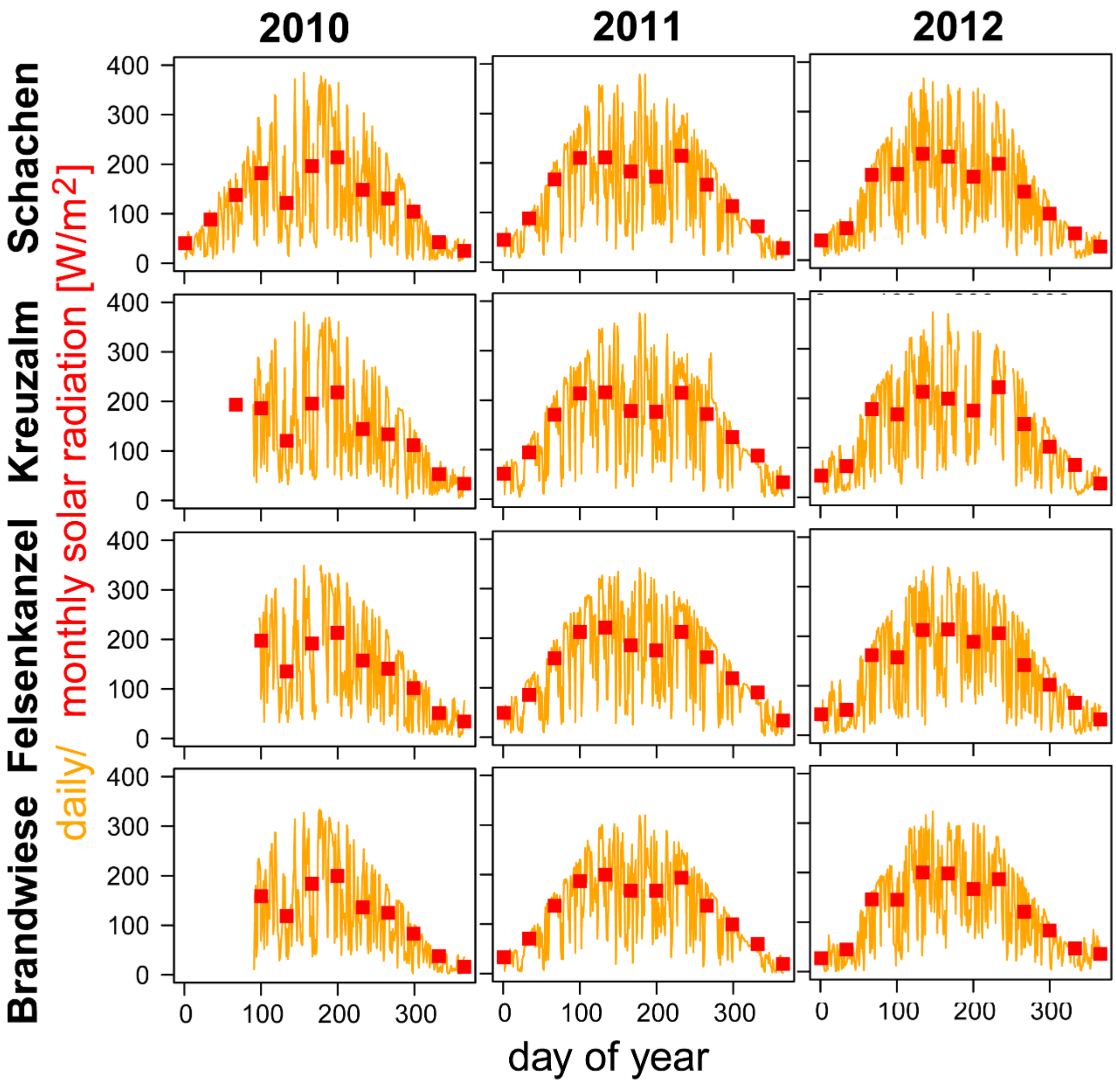


Figure 4.9 Daily (orange) and monthly mean (red) solar radiation at the four stations in the years 2010-2012.

Outlook

At the end of KLIMAGRAD, three stations (Brandwiese, Felsenkanzel, Kreuzeck) were handed over to the Chair of Ecoclimatology, Technische Universität München, and one (Schachen) to the Botanical Garden at Schachen, Botanischer Garten München-Nymphenburg. Contracts with the Bavarian State Ministry of the Environment and Public Health, the government of Upper Bavaria, the District Office of Garmisch-Partenkirchen and the Bavarian State Forest Enterprise have been prolonged until end of 2015. The Fraunhofer Institute (Fraunhofer-Institut für Bauphysik) will keep user rights for the Schachen data for their project Climate for Culture. A continuative project (KLIMAGRAD II) is planed.

The Schachen station provides important meteorological measurements for the initiated long-term phenological observations in the Alpine Botanical Garden Schachen. At the website of the Alpine Botanical Garden (http://www.botmuc.de/de/garten/schachen_alpengarten.html) and on an information panel in the Botanical Garden Munich actual measurements are shown. Actual data of all four stations also is accessible at the website of the Chair for Ecoclimatology (http://www.oekoklimatologie.wzw.tum.de). Registered users can view, plot and download the datasets of recorded parameters via the server of Sommer Company (https://mds.sommer.at) and use the data for individual calculations.

Operating the meteorological stations in the alpine surrounding needs constant observation and servicing, since from time to time some defects occur due to harsh and extreme weather conditions. Especially the removal and reassembly during the yearly Johanni fire requires personal attendance.

Recorded meteorological parameters of the four stations provide an important database for the Werdenfelser Land. The data is currently used and will be used in future research projects of the KLIMAGRAD institutes and cooperation partners.

4.3 Observation Sites and Logger Network

Sites for phenological observations and temperature/humidity measurements were installed along four gradients: Garmisch-Kramer (700-1700 m a.s.l.), Garmisch-Kreuzeck/Längenfelder (800-1800 m a.s.l.), Reintal/Brandwiese-Kreuzeck (900-1600 m a.s.l.) and Reintal-Schachen (800-1800 m a.s.l.). In total, 42 sites (Figure 4.10) were established and chosen according to the following criteria:

- 100 m altitudinal difference
- close to the path, several meters into the forest, less visible
- several tree species in direct surrounding with low branches (if possible)
- semi-shadow, but not directly under a tree
- accessibility in winter with snow shoes (medium slopes)

Each site was documented by GPS, manual mapping and photographs. They were named by a code of three letters for the gradient (KRA= Kramer, KRE= Kreuzeck, SCH= Schachen), three numbers for the elevation, exposition (N for northern, S for southern aspect and M for mast loggers) and site type (L for logger since in other related subprojects also B “Bestandsfläche” and F “Freilandfläche” were used). Some examples:

- SCH185ML: Reintal-SCHachen gradient, 1850 m a.s.l., Mast, Logger
- KRA130SL: Garmisch-KRAmer gradient, 1300 m a.s.l., S exposed, Logger
- KRE160NL: Garmisch-KREuzeck gradient, 1600 m a.s.l., N exposed, Logger
- KRE160SL: Brandwiese-KREuzeck gradient, 1600 m a.s.l., S exposed, Logger

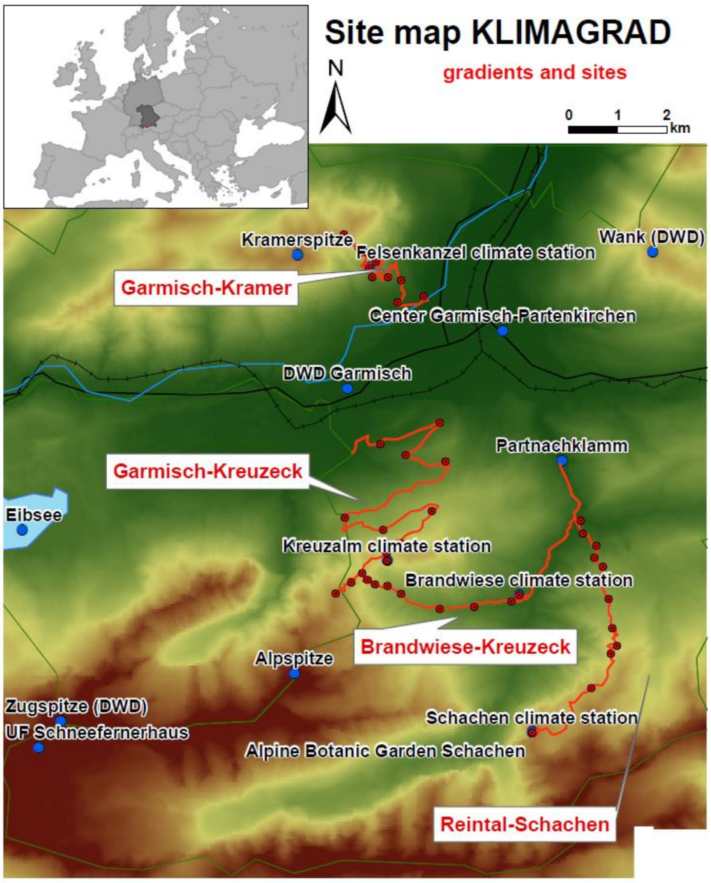


Figure 4.10 Location of the 42 observation sites for tree phenology and air temperature/humidity logger measurements in the study area.

Directly on each of the 42 sites a HOBO® Pro V2 Data Logger of the type U23-001 (Figure 4.11, Table 4.3, www.onsetcomp.com) was installed. Additionally, at each of the four meteorological stations a logger was mounted to ensure the comparability between logger and station data. Loggers included a temperature and a relative humidity sensor in a waterproof case. Batteries and sensors can easily be replaced. They were sheltered in Solar Radiation Shields (onset RS2) and fixed 2 m above the ground. Loggers and shields were labeled with the site code. For reading out data, the onset HOBOware® Pro Software was used (Getting Started Software for HOBO® Data Loggers & Devices Version 2.3.0 for Windows® XP/2000).

Figure 4.11 HOBO® Pro V2 Loggers (top) installed at 2 m height in solar radiation shields in the forest (left, right), reading data (bottom).

Table 4.3 HOBO® Pro V2 Loggers – Technical Information.

	Pro V2 with internal temperature sensor (U23-001)
Measurement range:	-40°C...+70°C 0...100% rH
Accuracy:	±0.2°C at 0...+50°C ±2.5% at 10%...90% rH
Release:	0,02°C at 25°C (12-bit) 0,03% rH (12-bit)
Reaction time:	40 min (Temp.) 10 min (rH)
Memory:	42 000 values
Measurement interval:	1 s - 18 h
Battery:	1/2 AA 3.6 V Lithium Battery
Battery life-time:	Ca. 3 years
Dimensions:	102 x 38 mm
Weight:	57 g

Operating the measurement network in alpine surrounding led to a few gaps in the data record. Due to snow cover, the HOBO stations were established in April 2010, thus January to March 2010 temperature data is missing. Temperatures were interpolated for each site based on DWD recordings in Garmisch-Partenkirchen (1st January 2010 until the first HOBO measurement day) and lapse rates of -0.3 °C 100 m^{-1} (January), -0.2 °C 100 m^{-1} (February), -0.3 °C 100 m^{-1} (March) and -0.4 °C 100 m^{-1} (April). These lapse rates are based on the Zugspitze - Garmisch-Partenkirchen lapse rates in the missing month.

The station SCH080NL, which was set up in mid April 2010 by students during a field work course, was brought to another location (50 m distance) three weeks later, because it was located too close to the flooding area of the Ferchenbach river. In fact, a mudflow event in the first week of June 2010 took away large parts of the riverside material. In summer 2010, HOBO station KRE160NL toppled over probably because of mountain pasture cows. In winter 2010/11 KRA160SL toppled over under snow pressure. They were not damaged and were rebuilt at the next observation visit. There were data losses from November to March at the stations KRA150SL and SCH090NL because of broken sensors. Data gaps were filled by interpolating the temperature with the mean value of the two closest stations (100 m above and 100 m below).

Measurements at the logger sites show parallel courses of the temperature with reduced absolute values at higher elevated sites (Figure 4.12) except in spring and autumn 2011 when stable inversion layers occurred. Using linear regressions of temperature against elevation, temperature lapse rates can be calculated for different time scales, e.g. monthly mean in Figure 4.13. Inversions in January/February and November 2011 resulted in positive lapse rates.

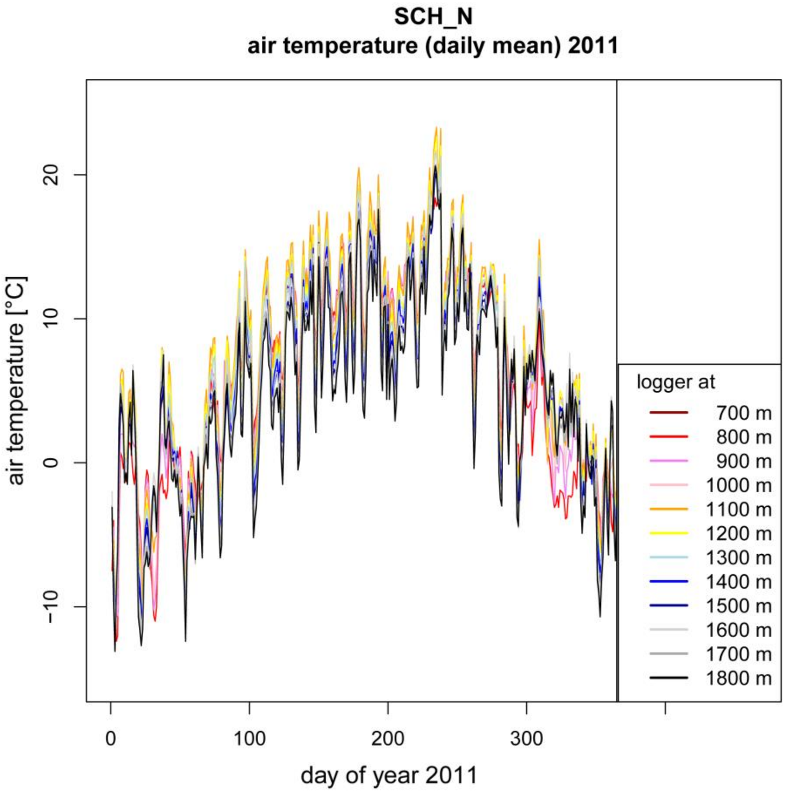


Figure 4.12 Example for the course of the air temperature (°C) measured in different elevations at the logger sites (700-1800 m a.s.l.) in the observation year 2011 (Schachen gradient).

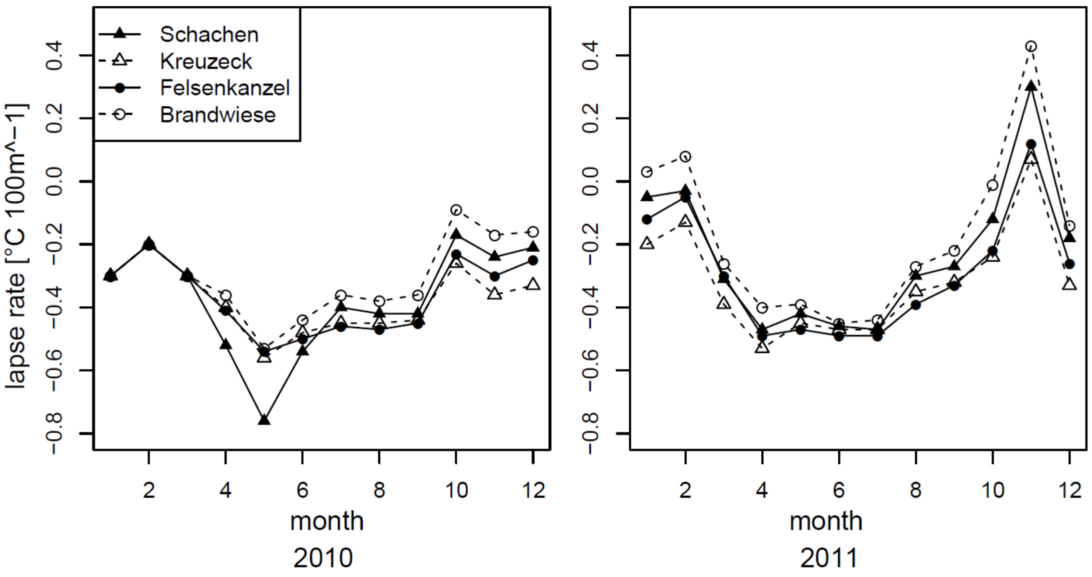


Figure 4.13 Monthly mean temperature lapse rates (°C 100 m^{-1}) at the four gradients in the observation years 2010 and 2011.

Additionally, the meteorological data of the four KLIMAGRAD stations and the DWD stations in Garmisch and Zugspitze were used for analyses.

4.4 Tree Phenological Observations

For phenological observations of typical mountain forest trees, seven species were chosen: *Abies alba* MILL., *Acer pseudoplatanus* L., *Fagus sylvatica* L., *Larix decidua* MILL., *Picea abies* L. (KARST), *Pinus mugo* TURRA and *Pinus sylvestris* L.. At each of the 42 sites along the four gradients, six individuals of each tree species present were included in the study. Three adult (1-3) and three juvenile (4-6) trees were marked by numbers. Each tree of the study was assigned by the site code, two letters for the species (e.g. AA for *Abies alba* or FS for *Fagus sylvatica*) and the tree number. In total, 571 tree individuals were observed: 220 *P. abies*, 133 *F. sylvatica*, 95 *A. pseudoplatanus*, 45 *A. alba*, 41 *P. mugo*, 20 *P. sylvestris*, 17 *L. decidua*.

P. sylvestris is only distributed at the southern aspect of the Kramer gradient. While *P. abies, F. sylvatica* and *A. pseudoplatanus* are the main tree species in the mixed mountain forests, *A. alba* is less frequently represented. Upper limits in the research area are 1500 m a.s.l. for *F. sylvatica* and 1600 m a.s.l. for *A. pseudoplatanus*. *P. abies* grow up to the tree line together with *L. decidua* and *P. mugo*. Less frequent are *Alnus* and *Sorbus* species. At the tree lines of Kreuzeck and Schachen, *P. cembra* is also present (1700-1800 m a.s.l.).

For all trees, spring phenology (e.g. bud burst, leaf unfolding, flowering) and at the deciduous trees also autumn phenology (leaf coloration and leaf fall) was observed. For each species, an individual observation key was developed according to the general BBCH Code (Figure 4.14, Meier 1997) and the general growth stage key for trees and woody plants (Finn et al. 2007). A general summarization of the keys is presented in Table 4.4 the individual keys moreover included photographs showing the exact phenological phase (Figure 4.15).

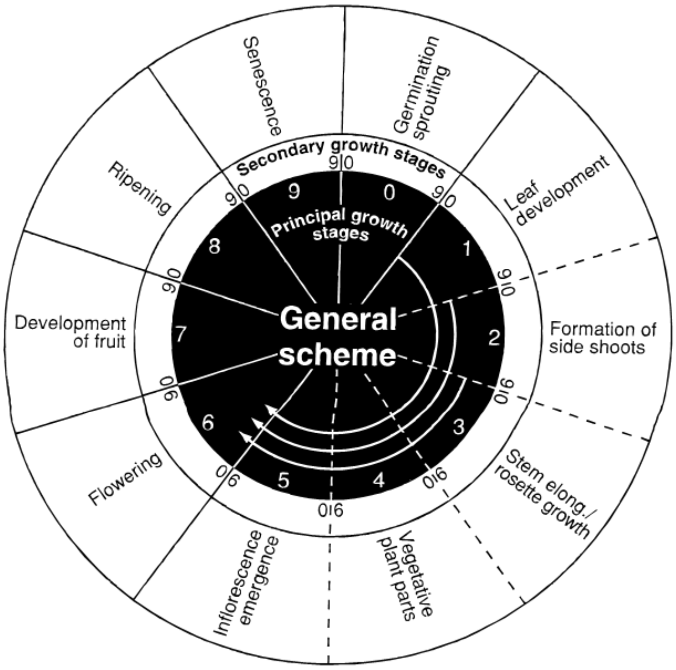


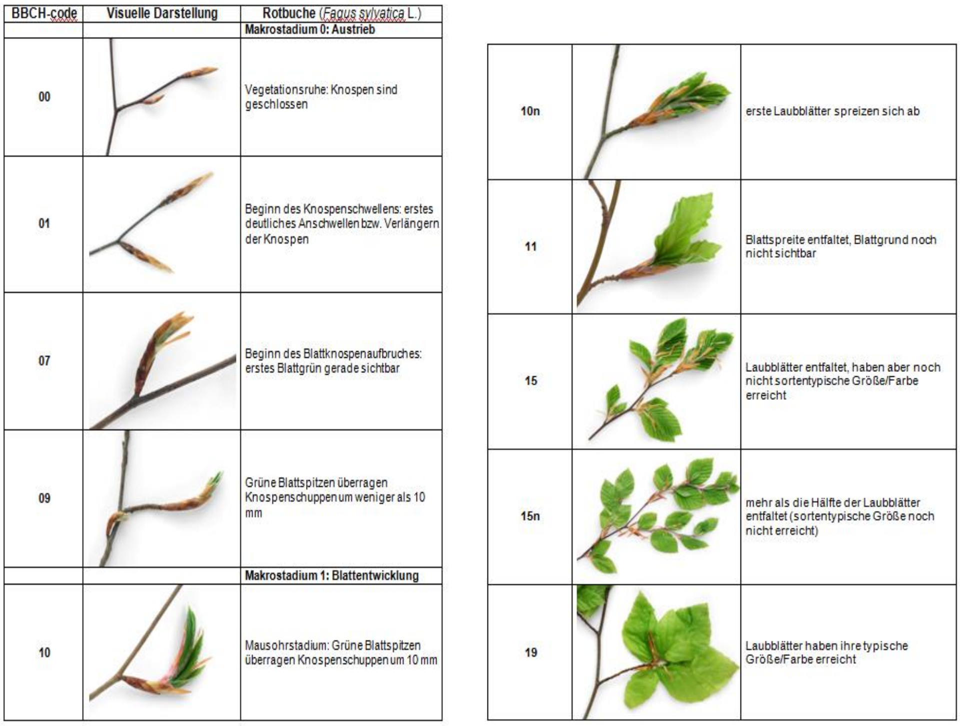
Figure 4.14 BBCH Code (Meier 1997).

Observations for the adult trees were separated for upper and lower crown; for the upper crown a binocular (8-fold magnification) was used. At every observation day, the most advanced phenological phase of an individual was noted. In autumn, the percentages of green, colored and fallen leaves of an individual was estimated and noted. All observations were made by the same person (the author), which minimizes subjectivity.
The observation period was from April to July for spring and September to October for autumn phenology in the years 2010 and 2011. The interval was weekly due to the high number of sites and the difficult terrain in the alpine mountains (3000 m elevation hiking up and down again per week, which summarizes in one year to approximately seven times climbing Mount Everest up and down from sea level). In general, on Mondays the gradients Garmisch-Kramer and Garmisch-Kreuzeck and on Tuesdays the gradients Brandwiese-Kreuzeck and Reintal-Schachen were visited.

Due to the harsh alpine weather conditions, there were some few shifts or gaps in the observation intervals. Heavy rain, thunderstorms or sudden snow in higher elevations made phenological observations difficult or impossible. Changing light conditions (bright sun, clouds, evening light and fog) particularly complicated the differentiation between BBCH 17 (full unfolded fresh green leaves) and BBCH 19 (darker leaves), therefore the latter one often was neglected for analysis. Sometimes it was difficult to observe flowering, especially for adult *A. alba*, which flowers are located at the top of the trees. In the two observation years 2010 and 2011, some trees also dropped out of the observation program due to human or nature impacts (harvested, deer grazing, wind/erosion).

Table 4.4 Overview of observed phenological phases (based on the BBCH Code, Meier 1997).

BBCH	Leaf unfolding (deciduous species)	Needle elongation
0	Buds closed	Buds closed
1	Begin of bud swelling	
7	Begin of bud burst (first green visible)	Begin of bud burst (first green visible)
9	Green leaf tops <10 mm out of bud scale	Green needles bunched, <10 mm
10	Green leaf tops >10 mm out of bud scale (mouse ear phase)	
10.5	First leaves start unfolding	
11	Leaf blade unfolded, leaf base not visible	Needles loose (not bunched), >10 mm, shoot growth starts
15	First leaves complete unfolded, light green and weak	Shoot and needles approx. ½ size, light green and weak
17	>50 % of leaves unfolded, approx. end size and color	>50 % of shoots and needles approx. end size and color
19	Leaves fully unfolded, final size and color	Shoots have final size and color
BBCH	**Flowering and Seed development**	
61	Beginning of flowering (10 % flowers open)	
65	Full flowering (50 % flowers open)	
69	End of flowering	
71	Beginning of fruit growth	
79	End of fruit growth (approx. final size)	
81	Beginning of ripening / fruit coloration	
89	End of ripening / fruit coloration, releasing seeds	
BBCH	**Senescence (deciduous species)**	
91	Leaves still green	
93	Begin of leaf coloring (5 % colored)	
95	50 % leaves still green, 50 % colored or fallen	
96	50 % leaves fallen	
97	End of leaf fall (95 % fallen)	



BBCH-code	Visuelle Darstellung	Rotbuche (*Fagus sylvatica* L.)
		Makrostadium 0: Austrieb
00		Vegetationsruhe: Knospen sind geschlossen
01		Beginn des Knospenschwellens: erstes deutliches Anschwellen bzw. Verlängern der Knospen
07		Beginn des Blattknospenaufbruches: erstes Blattgrün gerade sichtbar
09		Grüne Blattspitzen überragen Knospenschuppen um weniger als 10 mm
		Makrostadium 1: Blattentwicklung
10		Mausohrstadium: Grüne Blattspitzen überragen Knospenschuppen um 10 mm
10n		erste Laubblätter spreizen sich ab
11		Blattspreite entfaltet, Blattgrund noch nicht sichtbar
15		Laubblätter entfaltet, haben aber noch nicht sortentypische Größe/Farbe erreicht
15n		mehr als die Hälfte der Laubblätter entfaltet (sortentypische Größe noch nicht erreicht)
19		Laubblätter haben ihre typische Größe/Farbe erreicht

Figure 4.15 Observation key for tree phenology including BBCH codes, photograph and descriptions. Example for *Fagus sylvatica* leaf unfolding.

To derive onset dates for each phase, species, site and year from the observed BBCH phases, logistic regressions (A) were fitted on the data.

(A) $$y = \frac{e^{a+bx}}{1+e^{a+bx}}$$

y: percentage of spring development derived from BBCH observations

x: time (day of year)

a, b: coefficients fitted individually for each regression

This method is used to fill up gaps in observations in order to ensure a complete set of onset dates. Based on determined onset dates, phenological elevational rates were calculated for all species and phenological phases by linear regression (days 100 m^{-1}). These rates were combined with temperature lapse rates determined from the logger measurements (°C 100 m^{-1}) by using formula (B). In this way, phenological response rates to temperature (days $°C^{-1}$) were identified.

(B) $$prr\left[\frac{days}{°C}\right] = per\left[\frac{days}{100m}\right] * \frac{1}{tlr\ [\frac{°C}{100m}]}$$

prr: phenological response rate

per: phenological elevational rate

tlr: temperature lapse rate

Phenological response rates characterize the shift of phenological onset dates in days with increasing temperature of one degree. Thus, species differences in the response to climate change can be quantified.

4.5 Microcore Sampling

Eight of the 42 sites were chosen for microsampling: four at the south exposed Garmisch-Kramer gradient and four at the north exposed Garmisch-Kreuzeck gradient. Here, the altitudinal difference between sampling sites was 200 m, so sampling took place at 800, 1000, 1200 and 1400 m a.s.l. At each site two trees of *Picea abies* and of *Fagus sylvatica* were chosen for sampling from the phenologically observed trees (Table 4.5). Unfortunately, sampling was not possible for *F. sylvatica* at KRA 1400, as trees had bark wounds or an irregular diameter growth. Here, another individual was chosen as a substitute (FX).

Table 4.5 List of microcore sampling trees at Kramer (KRA) and Kreuzeck (KRE) gradient, elevation (800 – 1400 m a.s.l.), tree number (F = *Fagus sylvatica*, P = *Picea abies*), presence of individual phenology observation

site	tree	phenology	site	tree	phenology
KRA 800	F1	yes	KRE 800	F1	yes
KRA 800	P1	yes	KRE 800	F3	yes
KRA 800	P3	yes	KRE 800	P1	yes
KRA 1000	F1	yes	KRE 800	P2	yes
KRA 1000	F3	yes	KRE 1000	F1	yes
KRA 1000	P2	yes	KRE 1000	F2	yes
KRA 1000	P3	yes	KRE 1000	P1	yes
KRA 1200	F1	yes	KRE 1000	P3	yes
KRA 1200	F3	yes	KRE 1200	F1	yes
KRA 1200	P1	yes	KRE 1200	F2	yes
KRA 1200	P3	yes	KRE 1200	P1	yes
KRA 1400	F3	yes	KRE 1200	P2	yes
KRA 1400	FX	no	KRE 1400	F1	yes
KRA 1400	P1	yes	KRE 1400	P1	yes
KRA 1400	P2	yes	KRE 1400	P2	yes

For microsampling, a Trephor was used, an easy to handle tool (Figure 4.16) developed for microsampling of wood tissue by the University of Padua, Italy, (http://www.tesaf.unipd.it/Sanvito/trephorEn.asp). It provides high quality samples on both softwood and hardwood species with minimum damage to sampled trees. The standard size is used for microsamples (16 mm length and 2 mm diameter). The Trephor is inserted into the wood using a rubber hammer and then removed from the trunk. When choosing the sampling points, knurls of the trunk and reaction wood should be avoided.

Sampling took place every week from the 2nd of May to the 15th of July 2011, later in larger intervals of 10-14 days. In total, samples were collected at 18 days during the vegetation period (Julian days: 122, 129, 136, 143, 150, 157, 171, 181, 192, 206, 220, 234, 255, 269, 279, 290, 297). The last sampling date was the 24th of October 2011.

Samples were taken at breast height (1.3 m) at a side of the tree perpendicular to the slope. When necessary, the sampling area was cleaned carefully from thick bark (especially in *Picea abies*). Weekly samples took place at a horizontal distance of ca. 4 cm, re-samples (when the first sample was not good) at a vertical distance of 2 cm. Since we consider the vertical wound reaction to be stronger than the horizontal, a distance of ca. 8 cm was left to the next sampling row. Considering that each tree is an individual concerning bark, branches, wounds and radial growth, this scheme could not always be followed strictly.

Direct after sampling, microcores were stored in Eppendorf® reaction tubes filled with a mixture of ethanol, glycol and demineralized water (1:1:1). Many solution mixtures are used in practice, but all in all it is important to keep the samples wet and more or less in an osmotic equilibrium to prevent cell dehydration or destruction.

Figure 4.16 Trephor (top left), Microcores (top right), sampled tree (bottom left), all samples (bottom right).

After learning the microcore wood processing method with some additional samples and estimating the enormous time required, an external laboratory (Marcus Brückner Materialfotografie & Histologie, Mannheim, www.brueckner-m.de) was contracted to process the bulk of the 510 samples. In this way a constant quality of all the samples was ensured and the risk of sample loss due to single manual treatment was minimized. Moreover, our laboratory facilities in the university were not adequate for processing this number of samples.

Laboratory protocol of the sample processing, cutting and staining:

1. Processing of the samples
    - washing in 70 % alcohol (2 h), changed several times
    - dehydration in a rising alcohol series, 80 %, 90 % 96 %, 2 h each
    - pre-infiltration with Technovit 7100, 7-12 h
    - infiltration-solution Nr. I 7-12 h
    - infiltration-solution Nr. II 7-12 h
    - embedding in Technovit 7100, hardening 24 h
2. Preparation with the Microtome

    All samples were cut by a rotation microtome (Leica RM 2050 with hard metal knife d-grinding). It was worked with a free angle of 7° and slow cutting speed. Slices of 7-15 µm, depending on the sample.

3. Staining with Safranin-O-Astrablau
    - Safranin-O solution 5 min
    - Acetic acid 1 % 1 min (changed after each staining)
    - demineralized water 1 min
    - Astrablau 10 min
    - demineralized water 1 min
    - rinsing in a rising alcohol series (96 %, 96 %, 100 %, Xylol 1 and Xylol 2), 5-10 min
    - object slide covered with Leica CV Mount, Xylol basis
4. Labeling

During the explained procedure in the laboratory, several difficulties occurred. Some samples broke during the dehydration process before they were embedded. The following samples were lost in the laboratory: A8P3_297, E12P1_152 and E14P2_152. Samples which were embedded with fiber direction orthogonal to the cutting direction (Figure 4.17) sometimes moved before the resin finally hardened. So in some slices, the cells were visible in a more longitudinal cut, which makes it more difficult to determine the stage of the cell (growing/ wall thickening/ early- or latewood). Some of the slices could not be measured because they were broken at the cambial zone or differentiation of the cells was not visible because of a longitudinal cut.

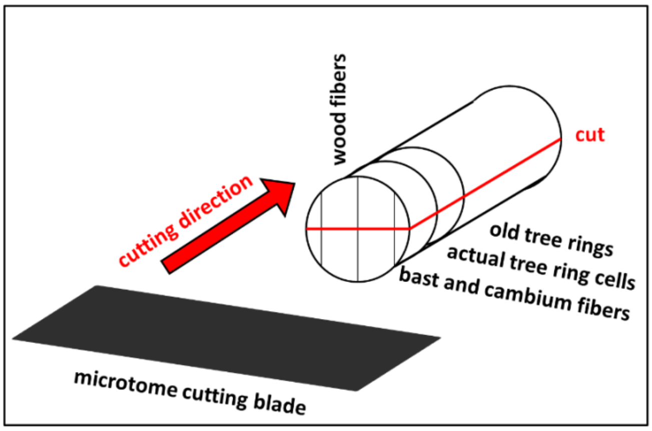


Figure 4.17 Thin section cutting of the microcore. Cutting direction orthogonal to the wood fibers for optimal results.

Slices were digitalized by taking photographs with a Kappa DX 0.32X® camera and Kappa Image Base Control® Software in a 63x magnification of a Leitz Variophot® microscope (Figure 4.18). The pictures have a dimension of 1296 x 1025 pixels with a resolution of 72 Px/inch and a scale was added. Sometimes, especially with *P. abies*, the whole tree ring was larger than one picture, so two or three pictures were taken and assembled by Photoshop CS3.
The ring width was measured three times per section by Photoshop CS3 with a scale factor of 400 (1 pixel = 0.0025, 805 pixel = 2 mm) and averaged. Seven different categories were differentiated:

1 phloem
2 cambium
3 total xylem
4 growing xylem cells
5 wall thickening xylem cells
6 lignified xylem cells
7 latewood cells (*P. abies*) or youngest vessel diameter (*F. sylvatica*)

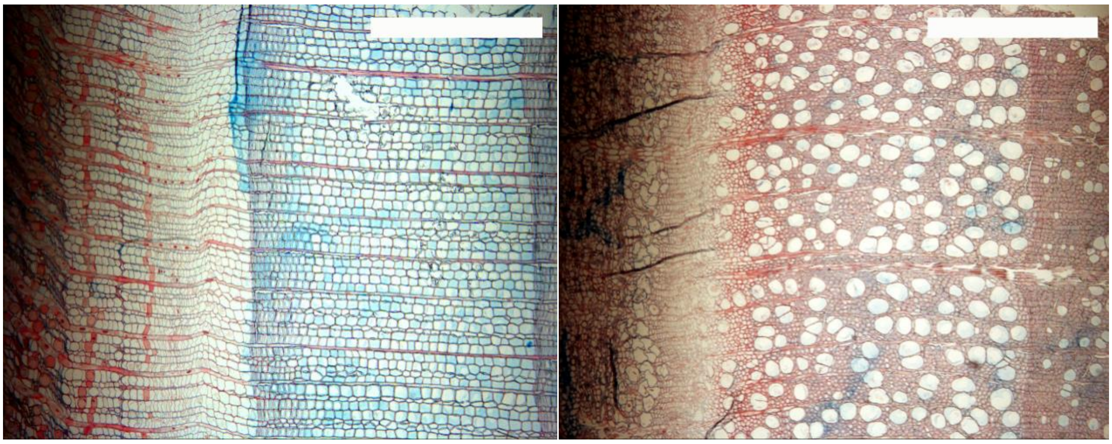


Figure 4.18 Examples for thin sections: *Picea abies* from KRA 800 m a.s.l. site at day 143 of the year 2011 (left) and *Fagus sylvatica* from KRA 800 m a.s.l. site at day 192 of the year 2011 (right). The white scale bar represents 1 mm.

To the averaged ring width of each sampling date, a smoothing growth curve was fitted. A Gompertz curve (A) for phloem, xylem and lignified cells was applied. For growing and wall thickening cells an adjusted three-parametric Hadwiger curve (B) was chosen, since for these categories the amount of cells in this stage first increases and then decreases after a maximum.

$$\text{(A)} \qquad d = ae^{be^{c\,doy}}$$

$$\text{(B)} \qquad d = \frac{a * b * (\frac{c}{doy})^{\frac{3}{2}}}{c} * e^{-b^2 * (\frac{c}{doy} + \frac{doy}{c} - 2)}$$

d: predicted ring width
doy: day of the year
a, b, c: variables
(b and c are negative for Gompertz)

On the basis of the fitted curve, following onset dates were determined for all categories: growth start date (one cell row, day of year), growth end date (95 % of the final ring width, day of year) and the growth period (difference between start and end date, days). Additional parameters of the Gompertz curve were maximum growth rate (slope at the inflection point, mm day^{-1}), maximum growth rate date (day of year) and the final ring width (mm).

Responses of the onset dates to elevation and temperature were determined similar to the phenological response rates. Rates and onset dates of tree ring growth and leaf phenology were related to one another.

5 Shifting and Extension of Phenological Periods with Increasing Temperature along Elevational Transects in Southern Bavaria

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5.1 Abstract

The impact of global warming on phenology has been widely studied and almost consistently advancing spring events have been reported. Especially in alpine regions, an extraordinary rapid warming has been observed in the last decades. However, little is known about phenological phases over the whole vegetation period at high elevations. We observed 12 phenological phases of seven tree species and measured air temperature at 42 sites along four transects of about 1000 m elevational range in the years 2010 and 2011 near Garmisch-Partenkirchen, Germany. Site- and species-specific onset dates for the phenological phases were determined and related to elevation, temperature lapse rates and site-specific temperature sums. Increasing temperatures induced advanced spring and delayed autumn phases, in which both yielded similar magnitudes. Delayed leaf senescence could therefore have been underestimated until now in extending the vegetation period. Not only the vegetation period, but also phenological periods extended with increasing temperature. Moreover, sensitivity to elevation and temperature strongly depends on the specific phenological phase. Differences between species and groups of species (deciduous, evergreen, high elevation) were found in onset dates, phenological response rates and also in the effect of chilling and forcing temperatures. Increased chilling days highly reduced forcing temperature requirements for deciduous trees, but less for evergreen trees.

The problem of shifted species associations and phenological mismatches due to species-specific responses to increasing temperature is a recent topic in ecological research. Therefore, we consider our findings by this novel dense observation network in an alpine area of particular importance to deepen the knowledge about phenological response to climate change.

Short Title: Shifting and extension of phenological periods
Key words: alpine forest, tree phenology, elevation gradients, BBCH, seasons

5.2 Introduction

Phenology has proved to be a good indicator of the impacts of climate change on vegetation (e.g. Murray et al. 1989, Hänninen 1991, Kramer 1994, Menzel et al. 2001). The growing period of trees has extended in recent decades due to global warming (e.g. Menzel & Fabian 1999, Linderholm 2006). This trend is mainly due to advanced spring events (bud burst; e.g. Ahas et al. 2002, Cleland et al. 2007) which are predominantly triggered by spring warming (Hickin & Vittum 1976, Castonguay et al. 1984) and a sufficient dormancy chilling period (Chuine & Cour 1999). Additionally, but less frequently, delayed leaf senescence is reported (Menzel et al. 2006, Vitasse et al. 2009a). In mountainous regions such as the Alps, a high impact of global warming has been detected in recent decades since these areas have warmed by almost double (1.5 °C) than the global average (0.7 °C; e.g. Theurillat & Guisan 2001, Schröter et al. 2005, Nogués-Bravo et al. 2007). Animals and plants often experience harsh or inhospitable living conditions here due to extreme climatic conditions, combined with a high variation in topography and habitats. Therefore they react with a high degree of specialization and adaption (Körner 2003). Faced with a higher speed of warming (left behind) and the lack of areas to retreat (nowhere-to-go), alpine species are considered as highly threatened by climate change (Beniston et al. 1997, Schröter et al. 2005). Moreover, climate warming will lead to an upward shift in species distribution, which initially increases species richness but enforces species competition at higher elevations and will result in a loss of biodiversity in longer time scales (Klanderud & Birks 2003, Parmesan 2006, Erschbamer et al. 2009, Lenoir et al. 2008).

Phenological observations along elevational transects allow studying phenological responses to a wide range of temperature in relatively short time (Dittmar & Elling 2006, Vitasse et al. 2009b). However, since observations in alpine surroundings require extensive efforts, detailed phenological data as recorded in our study are still rare. Only few studies have observed both spring flushing and leaf senescence (Vitasse et al. 2009b) and most studies only focused on a few phenological phases (such as bud burst and leaf coloration) and the length of the vegetation period. However, knowledge on the relations of phenology, temperature and elevation based on field observations helps to predict phenological changes under future global warming and to improve phenological model fitting. Many efforts have been undertaken to develop complex phenological models (Hänninen 1990, Hunter & Lechowicz 1992, Chuine & Cour 1999, Migliavacca et al. 2008), but also simple models provide convincing results (Rötzer et al. 2004).

At the forest covered slopes in the Bavarian Alps, we find optimal conditions for tree phenological studies on elevational transects. Along four transects, we installed 42 observation sites including temperature and relative humidity measurements and observed seven tree species according to a species-modified BBCH Code (Meier 1997) in the years 2010 and 2011. We determined responses of single phenological phases based on phenological elevational rates and temperature lapse rates as well as based on temperature sums. Finally, we compared phenological temperature response rates from both approaches.

The objectives of this study were (a) to identify species-specific response rates to elevation and temperature as we expected them to be highly variable. We wanted to quantify differences between (b) responses from a high number of phenological phases and (c) between species groups (MD: montane deciduous, ME: montane evergreen and HE: high elevation species). Since Davi et al. (2006) found in temperate trees that 55 % of the increase of the vegetation period is attributable to advanced spring and 45 % to delayed autumn events, another aim was (d) to compare phenological periods in their role of lengthening the total vegetation period. Additionally, we wanted (e) to determine the behavior of our seven tree species regarding chilling and forcing temperatures, since spring forcing (Hickin & Vittum 1976, Hunter & Lechowicz 1992) and winter chilling (Perry 1971) are known to be the main drivers of temperate spring phenology.

5.3 Materials and Methods

Study Area

The study area is located in southern Bavaria near the city of Garmisch-Partenkirchen (708 m a.s.l., 47°30’ N, 11°5’ E) and the Zugspitze (2962 m a.s.l., 47°25’ 16’ N, 10°59’ 11’ E), the highest mountain in Germany. In this alpine region annual precipitation varies from 1363 mm in Garmisch to 2003 mm at Zugspitze and annual mean temperature ranges from 6.5 °C (Garmisch) to -4.8 °C (Zugspitze, 1961 – 1990). Mixed mountainous deciduous-coniferous forest covers most of the slopes from 700 m a.s.l. in the valley up to the tree line at 1700 - 1900 m a.s.l. For the present study, four transects within the montane forest zone were installed (Figure 5.1): Garmisch-Partenkirchen – Kramer pass (700 - 1700 m a.s.l., S aspect, KRA), Garmisch-Partenkirchen – Kreuzeck/Längenfelder (800 - 1800 m a.s.l., N aspect, KRE), Reintal/Brandwiese – Kreuzeck (900 - 1600 m a.s.l., S aspect, BRA) and Reintal – Schachen (800 - 1800 m a.s.l., N aspect, SCH).

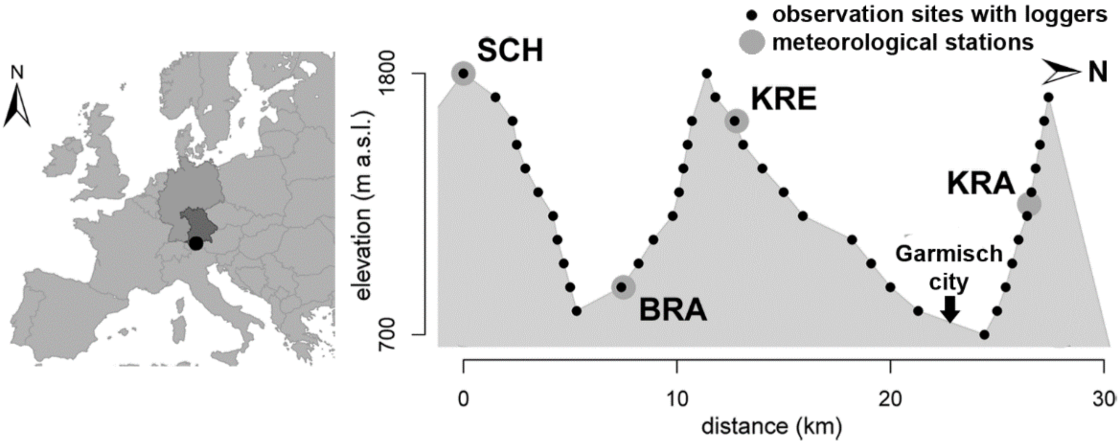

Figure 5.1 Study site in southern Bavaria, Germany (left), and transects around the city of Garmisch-Partenkirchen with logger and tree phenological observation sites (black points) as well as meteorological stations (grey points).

Meteorological Measurements

Four meteorological stations were installed in autumn 2009 and early spring 2010: one at each transect, but at different elevations, to provide data from different elevations (900 m a.s.l. at BRA, 1250 m a.s.l. at KRA, 1600 m a.s.l. at KRE and 1830 m a.s.l. at SCH). Air, surface and soil temperature, air humidity, precipitation, solar radiation, wind speed and wind direction have been recorded every ten minutes. Along the four transects, 42 observation sites in the forest have been chosen every 100 m in elevation (see Figure 5.1). At each forest site, air temperature and relative humidity have been measured using onset HOBO® PRO V2 loggers fixed in a solar radiation shield at 2 m height on a stake. Logger measurements have been recorded with a 30 min frequency from April 2010 onwards.

Phenological Observations

At each of the 42 sites, six individuals (three mature and three juvenile tees) from each species present were selected for phenological observations, resulting in 571 individual trees: *Abies alba* (45), *Acer pseudoplatanus* (95), *Fagus sylvatica* (133), *Larix decidua* (17), *Picea abies* (220), *Pinus mugo* (41), *Pinus sylvestris* (20). While *P. abies* is one of the dominant species everywhere, *A. alba* is only found in smaller numbers and not at all sites. Elevational limits for *A. pseudoplatanus* and *F. sylvatica* are around 1600 m a.s.l. and 1500 m a.s.l., respectively. *P. sylvestris* is present only at the KRA transect. *L. decidua* and *P. mugo* are mostly distributed at higher elevations above 1100 m a.s.l.

For each species, an observation guide was set up according to the general BBCH Code (Meier 1997) and the general growth stage key for trees and woody plants (Finn et al. 2007). The observation guide included eight phases for leaf development (BBCH phases 1, 7, 9, 10, 10.5, 11, 15, 17, see Table 5.1) and four phases for leaf senescence (93, 95, 96, 97, see Table 5.1). In this study, the most advanced phase found at an individual defined its actual development stage (status monitoring). In autumn, the percentage of green, colored and fallen leaves was estimated in 5 % intervals. Onset dates for the BBCH codes were calculated by logistic regression on the observations (see analysis methods). The annual observation period started with visible spring events (bud swelling) and ended when leaves were fully unfolded (end of April to end of July 2010, beginning of April to mid July 2011). The leaf senescence phases were observed weekly for *A. pseudoplatanus* and *F. sylvatica* in September and October 2010 and 2011. Observations took place regularly once a week using binoculars with tenfold magnification.

In addition to classical onset dates, we defined phenological periods between BBCH phases ($\text{onset}_{\text{BBCH b}}$ - $\text{onset}_{\text{BBCH a}}$ with BBCH a < BBCH b), e.g. leaf development period ($\text{onset}_{\text{BBCH 17}}$ - $\text{onset}_{\text{BBCH 7}}$), full leaf period ($\text{onset}_{\text{BBCH 93}}$ - $\text{onset}_{\text{BBCH 17}}$), leaf senescence period ($\text{onset}_{\text{BBCH 97}}$ - $\text{onset}_{\text{BBCH 93}}$) and vegetation period ($\text{onset}_{\text{BBCH 97}}$ – $\text{onset}_{\text{BBCH 7}}$).

Analysis Methods

Temperature lapse rates (°C 100 m^{-1}) were calculated by linear regression of mean air temperatures at the logger sites against elevation, separately for each month (monthly mean temperature), the spring (April to July) and autumn period (September to October, mean of monthly mean temperature lapse rates) and for annual mean temperatures.

In order to model spring leaf development and to derive site- and species-specific onset dates of each phase, logistic regressions (1) were fitted for each species at each site to the BBCH observations. For the regressions, the classes of BBCH phases had been converted to percentages of total leaf development before (see Table 5.1) and a binominal glm model was used in R (R Development Core Team 2009). Based on the respective parameters (a, b) of the regression, single onset dates for each phenological phase of each species at each site were calculated separately for 2010 and 2011.

(1) $$y = \frac{e^{a+bx}}{1+e^{a+bx}}$$

y: percentage of spring development derived from BBCH observations
x: time (day of year)
a, b: coefficients fitted individually for each regression

Table 5.1 Observed phenological phases, modified after Meier (1997) and Finn et al. (2007), phenological periods and development percentages for logistic regressions.

BBCH	Leaf unfolding (deciduous species)	Needle elongation	Percentage
0	Buds closed	Buds closed	0
1	Begin of bud swelling		5
7	Begin of bud burst (first green visible)	Begin of bud burst (first green visible)	10
9	Green leaf tops <10 mm out of bud scale	Green needles bunched, <10 mm	20
10	Green leaf tops >10 mm out of bud scale (mouse ear phase)		30
10.5	First leafs start unfolding		40
11	Leaf blade unfolded, leaf base not visible	Needles loose (not bunched), >10 mm, shoot growth starts	50
15	First leafs complete unfolded, light green and weak	Shoot and needles approx. ½ size, light green and weak	70
17	>50 % of leaves unfolded, approx. end size and color	>50 % of shoots and needles approx. end size and color	90
BBCH	**Senescence (deciduous species)**		
91	Leaves still green		
93	Begin of leaf coloring (5 % colored)		
95	50 % leaves still green, 50 % colored or fallen		
96	50 % leaves fallen		
97	End of leaf fall (95 % fallen)		
Periods			
Spring leaf development period (onset$_{BBCH\ 17}$ - onset$_{BBCH\ 7}$, days)			
Summer full leaf period (onset$_{BBCH\ 93}$ - onset$_{BBCH\ 17}$, days)			
Autumn leaf senescence period (onset$_{BBCH\ 97}$ - onset$_{BBCH\ 93}$, days)			
Vegetation period (onset$_{BBCH\ 97}$ - onset$_{BBCH\ 7}$, days)			

Onset dates for the autumn phases were also calculated by logistic regressions (1) on the observed percentages of green (BBCH 93 and 95) and fallen leaves (BBCH 96 and 97). This logistic regression method is suitable to fill up gaps in observations in order to ensure a complete set of consistent onset dates. In literature, the most common phenological phases are BBCH 7 (bud burst), BBCH 10.5 (leaf unfolding for deciduous trees) in spring and BBCH 95 (50 % leaves colored or fallen, 50 % still green) in autumn. Thus, response rates of all phases we determined are presented, but not all of them are discussed.

Phenological elevational rates were calculated for all species and BBCH phases by linear regression of determined onset dates against elevation (per, days 100 m^{-1}). Combining per (days 100 m^{-1}) with the temperature lapse rates measured by the logger network (tlr, °C 100 m^{-1}) by using formula (2), phenological response rates (prr, days °C^{-1}) were determined for 2010, 2011 and 2010/11.

$$prr\left[\frac{days}{^\circ C}\right] = per\left[\frac{days}{100m}\right] * \frac{1}{tlr\,[\frac{^\circ C}{100m}]} \tag{2}$$

prr: phenological response rate
per: phenological elevational rate
tlr: temperature lapse rate

Mean phenological response rates were determined for the groups montane deciduous species (MD: *A. pseudoplatanus*, *F. sylvatica*), montane evergreen species (ME, *A. alba*, *P. abies, P. sylvestris*) and species in high elevation (HE: *L. decidua*, *P. mugo*).

The response of phenology to temperature was tested by a second method: First, we calculated respective temperature sums (3) for each of the phenological periods defined.

(3) $$Tsum = \sum_{onsetBBCHa}^{onsetBBCHb} T$$ Onset dates of all BBCH phases with BBCH a < BBCH b

Then, the lengths of the phenological periods were correlated with the temperature sums by Pearson correlations. The resulting regression slopes indicates the extensions of the respective periods with increasing temperature sum (days $\sum °C^{-1}$) and can be interpreted as the sensitivity of the phenological periods to temperature. Again, mean phenological response rates were determined for the groups MD, ME and HE to compare with the lapse rate method.

For all bud burst onset dates in 2011 we calculated the number of chilling days (daily mean temperature ≤5 °C) in the period from BBCH 97 to BBCH 7 for deciduous and from 1st Nov to BBCH 7 for evergreen species. Equally, the number of forcing days as well as the forcing temperature sum (daily mean temperature >5 °C, 1st January to BBCH 7) was determined. The threshold of 5 °C is commonly used in literature (e.g. Murray et al. 1989, Hunter and Lechowicz 1992, Heide 2003). Since there was a huge variation in winter days due to the elevational difference of around 1000 m of each transect, we also calculated the relative number of chilling days (4a), forcing days (4b), and the relative forcing temperature sum (4c). We then correlated the number of chilling days with forcing days / temperature sums for all species.

(4a) $$relative\ chilling\ days = \frac{\sum_{BBCH\ 97\ or\ 1st\ Nov.}^{BBCH\ 7} chilling\ days\ (\leq 5°C)}{\sum_{BBCH\ 97\ or\ 1st\ Nov.}^{BBCH\ 7} all\ days}$$

(4b) $$relative\ forcing\ days = \frac{\sum_{1st\ Jan.}^{BBCH\ 7} forcing\ days > 5°C)}{\sum_{1st\ Jan.}^{BBCH\ 7} all\ days}$$

(4c) $$relative\ forcing\ sum = \frac{\sum_{1st\ Jan.}^{BBCH\ 7} forcing\ temperature\ (> 5°C)}{\sum_{1st\ Jan.}^{BBCH\ 7} all\ temperature\ (\geq 0°C)}$$

5.4 Results

Meteorological Data

Mean air temperatures at the four meteorological stations in 2011 were generally warmer than in 2010 (Figure 5.2). In detail, the spring period (April to July) was 0.63 °C warmer in 2011 (BRA +0.53 °C, KRA +0.51 °C, KRE +0.74 °C, SCH +0.72 °C), especially at higher elevations (KRE, SCH). Mean autumn temperature (September to October) in 2011 was even 2.78 °C warmer than in 2010 (BRA +2.01 °C, KRA +3.08 °C, KRE +3.00 °C, SCH +3.04 °C). Consequently, relative humidity was lower in 2011 than in 2010 at all stations (-3.9 % in spring and -6 % in autumn). A special situation was recorded in November 2011 (see also Figure 5.2): While for whole Germany, mean air temperature was only 0.5 °C above the long term mean, in mountainous regions, new temperature and sunshine records were measured (DWD 2011). Moreover it was the driest month since the start of meteorological observations in 1881 (DWD 2011).

Predominantly, negative monthly mean temperature lapse rates at the transects indicate the expected decrease in temperature with elevation (Figure 5.2). Lapse rates were pronounced in spring (April to July) and moderate in winter (October to January). Maximum and minimum were +0.43 (November 2011, BRA) and -0.76 °C 100 m^{-1} (May 2010, SCH). Here too, in November 2011 there were extraordinary high (positive) lapse rates at all transects due to frequent inversion situations. The spring and autumn means of monthly lapse rates are also indicated in Figure 5.2: for spring leaf development period (April to July), mean of monthly mean temperature lapse rate was -0.48 °C 100 m^{-1} in 2010 and -0.46 °C 100 m^{-1} in 2011 (-0.47 °C 100 m^{-1} for 2010/11). In the leaf senescence period (September – November), lapse rates were less strong due to frequent inversion situations: -0.3 °C 100 m^{-1} in 2010 and -0.22 °C 100 m^{-1} in 2011 (-0.26 °C 100 m^{-1} for 2010/11). These lapse rates were used to determine phenological response rates out of the phenological elevational rates.

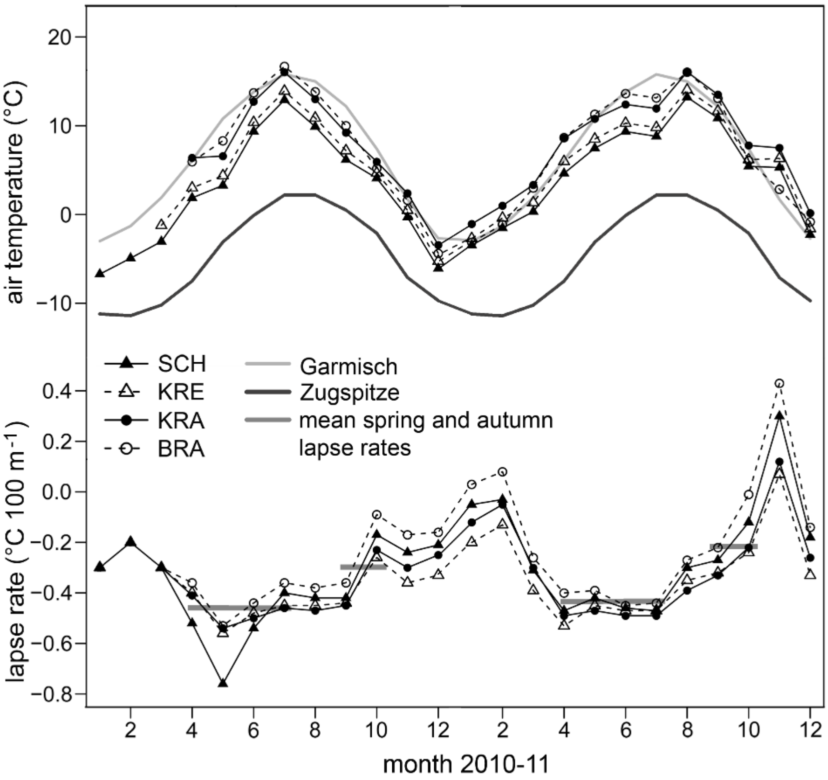

Figure 5.2 Course of the 2010 and 2011 monthly mean temperature at the four meteorological stations compared to the long-term mean of Garmisch and Zugspitze (1961–1990) and the monthly mean temperature lapse rates at the four transect in 2010 and 2011.

Phenological Elevational and Response Rates

134 logistic regressions were calculated to determine the site and species-specific onset dates for 2010, 139 for 2011. The numbers of significant regressions were: 80 ($p < 0.001$), 36 ($p<0.01$), 7 ($p<0.05$), 16 (not significant) in 2010 and 114 ($p < 0.001$), 16 ($p<0.01$), 5 ($p<0.05$), 4 (not significant) in 2011. Here can be seen, that results of onsets dates in 2011 are based on slightly better fittings than the onset dates of 2010. Significance parameter p varied from 3.5E-7 to 0.32 (2010) and from 4.9E-8 to 0.39 (2011).

Phenological onset dates in spring were generally delayed, onset dates in autumn advanced with elevation (Figure 5.3, Table 5.2). For early spring phases, *L. decidua*, *A. pseudoplatanus* and *P. abies* showed the highest response rates, followed by *F. sylvatica*. *A. alba* and the *Pinus* species revealed lower response rates. We found a strong effect of elevation on early spring phases and late autumn phases compared to late spring and early autumn phases. In fact, phenological elevational rates decreased from early to late spring phases and increased again from early to late autumn phases (Table 5.2). This effect is more pronounced for deciduous species and less for evergreen species. *A. alba* and *P. sylvestris* even showed approximately constant phenological elevational rates for all spring BBCH phases. Based on the phenological elevational rates we calculated phenological response rates using the mean lapse rates of the respective phenological period (see meteorological data results). Due to the constant factor (lapse rate), the pattern of decreasing response rates in spring and increasing response rates in autumn persists.

The difference in rates between the two years 2010 and 2011 is small relative to their standard error, except for *L. decidua* and *P. sylvestris*, the two species with the lowest number of individuals in the study. Rates of *L. decidua* were not significant in 2010; rates of *P. sylvestris* were not significant in 2011. Here, the variance between individuals might strongly influence the rate and lead to higher differences between the years. In the following, mean data of both years (2010/11) is presented since the higher number of observations lead to more significant results.

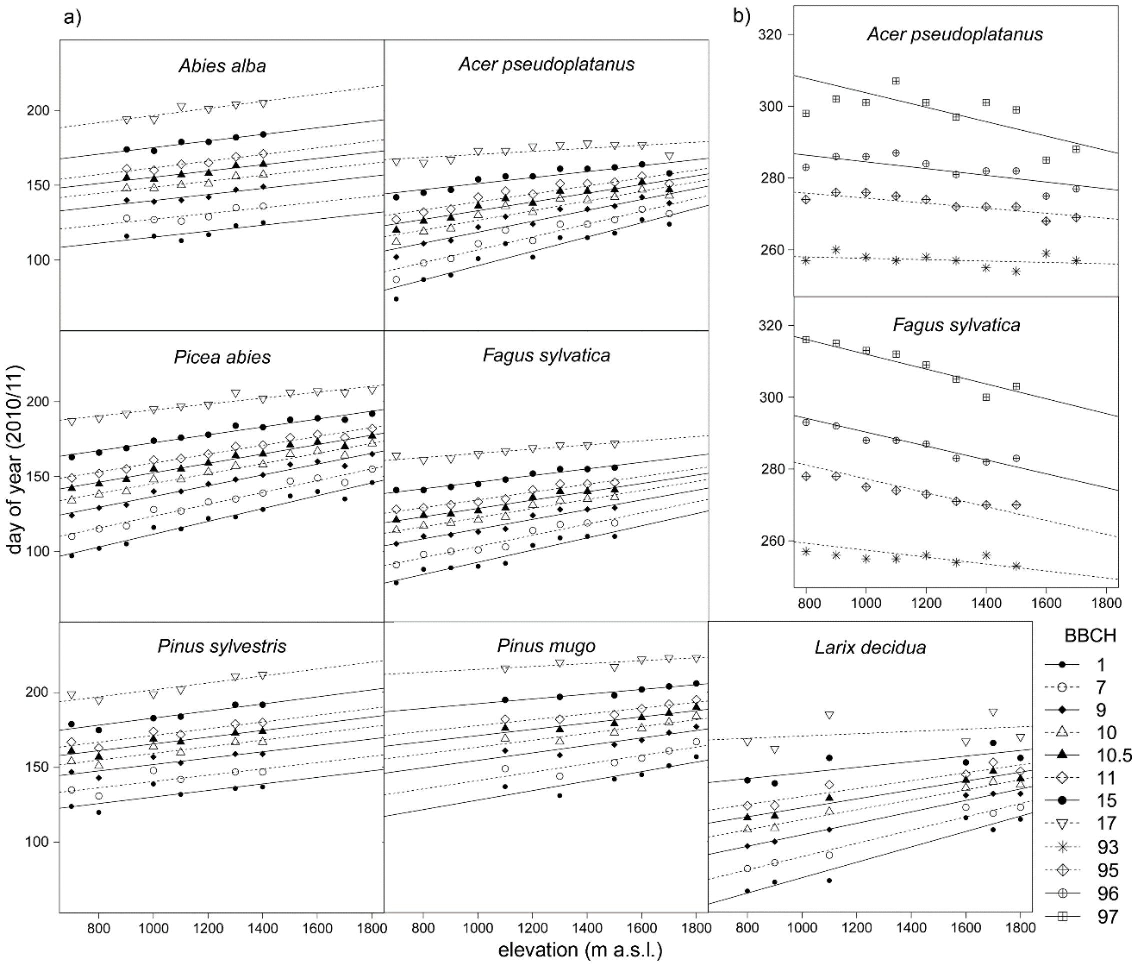

Figure 5.3 Linear regression of BBCH onset dates (mean 2010/2011 data) for the seven species in spring (a) and the two deciduous species in autumn (b) on elevation. Slopes of the regression lines (phenological elevational rates) are given in Table 5.2.

Table 5.2 Phenological response to elevation and temperature for leaf unfolding and senescence BBCH phases (2010, 2011 and 2010/11 data), phenological elevational rate (per, days 100 m^{-1}) with standard error and significance level (* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$), R^2, onset day at 1000 m elevation (day of year), phenological response rate (prr = per * (1 / tlr), days °C^{-1}), mean temperature lapse rates (tlr). (Continued the next page).

		2010				2011				2010/11			
species	**BBCH**	**per ± SE**	**R^2**	**onset**	**prr**	**per ± SE**	**R^2**	**onset**	**prr**	**per ± SE**	**R^2**	**onset**	**prr**
Abies alba	7	1.6 ± 0.3**	0.90	138	-3.3	1.9 ± 0.7*	0.67	124	-4.2	1.9 ± 0.6*	0.71	127	-4.1
	9	1.9 ± 0.3**	0.93	148	-3.9	2.0 ± 0.6*	0.71	135	-4.3	2.0 ± 0.5*	0.83	139	-4.3
	11	2.1 ± 0.6*	0.75	167	-4.4	1.9 ± 0.6*	0.76	155	-4.2	2.2 ± 0.3**	0.92	160	-4.7
	15	2.3 ± 0.8	0.65	178	-4.7	1.9 ± 0.6*	0.74	167	-4.2	2.2 ± 0.4**	0.91	173	-4.7
	17	2.6 ± 1.2	0.53	195	-5.5	1.9 ± 0.8	0.61	186	-4.2	2.4 ± 0.6*	0.80	194	-5.0
Acer pseudoplatanus	1	4.6 ± 0.6***	0.88	125	-9.5	4.1 ± 1.0**	0.64	94	-8.9	4.8 ± 0.5***	0.91	101	-10.2
	7	4.1 ± 0.5***	0.90	132	-8.4	3.7 ± 0.9**	0.65	104	-8.1	4.3 ± 0.5***	0.91	111	-9.1
	9	3.5 ± 0.4***	0.91	139	-7.3	3.4 ± 0.7**	0.70	115	-7.4	3.7 ± 0.4***	0.90	122	-7.8
	10	3.1 ± 0.3***	0.92	144	-6.5	3.1 ± 0.6***	0.72	123	-6.6	3.2 ± 0.4***	0.89	130	-6.9
	10.5	2.9 ± 0.3***	0.93	147	-6.0	2.8 ± 0.5***	0.75	129	-6.2	2.9 ± 0.4***	0.88	136	-6.2
	11	2.6 ± 0.3***	0.93	151	-5.4	2.6 ± 0.5***	0.76	135	-5.7	2.7 ± 0.3***	0.87	142	-5.7
	15	2.1 ± 0.3***	0.89	158	-4.3	2.3 ± 0.3***	0.83	146	-4.9	2.0 ± 0.3***	0.80	154	-4.3
	17	1.2 ± 0.3**	0.60	170	-2.4	1.5 ± 0.2***	0.82	165	-3.3	1.0 ± 0.4*	0.48	173	-2.2
Fagus sylvatica	1	5.8 ± 0.5***	0.95	107	-12.1	4.2 ± 0.5***	0.92	82	-9.1	4.1 ± 0.4***	0.92	90	-8.7
	7	5.0 ± 0.4***	0.96	115	-10.4	3.8 ± 0.4***	0.93	94	-8.3	3.7 ± 0.4***	0.93	101	-7.9
	9	4.2 ± 0.3***	0.96	124	-8.7	3.4 ± 0.3***	0.94	106	-7.3	3.3 ± 0.3***	0.94	113	-6.9
	10	3.6 ± 0.3***	0.97	130	-7.4	3.1 ± 0.2***	0.96	115	-6.7	3.0 ± 0.2***	0.96	121	-6.4
	10.5	3.1 ± 0.2***	0.97	135	-6.5	2.9 ± 0.2***	0.95	121	-6.3	2.8 ± 0.3***	0.95	127	-5.9
	11	2.7 ± 0.3***	0.94	139	-5.7	2.6 ± 0.2***	0.96	128	-5.6	2.6 ± 0.2***	0.95	133	-5.5
	15	1.8 ± 0.3***	0.81	148	-3.8	2.2 ± 0.1***	0.99	141	-4.7	2.2 ± 0.2***	0.96	145	-4.7
	17	0.4 ± 0.5	0.07	163	-0.7	1.5 ± 0.1***	0.99	161	-3.3	1.4 ± 0.2***	0.87	165	-3.0
Larix decidua	7	1.8 ± 0.8	0.71	114	-3.8	4.7 ± 0.9**	0.87	82	-10.1	4.4 ± 0.4***	0.97	99	-9.4
	9	2.1 ± 0.3*	0.95	125	-4.3	4.0 ± 0.7**	0.89	96	-8.7	3.8 ± 0.3***	0.98	115	-8.1
	11	2.4 ± 0.5*	0.93	147	-5.0	2.9 ± 0.5**	0.91	121	-6.3	2.7 ± 0.5**	0.89	140	-5.6

	15	2.7 ± 1.0	0.81	156	-5.7	2.3 ± 0.3***	0.95	138	-4.9	1.9 ± 0.7	0.65	155	-4.0
	17	3.2 ± 1.6	0.65	173	-6.6	1.2 ± 0.1***	0.98	161	-2.7	0.8 ± 1.1	0.10	180	-1.6
Picea abies	7	4.1 ± 0.2***	0.97	143	-8.5	4.0 ± 0.2***	0.97	122	-8.6	4.0 ± 0.2***	0.97	128	-8.4
	9	3.6 ± 0.2***	0.97	153	-7.6	3.5 ± 0.2***	0.97	134	-7.6	3.6 ± 0.2***	0.97	140	-7.7
	11	2.9 ± 0.2***	0.97	169	-6.1	2.6 ± 0.2***	0.94	154	-5.7	3.0 ± 0.2***	0.97	161	-6.3
	15	2.4 ± 0.2***	0.96	179	-5.0	2.1 ± 0.2***	0.90	165	-4.7	2.6 ± 0.2***	0.96	174	-5.6
	17	1.7 ± 0.2***	0.87	195	-3.4	1.4 ± 0.2***	0.77	185	-2.9	2.0 ± 0.2***	0.92	195	-4.2
Pinus mugo	7	2.6 ± 0.5**	0.87	144	-5.4	2.9 ± 0.9*	0.70	125	-6.2	2.8 ± 0.8*	0.78	146	-5.9
	9	2.3 ± 0.4**	0.91	155	-4.8	2.5 ± 0.8*	0.73	140	-5.4	2.5 ± 0.6*	0.82	158	-5.3
	11	1.6 ± 0.2**	0.92	176	-3.3	1.9 ± 0.5*	0.82	164	-4.2	1.9 ± 0.4**	0.88	176	-4.1
	15	1.3 ± 0.2**	0.91	187	-2.6	1.7 ± 0.4**	0.84	179	-3.6	1.6 ± 0.2**	0.92	187	-3.4
	17	0.7 ± 0.3	0.58	204	-1.4	1.1 ± 0.4	0.61	202	-2.3	1.0 ± 0.3*	0.68	207	-2.1
Pinus sylvestris	7	3.4 ± 0.6**	0.88	161	-7.0	2.0 ± 0.8	0.59	141	-4.3	2.1 ± 0.8	0.65	148	-4.5
	9	3.2 ± 0.5**	0.92	167	-6.6	1.6 ± 0.7	0.57	151	-3.5	2.1 ± 0.6*	0.76	157	-4.5
	11	3.0 ± 0.4**	0.94	179	-6.3	0.9 ± 0.5	0.46	167	-1.9	2.3 ± 0.5**	0.86	174	-4.8
	15	2.9 ± 0.4**	0.92	186	-6.1	0.4 ± 0.4	0.17	177	-0.8	2.4 ± 0.4**	0.89	183	-5.0
	17	2.8 ± 0.6**	0.85	197	-5.9	-0.2 ± 0.5	0.05	193	0.5	2.3 ± 0.5*	0.83	199	-4.9
Acer pseudoplatanus	93	-0.2 ± 0.1	0.14	258	0.6	-0.1 ± 0.3	0.02	264	0.5	-0.2 ± 0.2	0.14	258	0.7
	95	-0.9 ± 0.1***	0.88	272	3.0	-0.5 ± 0.2	0.31	282	2.2	-0.7 ± 0.1***	0.75	276	2.7
	96	-1.2 ± 0.2***	0.84	282	3.9	-0.5 ± 0.3	0.18	291	2.2	-0.9 ± 0.2**	0.65	286	3.6
	97	-2.8 ± 0.7**	0.66	294	9.3	-0.6 ± 0.6	0.09	305	2.6	-2.0 ± 0.6**	0.58	301	7.7
Fagus sylvatica	93	-0.5 ± 0.2*	0.50	258	1.8	-1.1 ± 0.6	0.30	254	4.8	-1.0 ± 0.4*	0.49	255	3.7
	95	-2.0 ± 0.4***	0.81	274	6.7	-1.8 ± 0.4**	0.71	277	8.0	-1.9 ± 0.4**	0.79	275	7.4
	96	-2.0 ± 0.2***	0.91	284	6.7	-1.8 ± 0.3***	0.82	292	8.0	-1.9 ± 0.2***	0.90	288	7.4
	97	-2.3 ± 0.3***	0.90	303	7.7	-1.9 ± 0.4**	0.74	320	8.6	-2.1 ± 0.3***	0.90	313	8.0
Mean tlr used to calculate prr	spring		-0.48				-0.46				-0.47		
	autumn		-0.30				-0.22				-0.26		

Species Groups

Comparing different groups of species (MD montane deciduous, ME: montane evergreen and HE: high elevation), mean onset dates (day of year, 2010/11 data) were 111 ± 12, 133 ± 14 and 138 ± 27 for bud burst (BBCH 7) and 170 ± 6, 200 ± 8 and 204 ± 23 for the end of leaf development (BBCH 17). For MD, mean onset dates for BBCH 93 and BBCH 97 were 257 ± 4 and 304 ± 9. Therefore, the mean length of leaf development period was 59, 67 and 66 days (MD, ME, HE). For MD in the study area, mean length of full leaf, leaf senescence and vegetation period were 87, 47, 193 days. Mean phenological response rates for bud burst (BBCH 7) were -8.5 ± 0.4, -5.7 ± 1.1 and -7.7 ± 1.2 days $°C^{-1}$ for MD, ME and HE. End of leaf unfolding (BBCH 17) advanced by -2.6 ± 0.3, -4.8 ± 0.2 and -1.9 ± 0.1 days $°C^{-1}$, respectively. Mean delay of autumn phases for MD was 1.5 ± 0.6 and 7.9 ± 0.1 days $°C^{-1}$ (BBCH 93 and BBCH 97). Combining these phenological response rates (prr) of deciduous trees for specific periods, the vegetation period was extended by 16.4 days $°C^{-1}$ ($|prr_{BBCH\ 7}| + |prr_{BBCH\ 97}|$), leaf development by 5.9 days $°C^{-1}$ ($|prr_{BBCH\ 7}| - |prr_{BBCH\ 17}|$) full leaf period by 4.1 days $°C^{-1}$ ($|prr_{BBCH\ 17}| + |prr_{BBCH\ 93}|$), and leaf senescence period by 6.4 days $°C^{-1}$ ($|prr_{BBCH\ 97}| - |prr_{BBCH\ 93}|$) for MD. For ME and HE, leaf development extended by 0.9 days $°C^{-1}$ and 5.8 days $°C^{-1}$ ($|prr_{BBCH\ 7}| - |prr_{BBCH\ 17}|$).

Extension of Phenological Periods

For all species, the length of leaf development, leaf senescence, full leaf and vegetation period was highly correlated with the respective temperature sum (Figure 5.4, Table 5.3). Even the lengths between two phases were extended (not shown). Since temperature sums are calculated with daily means, with a general warming of one degree, the temperature sum within a period will increase by the number of days of this period. The increased length of the period is the previous length of the period multiplied by the slope. Therefore, the regression slope can be interpreted as percental increase of the period length per degree (i.e. a slope of 0.05 would lengthen a period by 5 %). Regarding the groups (MD montane deciduous, ME: montane evergreen and HE: high elevation), mean values were 9.1 %, 3.7 %, 10.5 % and 7.1 % for MD (leaf development, full leaf, leaf senescence, vegetation period) and 7.7 % and 7.9 % for ME and HE respectively (leaf development, correlation coefficients ranged from 0.87 to 0.95). Applying this percental increase on the mean length of the respective period (2010/11 data), we calculated lengthening of 5.1, 3.5, 4.5 and 13.7 days per degree for MD (leaf development, full leaf, leaf senescence and vegetation period; Table 5.3 2010/11 data). Leaf development period for ME and HE is extended by 5.1 and 4.8 days per degree, respectively.

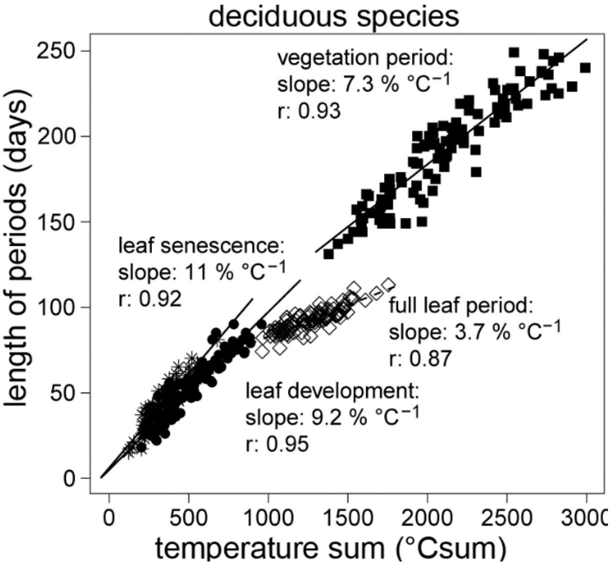

Figure 5.4 Correlation between the length of phenological periods and the corresponding temperature sums. Percentage increase (perc) of the period length per degree and Pearson's correlation coefficients r are given.

Table 5.3 Extension of the length of phenological periods with increasing temperature for 2010, 2011 and 2010/11 data, percental increase (perc, % °C^{-1}) with standard error and significance level (* p ≤ 0.05, ** p ≤ 0.01, *** p ≤ 0.001), R^2, mean length of the periods (mL, days).

species	period BBCH	2010			2011			2010/11		
		perc ± SE	R^2	mL	perc ± SE	R^2	mL	perc ± SE	R^2	mL
Abies alba	1-17	9.6 ± 0.9***	0.91	72	9.1 ± 1.1***	0.86	72	8.7 ± 0.8***	0.83	72
Acer pseudoplatanus	1-97	6.3 ± 0.6***	0.83	160	4.9 ± 0.4***	0.86	204	7.0 ± 0.4***	0.86	183
	1-17	9.1 ± 0.8***	0.85	36	7.9 ± 0.7***	0.85	67	9.8 ± 0.4***	0.93	52
	17-93	3.5 ± 0.4***	0.81	90	3.7 ± 0.3***	0.82	97	3.9 ± 0.3***	0.81	93
	93-97	14.2 ± 1.2***	0.83	32	11.4 ± 1.0***	0.82	40	12.0 ± 0.7***	0.84	36
Fagus sylvatica	1-97	7.2 ± 0.6***	0.83	184	5.2 ± 0.6***	0.79	224	7.1 ± 0.4***	0.89	204
	1-17	10.1 ± 1.2***	0.74	48	6.5 ± 0.7***	0.77	73	8.4 ± 0.4***	0.88	60
	17-93	2.7 ± 0.5***	0.60	93	4.2 ± 0.5***	0.77	93	3.5 ± 0.3***	0.68	93
	93-97	11.4 ± 1.4***	0.70	43	8.1 ± 0.9***	0.76	58	9.0 ± 0.5***	0.84	50
Larix decidua	1-17	9.1 ± 1.1**	0.96	36	8.0 ± 1.2***	0.91	72	10.0 ± 1.0***	0.91	57
Picea abies	1-17	7.5 ± 0.4***	0.91	60	6.2 ± 0.2***	0.96	68	6.9 ± 0.4***	0.83	64
Pinus mugo	1-17	4.7 ± 0.6***	0.87	56	4.8 ± 0.8***	0.78	74	5.8 ± 1.1***	0.56	65
Pinus sylvestris	1-17	6.5 ± 1.4**	0.84	51	5.3 ± 0.8**	0.92	70	7.4 ± 1.1***	0.82	61

Comparing the lengthening of phenological periods based on temperature sums at the specific sites with the lengthening of the periods resulting out of the lapse rate method (combination of phenological response rates for the start and end of each period), both methods yielded similar results (Figure 5.5, example for *A. pseudoplatanus* and *F. sylvatica*, 2010/11 data, see also Table 5.2 and Table 5.3). In our observation years, the contribution of delayed leaf senescence to the lengthening of the total vegetation period was as high as or even higher than the advance of leaf development. Only for *A. pseudoplatanus* in the lapse rate method (Figure 5.5, black arrows) we had approximately the 55 % contribution of advanced spring (BBCH 7) and 45 % of delayed autumn (BBCH 97) to the lengthening of the vegetation period like Davi et al. (2006).

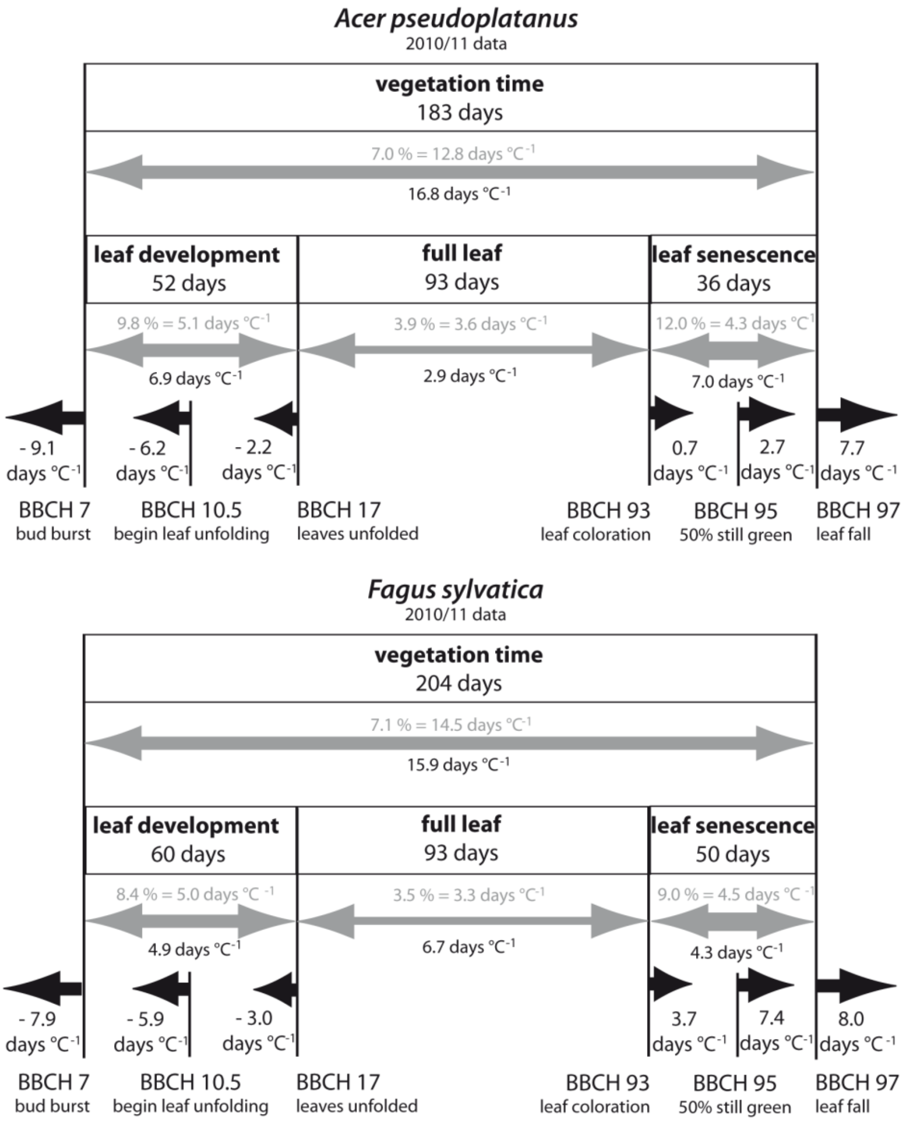

Figure 5.5 Advance of spring and delay of autumn onset dates based on the lapse rate calculation (black arrows) and extension of phenological periods based on two methods [lapse rates (black values at two-sided arrows) and percentage increase determined on site-specific temperature sums (grey values at two-sided arrows) for *Acer pseudoplatanus* and *Fagus sylvatica* 2010/2011 data obtained along the elevational transects.

Chilling and Forcing

All linear regressions between chilling and forcing days (or temperature sums) had negative slopes, except for *L. decidua*. This indicates that the more chilling days were experienced, the less forcing days or temperature sums were required for bud burst. The regressions between relative chilling days and relative forcing days revealed similar slopes for all species: -1.26 ± 0.04 (*F. sylvatica*), -1.27 ± 0.07 (*A. pseudoplatanus)*, -1.24 ± 0.03 *(A. alba)*, -1.23 ± 0.01 *(P. abies)*, -1.10 ± 0.06 *(P. sylvestris)*, -1.25 ± 0.02 *(P. mugo)* and -1.11 ± 0.13 *(L. decidua).* However, slopes of the regressions between relative chilling days and relative forcing sums were similar for deciduous trees (-1.28 ± 0.15 *F. sylvatica*, -1.33 ± 0.23 *A. pseudoplatanus*), but lower for evergreen species (Figure 5.6). Mean absolute chilling days ranged from 115.8 days (700 m a.s.l.) to 160.3 days (1800 m a.s.l.). With regard to the suggested natural required chilling of 145 days (Murray et al. 1989), this amount was only achieved at higher elevations (≥1300 m a.s.l. *F. sylvatica* and *A. pseudoplatanus*, ≥1400 m a.s.l. *A. alba* , ≥1500 m a.s.l. *P. abies*, ≥1700 m a.s.l. *P. mugo*, not achieved on south-faced sites for *L. decidua* and *P. sylvestris*).

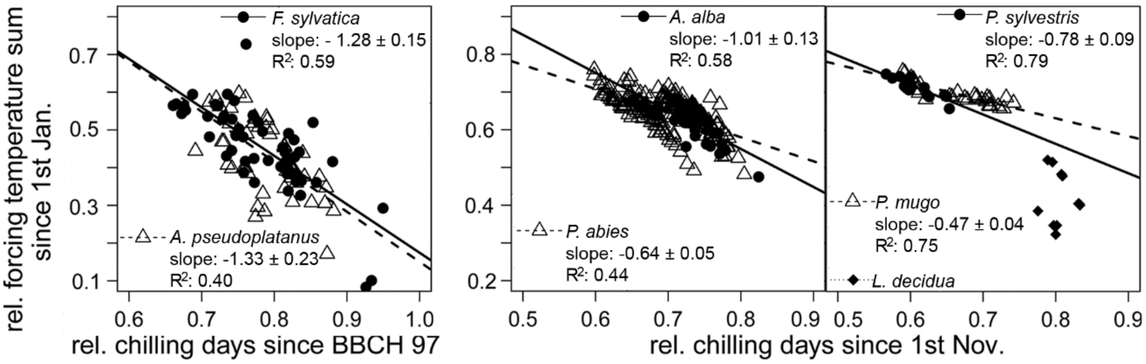

Figure 5.6 Linear correlation between relative number of chilling days (≤5 °C, BBCH 97 - BBCH 7 for deciduous and 1 November - BBCH 7 for evergreen species) and relative forcing temperature sum before bud burst (>5 °C, 1 January - BBCH 7) in 2011.

5.5 Discussion

Referring to our initial questions, we could (a) prove that phenological responses to elevation and temperature highly vary between species and we were able to determine species-specific rates. A surprising result was the relatively high temperature response of *F. sylvatica*, which is known to be less sensitive to temperature (Vitasse et al. 2009a, Čufar 2012). We also were able to quantify (b) responses from a set of phenological phases. As expected, they were different, but we found a homogenous pattern: Spring response rates decrease and autumn response rates increase again with later phases. Between species groups (c), bud burst and end of leaf development onset dates were similar between ME and HE and about four weeks earlier for MD. However, sensitivity of bud burst to elevation and temperature was high for MD and HE, but smaller for ME. Moreover, elevational and temperature response rates strongly decreased with later phases (end of leaf development) for MD and HE, but less for ME. Regarding the role of spring and autumn phases in lengthening the vegetation period (d), we found the same or even a stronger influence of delayed autumn phases. This result is probably highly influenced of the warm autumn 2011. But this circumstance shows clearly that the contribution of phenological periods to the lengthening of the vegetation period strongly depends on the time of the year experiencing the highest warming. Last but not least, we showed that (e) the two deciduous species (*A. pseudoplatanus* and *F. sylvatica*) seem to reveal approximately the same correlation between reduced chilling days and increased forcing temperature in contrast to the other species.

Meteorological Data

For calculations of the phenological response rates, of course, there is a high influence of the lapse rates used. Lapse rates smooth temperature variation to linear reduction with elevation and neglects for example special microclimates due to topography or thermal inversions. However, our dense measurement network directly at the phenological observation sites gives us the possibility to calculate lapse rates and especially temperature sums individually for all transects, sites and seasons. Compared to other published lapse rates in the Alpine region (e.g. -0.54 to -0.58 °C 100 m^{-1}; Rolland 2003) and the commonly used mean lapse rate of -0.65 °C 100 m^{-1} (Minder et al. 2010), our measured lapse rates were less expressed due to the temperature buffer effect of the forest (loggers are installed within the forest). Other studies reported annual mean lapse rates around -0.47 to -0.48 °C 100 m^{-1} for the Bavarian Alps (Ewald 1997) and -0.32 (December) to -0.62 °C 100 m^{-1} (spring; Kirchner et al. 2012) in Garmisch-Partenkirchen. Here, our measured lapse rates (with mean lapse rate of -0.47 °C 100 m^{-1}) yield similar values due to the regional proximity of the study areas.

The regional and annual differences in the lapse rates underline the importance of site-specific temperature measurements at the sites and transects instead of commonly used values. Since temperature loggers became affordable, in most studies, site-specific measurements in phenological studies become more and more common. With this data, it is also possible to focus on phenological differences due to small scaled meteorological conditions we find in complex terrain mountainous regions. Any variations in seasonal weather conditions from year to year (e.g. 2010 vs. 2011) would definitively result in different phenological elevational rates. However, taking into account results in temperature lapse rates including thermal inversion situations will result in more precise temperature response rates.

Phenological Elevational and Response Rates

In this study, differences between N and S facing aspects have not been included, since our first analyses of the two years' dataset did not lead to consistent results. Since we expect phenological differences related to aspect, a long-term study would be necessary. Moreover, comparing the two years 2010 and 2011, phenological elevational rates were within their standard errors, except for *L. decidua* and *P. sylvestris*. Due to the specialized occurrence of the species in the mountainous forest, we had a small number of individuals for *L. decidua* and *P. sylvestris* in our study which obviously was not sufficient for to achieve consistent results. More observation years and more individuals included in the study would likely consolidate the results. Since the elevational transects are ranging over 1000 m and not all species have the same elevational distribution (e.g. *L. decidua* and *P. mugo* in high elevations), there is also some uncertainty by mixing responses from different ecotypes. Our response rates for these species therefore have to be handled with care and could be revised by continuing studies.

Phenological elevational rates and phenological response rates in Table 5.2 confirm an advance of spring and a delay of autumn phases with increasing temperature. Our phenological elevational rates for *F. sylvatica* and *A. pseudoplatanus* bud burst and leaf unfolding (BBCH 7 and BBCH 10.5) in southern Germany fit perfectly to rates reported in literature: Vertical changes in *F. sylvatica* flushing are reported as 1 to 4 days 100 m^{-1} (Schnelle 1955, König & Mayer 1988, Menzel 1997, Pellerin et al. 2012). Vitasse et al. (2009b) found advanced flushing of 1.9 to 6.6 days °C^{-1} and delayed senescence of 0.0 to 5.6 days °C^{-1} for deciduous trees in the Pyrenean Mountains. For leaf unfolding of *Pinus* species and *A. alba*, Davi et al. (2011) determined phenological elevational rates of 4.4 and 2.8 days 100 m^{-1}. Our rates are somehow lower, but in the same magnitude. Comparing the species, *A. pseudoplatanus*, *L. decidua* and *P. abies* phenology turned out to be highly sensitive to elevation and temperature (response of >4 days 100 m^{-1}). Surprisingly, *F. sylvatica*, which is known to be less sensitive to temperature (Vitasse et al. 2009a, Čufar 2012), was following closely (3.7 days 100 m^{-1}). *A. alba* and the two *Pinus* species had smaller response rates <3 days 100 m^{-1}.

Phenological elevational rates determined by linear trends are quite trustful. However, the determination of temperature response rates by combination of phenological elevational rates with temperature lapse rates is an approximation. Lapse rates are smoothening real site conditions and give the linear temperature response with elevation. But to interpret them for temperature responses in future under global warming conditions, it must be considered that temperature sensitivity becomes non-linear with increased warming (Pope et al. 2013, Jochner et al. 2013b). Then, other factors (reduced chilling, photoperiod) could gain relevance. Especially in autumn, photoperiod plays an important role besides temperature (Migliavacca et al. 2008). However, the advantage of our method is to determine responses to temperature in a relatively short time of observations and is more accurate and site-specific than common elevational rates.

As we showed, elevation and temperature sensitivity strongly depends on the BBCH phase. Early spring and late autumn phases show higher values than late spring and early autumn phases, respectively. Most likely this is the consequence of a more explicit vertical temperature decrease in early spring and late autumn compared to the mid of the vegetation period. But this also means that leaf development and senescence processes are faster in higher elevations. This could be due to several reasons, which remain to verify: Either, trees in high elevations are adapted to a shorter vegetation period and/or they perform smaller leaves than in the valley. It also might be that, since spring phases in high elevations start later, the increase of temperature from day to day is much faster than in early spring which could lead to a faster development. Moreover, our results underline the need to clearly define observed phases in phenological studies. Otherwise comparing values of different studies will lead to inaccurate conclusions.

Species Groups

Mean values of species groups (MD, ME, HE) show obvious traits. Later spring onset dates for evergreen species compared to deciduous species can be explained by the fact that they have no need to expose themselves to the risk of late frosts since they are able to start photosynthesis at any time. Late onset dates of high elevation species can easily be explained by the temperature conditions required only are fulfilled later in the year. ME temperature response rates also differ in another feature from MD and HE. Whereas response rates of the latter ones decreased from bud burst to end of leaf unfolding, the ME response is relatively unchanged during spring development. This circumstance could be interpreted that species of MD and HE groups have to be more flexible to react to temperature since they are forced to adapt their leaf development to given environmental conditions, whereas evergreen species with late leaf-out seem to be relatively fixed in their course of leaf development. However, in the method based on temperature sums, the lengthening of leaf development period per degree did not reveal any big differences between the groups. Since these groups are only represented by few species, it might be too early to draw general conclusions.

Extension of Phenological Periods

Correlations of the length of phenological periods with corresponding temperature sums revealed the expected result of higher temperature leading to a longer vegetation period. In our study, not only the vegetation period, but also phenological periods and lengths between single phenological phases were extended with higher temperature sums available. With earlier onset in the year, more time might be necessary to fulfil required temperature sums. An observed lengthening of the vegetation period with warming due to earlier bud burst and later leaf fall has often been reported (Menzel & Fabian 1999, Vitasse et al. 2009b). For *F. sylvatica*, Vitasse et al. (2009b) found an extended vegetation period of 6.7 to 13 days °C^{-1}. Dittmar & Elling (2006) reported changes of 2.7 to 3.4 days 100 m^{-1}, which is equal to an extension of the vegetation period by 5.7 to 7.2 days °C^{-1} (based on our 0.47 days °C^{-1} spring lapse rate).

Changes in autumn period are reported as smaller (Menzel & Fabian 1999, Estrella & Menzel 2006, Röthlisberger 2010) or similar (Vitasse et al. 2009b) to the advance of phenological spring phases. However, principal climate factors inducing the beginning of leaf coloring have not clearly been identified yet (Estrella & Menzel 2006). Besides temperature, day length may be an important parameter (Larcher 2003). Between individuals at the same site, beginning of coloring is highly variable but not the end of leaf fall (Röthlisberger 2010). Both facts may explain why leaf coloring in our study showed less dependency on elevation and temperature than leaf fall. Davi et al. (2006) reported a 55 % contribution of early leaf unfolding to the extension of the vegetation period and a 45 % contribution of delayed leaf fall, which fits almost perfectly to advanced bud burst and delayed leaf fall dates using the lapse rate method for *A. pseudoplatanus*.

But in general, we found leaf senescence as sensitive to temperature as leaf development since it showed the same or even higher contribution to vegetation period lengthening. On the one hand, there is a high influence of the mean spring and autumn lapse rates used, since a smaller lapse rate (e.g. in autumn 2011) leads to a higher calculated phenological response rate. In 2011, autumn temperatures were 3 °C higher than in 2010, but spring temperatures only increased by <1 °C, thus this influenced the extension of the leaf senescence period in this study. But consequently, the period which experiences higher warming will mainly influence the lengthening of the vegetation period.

As we showed, the full leaf period is extended with increasing temperature (even though less than leaf development and senescence), due to an earlier end of leaf development and a later start of leaf coloration. This provides advantages especially for deciduous trees by a longer period of photosynthesis and secondary stem growth.

There are only slight differences in the results using the lapse rate or the temperature sum calculation (Figure 5.5). However, results of both methods were influenced by the extremely warm autumn 2011. We assume the results based on site-specific temperature sums could be more accurate than the method based on lapse rates since lapse rates neglect or soften the effect of site-specific microclimate and inversion influences.

Chilling and Forcing

Chilling thresholds are reported to be between 0 and 7.2 °C (Eggert 1951). However, exact thresholds and range of temperatures for chilling are still unknown. The definition of a uniform 5 °C threshold for chilling and forcing, as well as the two starting points 1st November for chilling for evergreen species and 1st January for forcing temperatures in this study are arbitrary, but often and commonly used in literature (e.g. Murray et al. 1989, Hunter & Lechowicz 1992). Moreover, differences between species in the required threshold are less studied yet and may be highly variable (Cesaraccio et al. 2004). This is definitively true for *L. decidua* since it was the one of the seven species without clear linear relationship of chilling and forcing temperatures with the 5 °C threshold.

For the other species, our results showed like several other studies (Murray et al. 1989, Chuine & Cour 1999, Heide 2003) that with increasing chilling period, decreasing forcing temperature was required for bud burst. The slopes in the regression between chilling days and forcing days, which mainly vary slightly around -1.25, can be interpreted, that for a 4 % increase in chilling days, 5 % less forcing days are required. The correlation between chilling days and temperature sums however is different between deciduous and evergreen trees. For deciduous species, an increase in chilling highly reduces forcing temperature requirements, which is consistent to previous studies (e.g. Heide 2003). Moreover, *F. sylvatica* is known to have high chilling requirements compared to other deciduous species (Caffarra & Donnelly 2011). For evergreen species in our study, the effect of longer chilling leading to less required forcing temperature is less distinct and highly variable between species of our study. The obvious difference between deciduous and evergreen species may also be related to the different starting dates for the calculation of chilling (end of leaf fall as a "true" phenological phase, varying from mid-October to mid-November, for deciduous and since 1st November for evergreen species). However, it is obvious that the two deciduous species seem to have quite the same reaction to reduced chilling whereas evergreen species compared to each other highly varied in their chilling requirements. In literature, where mostly only a few species are discussed, also different chilling requirements for evergreen species are reported (e.g. Nienstaedt 1967, Hänninen & Pelkonen 1989, Hänninen et al. 2007). Thus, under future global warming conditions, especially bud burst of deciduous trees might be delayed due to decreasing chilling partly counterbalancing spring warming (Heide 2003).

A natural chilling requirement of 145 days, as reported e.g. by Murray et al. (1989) was only achieved in high elevations, surely also influenced by the warm spring 2011. But this value should not be generalized for all species. In some studies, higher temperatures induce negative chilling when exceeding the upper threshold, whereas temperatures below a lower threshold (generally 0 °C) are not considered effective for chilling (e.g. Richardson et al. 1974, Cesaraccio et al. 2004). The idea that negative temperatures also would have a negative chilling effect would even mean that trees in high elevations experience less chilling than those in lower elevations.

5.6 Conclusions

Species phenological sensitivity to elevation and temperature is similar whether based on lapse rates or temperature sums. However, in the complex terrain of mountainous regions, microclimate at different locations is highly variable and does not always follow the lapse rate. Thus, results calculated with temperature sums originating from each specific site seem to be more reliable. Seasonal variation in elevational and temperature response rates of the single phenological phases observed here (decrease with later spring, increase with later autumn phases) underline the importance of clearly defined phenological phases when comparing results from different studies. Spring temperature response of deciduous and high elevation species seem to be more distinct and therefore more flexible than of evergreen species, because the latter ones are less forced to benefit of short term favorite growing conditions. Evergreen species leaf development instead seems to be more independent when once the temperature threshold for bud burst is reached. However, the effect of a reduced chilling period on the required temperature sum for bud burst is more distinct for deciduous species, which could counterbalance the advance in spring with increasing temperatures to some degree.

The lengths of the vegetation period and phenological periods (leaf development, full leaf, leaf senescence) increased with increasing temperature. This could be due to earlier onset dates leading to a longer time span necessary until temperature sums requirements for the next phase are fulfilled. In our study, senescence phases were delayed in similar magnitudes as leaf development phases advanced. Thus, the period, which experiences higher warming, mainly influences the lengthening of the vegetation period. Senescence phases therefore could have been underestimated concerning their influence on the lengthening of the vegetation period. According to our results, it plays an important role in which time of the year temperatures will change most in a future climate warming, especially since phenological response is variable between species, phenological periods and phenological phases.

Some questions have to remain unanswered and could be investigated by long term observations along elevational transects: How does N and S aspect influences phenology? Which differences there are in mature and juvenile tree phenology? How do changes in flowering and seed development phenology affect the reproduction of trees? How much do the different tree species profit from a lengthened vegetation period for secondary stem growth and carbon allocation? Answers to all small parts of the mosaic of interactions between climate and biosphere will lead to a whole picture in the end.

5.7 Acknowledgments

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6 Frequency of Inversions affects Senescence Phenology of *Acer pseudoplatanus* and *Fagus sylvatica*

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6.1 Abstract

In mountainous regions, inversion situations with cold-air pools in the valleys occur frequently, especially in fall and winter. With the accumulation of inversion days, trees in lower elevations experience lower temperature sums than those in middle elevations. In a two-year observational study, deciduous trees, such as *Acer pseudoplatanus* and *Fagus sylvatica*, on altitudinal transects responded in their fall leaf senescence phenology. Phenological phases were advanced and senescence duration was shortened by the cold temperatures in the valley. This effect was more distinct for late phases than for early phases since they experienced more inversion days. The higher the inversion frequency, the stronger the signal was. *Acer pseudoplatanus* proved to be more sensitive to cold temperatures compared to *Fagus sylvatica*. We conclude that cold-air pools have a considerable impact on the vegetation period of deciduous trees. Considering this effect, trees in the mid hillside slopes gain advantages compared to lower elevations. Our findings will help to improve knowledge about ecological drivers and responses in mountainous forest ecosystems.

Key words: altitudinal gradients, transects, deciduous trees, fall, sycamore, beech, temperature sensitivity

6.2 Introduction

Fall Senescence Phenology

At the end of the year, our deciduous forests display in red and yellow colors and show their beauty one last time before winter. In some regions this event is a real tourist attraction; in phenological research it represents the last stages in the leafing period, before the seasonal cycle restarts the next year. The process of leaf coloration and leaf fall is fascinating for both hikers and scientists since it represents a natural spectacle with still unexplained complex mechanisms (Estrella & Menzel 2006, Röthlisberger 2010). In this article we study how deciduous tree leaf senescence in mountainous areas is affected by the frequency of inversion situations, which mostly occur in fall and winter.

Leaf senescence begins with reduced photosynthetic activity and a loss of proteins, followed by chlorophyll and lipid degradation and finally ends in leaf death (Buchanan-Wollaston et al. 2003). In other words, the breakdown of the chloroplasts is the most significant change in the leaf structure; carbon assimilation via photosynthesis is replaced by catabolism (Lim et al. 2007). When yellowing is seen, the peak in the senescence process occurs (Buchanan-Wollaston et al. 2003). Leaf senescence is a highly complex process and questions about the triggers are still only partially answered. Many factors following different pathways play a role in the process (Nam 1997, Buchanan-Wollaston et al. 2003). Hence, senescence is not a passive, but an active process, since new genes are expressed and new proteins are synthesized (Noodén et al. 1997) whereby more than 800 genes are regulated during leaf coloring (Lim et al. 2007). Many biotic and abiotic factors trigger senescence (pathogens, shading, competition, heat, frost, drought, nutrients, UV-B irradiation, ozone), cause stress to the plants and lead to premature senescence (Lim et al. 2003). Out of 43 senescence transcription factor genes, 28 are also induced by stress (Lim et al. 2007), but this does not answer the question whether senescence is induced by stress or senescence itself leads to stress responses (Buchanan-Wollaston et al. 2003). Often senescence is a result of the redistribution of nutrients (especially N, K, P, Mg, Na, Cl) from older to younger tissue within the plant and therefore could also be a consequence of local deficiency (Williams 1955, Thomas & Stoddart 1980). Leaf senescence at the level of organs is closely related to cellular death, which is often pre-programmed and controlled by diverse genetic programs (Cao et al. 2003).

Besides genetics, which is highly variable between life trait and species, light in terms of day length/ photoperiod and temperature are the most important abiotic drivers of senescence (Thomas & Stoddart 1980, Estrella & Menzel 2006, Delpierre et al. 2009, Caffarra & Donnelly 2011). The role of photoperiod in triggering leaf senescence seems to be of less importance than temperature (Menzel & Fabian 1999, Yang et al. 2012) and also differs between species (Cleland et al. 2007, Vitasse et al. 2011). Heide (1993) found the photoperiodic effect especially pronounced in *F. sylvatica*. Whereas, *F. sylvatica* requires about 12 hours of daylight in spring to start leaf development (Wareing 1953, Heide 2003, Caffarra & Donnelly 2011, Čufar et al. 2012) the critical day length for onset of leaf coloring onset dates is largely unknown. Moreover, Archetti et al. (2013) showed that inter-annual variation of leaf senescence phenology was also correlated with inter-annual variation of precipitation.

In this article, the endogenic factors inducing leaf senescence are of less interest than the exogenic ones which regulate the course and the speed of leaf coloring and leaf fall. The most important fact is that the rate of leaf senescence - once initiated - is highly correlated to temperature (Thomas & Stoddart 1980). Leaf senescence of *F. sylvatica* is generally advanced with increasing altitude by about 2 days 100 m^{-1} (Menzel 1997, Dittmar & Elling 2006, Čufar et al. 2012, Vitasse & Basler 2013, Schuster et al. 2013) and delayed by higher temperatures with a response rate of 5-7 days °C^{-1} (Menzel & Fabian 1999, Schuster et al. 2013). For *A. pseudoplatanus*, Richardson et al. (2006) reported an advance of senescence by 2.5 days 100 m^{-1}, whereas Vitasse et al. (2009) could not confirm any elevational trend. Here, one has to keep in mind that different phenophases show different responses to altitude (Schuster et al. 2013) and also to climate warming (Archetti et. al. 2013); in particular, later fall phases respond more than early ones (Schuster et al. 2013).

Altitudinal Temperature Regime and Inversions in the Study Area

The variation of air temperature along altitudinal transects in different parts of the European Alps is described by Machalek (1974) and Kaiser (1992); the climatic situation in the area of Garmisch-Partenkirchen has been described by several authors, e.g. Reiter & Kanter (1972) and Werner et al. (1999). Kirchner et al. (2012) discussed temperature lapse rates between the Loisach valley and Mount Zugspitze in detail for the period 1951-2008, using the definition of Fang and Yoda (1988). On the basis of daily means, the lapse rates varied between -0.32°C 100 m^{-1} in December and -0.62 °C 100 m^{-1} in late spring (April/May) and in summer (June). Steep lapse rates (i.e. strong vertical temperature differences after Pepin 2001), are associated with frontal passages (cyclonic weather types); while shallow (i.e. less strong vertical temperature differences after Pepin 2001), or positive lapse rates (inversions) occur with anticyclonic weather types or sometimes with foehn events (Kirchner et al. 2012).

In mountainous regions, inversions do occur throughout the year, but are more frequent during night and in fall and winter (Micu 2009, Pepin & Seidel 2005, Rolland 2003). They can be most frequently observed during high pressure situations with clear nights and cold air downward drainage which is often accompanied by valley fog and warm conditions at higher elevations. Figure 6.1 shows a typical inversion situation in Garmisch-Partenkirchen with an inversion layer at about 1100 m a.s.l.

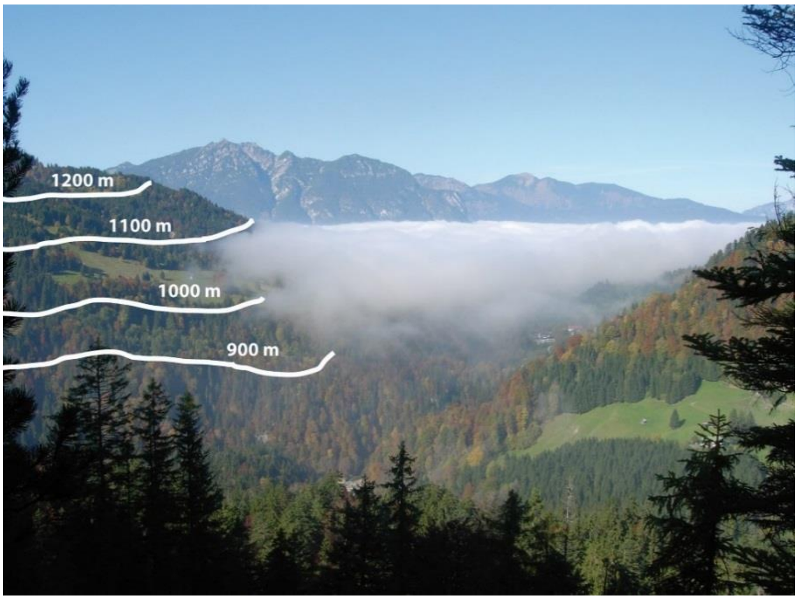

Figure 6.1 Inversion on 11th October 2010 in the area of Garmisch-Partenkirchen with an upper limit at about 1100 m a.s.l.

Response of Senescence Phenology to Inversions

With accumulation of inversion days, trees in lower elevations face colder temperatures than in situations with regular vertical temperature gradients – and even colder temperatures than the trees in middle elevations. With leaf senescence rates being related to temperature, frequent inversion situations should affect the timing of phenological senescence phases. In general, minimum temperatures play an important role in frost damage in trees. Therefore, many existing studies have focused on risks of late spring frosts associated with an extended vegetation period due to global warming (Hänninen 1991, Kramer 1994, Hänninen 1996, Linkosalo et al. 2000, Jonsson et al. 2004, Dittmar et al. 2006, Gu et al. 2008). However, other influences of cold air pools on trees, besides frost damages, are less frequently discussed in the current literature (Baumgartner 1962, Bastian & Steinhardt 2002). Existing studies are mostly restricted to calcareous karst sink holes (Sauberer & Dirmhirn 1954, Wegener 2006) or lower hilly mountain ranges (Baumgartner 1962), but are rare in the alpine area.

Recent studies showed that leaf coloration duration in fall is extended by warmer temperatures, and thus shortened by colder temperatures (Archetti et al. 2013, Schuster et al. 2013). A shortened vegetation period in alpine valleys due to inversion-induced cold air pools may influence other processes such as tree growth and carbon allocation. Therefore trees in mid elevations above frequent inversion layers could either gain carbon by a longer growing period (Dragoni et al. 2011) or suffer by a longer respiration (Piao et al. 2008, Wu et al. 2012, Archetti et al. 2013) compared to the trees in valleys.

At four altitudinal transect research sites around Garmisch-Partenkirchen in southern Germany we observed leaf senescence using the BBCH-Code (Meier 1997) and measured temperature directly at the observation sites in 2010 and 2011. The inversion situation in terms of frequency and inversion height was characterized based on temperature records. The aim was to study whether a high occurrence of inversion days was also related to leaf senescence since temperature is a main trigger of fall phenology. We also aimed to test whether responses to inversion-induced cold temperatures differed systematically between species and phenophases.

6.3 Material and Methods

Regional Setting and Site Infrastructure

Garmisch-Partenkirchen (708 m a.s.l., 47.49° N, 11.10° E) is located in southern Bavaria, at the northern edge of the Alps, next to Zugspitze, the highest mountain in Germany (2962 m a.s.l., 47.44° N, 11.02° E). Mean annual precipitation is 1363 mm in Garmisch and 2003 mm at Zugspitze; annual mean temperature is 6.5°C and -4.8°C respectively (1961-1990, German Meteorological Service).

In the mountains, mixed forests cover most of the slopes up to the tree line at 1700-1800 m a.s.l. *Acer pseudoplatanus* and *Fagus sylvatica* are the two most common deciduous tree species with upper limits of 1700 m a.s.l. (*A. pseudoplatanus*) and 1500 m a.s.l. (*F. sylvatica*). In this region, which is particularly suitable for altitudinal transect research, our study sites are located along four transects in the submontane to subalpine forest zone (Figure 6.2): Garmisch-Partenkirchen – Kramer pass (700-1700 m a.s.l., southern aspect, KRA_S), Garmisch-Partenkirchen – Kreuzeck/Längenfelder (800-1800 m a.s.l., northern aspect, KRE_N), Brandwiese – Kreuzeck (900-1600 m a.s.l., southern aspect, KRE_S) and Reintal – Schachen (800-1800 m a.s.l., northern aspect, SCH_N). The elevations of the valley floor differ: KRA_S and KRE_N are in the Loisach valley with a base at approximately 700 m a.s.l. The Reintal valley at about 800 m a.s.l. is the base for the SCH_N transect and Brandwiese in the Bodenlaine valley at about 900 m a.s.l. is the base for the KRE_S transect. Along the four transects separated by 100 m in altitude, a total of 42 observation sites were selected in the forest between 700 and 1800 m a.s.l.

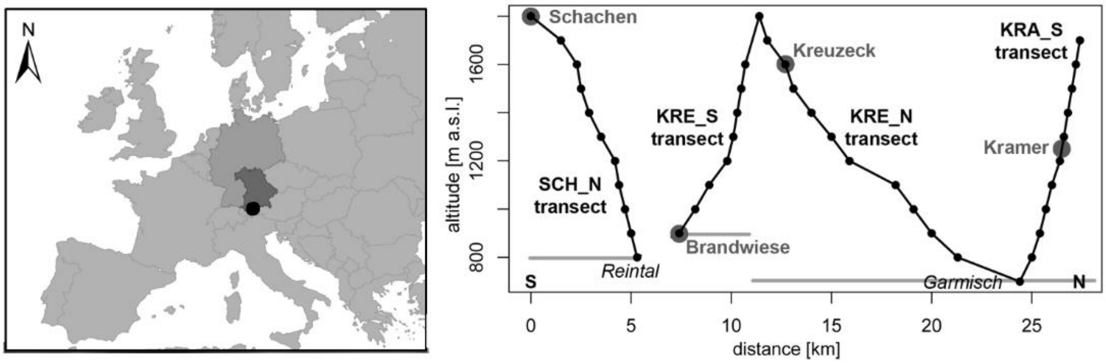

Figure 6.2 Transects in the area of Garmisch-Partenkirchen with positions of the observations sites (black points), the four meteorological stations (grey points) and transect specific valley floors (grey lines). A detailed geographical map can be found in the Online Supplements.

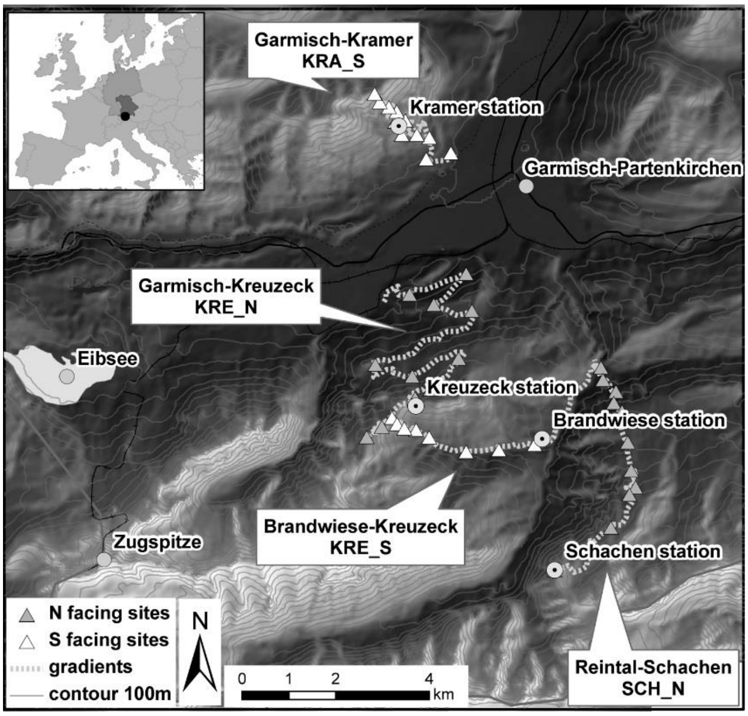

Figure 6.2 supplement: Geographical map of the four transects with observation sites in the area of Garmisch-Partenkirchen (708 m a.s.l., 47.4918° N, 11.0955° E) and Zugspitze (2962 m a.s.l., 47.4357° N, 11.0179° E).

Meteorological Measurements and Analyses

At each site, a temperature/humidity logger (onset HOBO® PRO V2 in a radiation shield fixed at the top of a 2 m pole) measured temperature and relative humidity at 30 min intervals since April 2010. Monthly lapse rates were calculated based on mean temperatures recorded by these loggers. Monthly minimum temperatures were used to illustrate the effect of inversions in the different altitudes. More detailed meteorological information (air-, surface- and soil-temperature, relative humidity, precipitation, solar radiation as well as wind velocity and direction, every 10 min) was provided by four climate stations at the transects (Brandwiese 900 m a.s.l., Felsenkanzel at Kramer 1250 m a.s.l., Kreuzeck 1600 m a.s.l. and Schachen 1830 m a.s.l.). For the period likely affecting fall phenology (August to November), monthly mean values based on the climate station data were used to compare fall 2010 and 2011.

Based on daily minimum temperatures measured by the loggers, inversion altitudes and frequencies were determined: Two linear regressions of altitude against minimum temperature were calculated for each day during autumn, one equal and above and one equal and below the altitude with the warmest minimum temperature (Figure 6.3a). The inversion altitude was then defined as the intersection point of both regressions. For inversion situations there is a positive slope for the regression below and a negative one for the regression above the inversion layer. Without inversion, the highest temperature is expected in the valley with decreasing temperatures with altitude. Consequently for these conditions only one regression with negative slope was determined. Altitudinal temperature rates (°C 100 m^{-1}) were determined from the slope of the regression of minimum temperature on altitude.

The number of inversion days which affect fall phenology was determined as counts of positive daily slopes in lower elevations between the beginning of August and the end of November. In some cases, temperature increased constantly with increasing altitude within our measurement sites (700-1800 m a.s.l.). These days were counted as inversion days, but no inversion altitude could be calculated.

Since the elevation of the valley floor is different in the valleys of Loisach (app. 700 m a.s.l., KRA_S, KRE_N), Reintal (app. 800 m a.s.l., SCH_N) and Bodenlaine (app. 900 m a.s.l., KRE_S), the inversion height was calculated by subtracting the valley floor altitude from the inversion altitude. The width of the valley can also influence the height of cold air pillows, but this was not considered. Day lengths at the onset dates of fall phenophases were determined by the R software package "geosphere" and based on 47.49° latitude for Garmisch-Partenkirchen. The free R software was also used for all figures and calculations (R Development Core Team 2009).

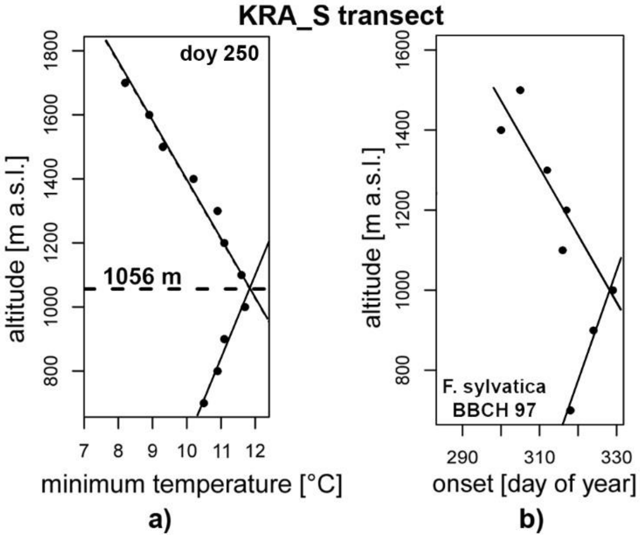

Figure 6.3 Method to determine the inversion altitude by two regressions of temperature (or phenological onset dates) on altitude (above and below the altitude with the highest minimum temperature or latest onset date). Examples show (a) minimum temperatures with altitude on the 7th September 2011 (day of year 250) and (b) end of leaf fall dates with altitude in 2011 on the KRA_S transect.

Phenological Observations and Analyses

At each site three adult and three young trees per species were marked for phenological observations. In total, 95 individuals of *Acer pseudoplatanus* and 133 of *Fagus sylvatica* at 35 (700-1600 m a.s.l.) of the 42 (700-1800 m a.s.l.) sites were observed. Phenological field observations took place once a week in September and October 2010 and 2011. The percentages of green, colored and fallen leaves were estimated for each marked individual. In addition, minimum and maximum development stages as well as an overall mean of all trees at the altitudinal level was recorded. Thus, the data basis consists of nine observations per week and site or 36 observations per week, altitude and species. Following the BBCH Code (Meier 1997) and the general growth stage key for trees and woody plants (Finn et al. 2007) five stages of leaf senescence were defined:

BBCH 91: all leaves still green
BBCH 93: 95% leaves still green (= beginning of leaf discoloration)
BBCH 95: 50% leaves still green, 50% leaves colored or fallen
BBCH 96: 50% leaves fallen
BBCH 97: 95% of leaves fallen (= end of leaf fall)

Site- and species-specific onset dates (day of year) were calculated by logistic regressions on the observations of still green (BBCH 93 and BBCH 95) or fallen leaves (BBCH 96 and BBCH 97) against time (day of the year). Altitudinal phenological rates (days 100 m^{-1}) were determined by the slope of the regression of the onset dates against altitude. Senescence duration was calculated for each site by the difference between BBCH 97 and BBCH 93 onset dates. Altitudinal distribution of senescence duration was visualized by linear regression and GAM (GAM is a function for fitting generalized additive models and uses the back-fitting algorithm to combine different fitting methods, R gam-package; Hastic 2013).

The influence of the inversion layer was studied similarly to the method in the temperature dataset by calculating two regressions: one equal and above and one equal and below the altitude with the latest onset day of each phenological phase (Figure 6.3b). Under non inversion conditions, the latest onset date in fall was expected in the valley with a negative slope (i.e. earlier onset dates with altitude). When phenology was affected by inversions, the latest onset date would be expected in mid-elevations with a positive slope (i.e. later onset dates with altitude) in lower and a negative slope (i.e. earlier onset dates with altitude) in higher elevations. For all fall phases, the overall slopes (without separation by inversion layers) were calculated for 2010 and 2011. These are expected to be steeper (i.e. a strong change with altitude) without inversion influence, and less steep (i.e. a less strong change with altitude) with increasing inversion frequency.

6.4 Results

Basic Climate Parameters, Lapse Rates and Inversions

The meteorological conditions in fall (August to November) were quite different in the two study years as the difference of mean values reveals (2011 minus 2010). Air- (+3.8°C), soil- (+0.7°C) and surface-temperatures (+2.1°C) as well as solar radiation (+32.6 W/m^2) were higher in fall 2011, and consequently relative air humidity was lower (-15.7%). For each transect and month the differences are given in Table 6.1a. November 2011 was the driest November since the beginning of the recordings of the German Meteorological Service (DWD 2011). Wind speed, as a driver of leaf fall, did not show huge differences between the study years (0.0 m s^{-1} for mean, -2.8 m s^{-1} for averaged maximum velocity, 2011 minus 2010). Therefore, in this study we ignore the potential influence of wind on leaf fall.

Table 6.1 Parameters measured at the meteorological stations Kramer, Kreuzeck, Brandwiese and Schachen (s) and at respective transects KRA_S, KRE_N, KRE_S and SCH_N (t, transects with temperature loggers and phenological observations) for the months relevant to leaf senescence and fall inversions (August to November) in 2010 and 2011.

- **a) Comparison of the two fall seasons by differences of the parameter mean values (2011 minus 2010) based on meteorological station data**
- **b) Lapse rates calculated on the mean and minimum temperatures measured by the 42 temperature loggers**
- **c) Inversion frequency (number of inversion days) and overall mean inversion altitude (m a.s.l.). (Note: At northern aspects, there are two separate peaks in the mean inversion altitude, see also Figure 6.5)**
- **d) Phenological rates determined by linear regression on weekly observation data for senescence phenophases (BBCH 93 to 97) vs. altitude at the 35 deciduous forest sites**

Note: Altitudinal rates (days 100 m^{-1} or °C 100 m^{-1}) result from separate regressions of onset dates or temperature on altitude. In the figures, altitude is often on the y-axis to support the visualization of the phenomena with altitude. An additional table containing the associated standard deviations can be found in the supplements (Online Resource 1).

			station (s) / transect (t)	**Kramer / KRA_S**				**Kreuzeck / KRE_N**				**Brandwiese / KRE_S**				**Schachen / SCH_N**				**mean**
			month	**8**	**9**	**10**	**11**	**8**	**9**	**10**	**11**	**8**	**9**	**10**	**11**	**8**	**9**	**10**	**11**	
	parameter	**data**	**year**																	
a	air temperature [°C]	s	diff. 2011-2010	3.1	4.3	1.9	5.1	3.2	4.5	1.5	5.9	2.2	3.1	0.9	1.2	3.3	4.7	1.4	5.6	3.8
	relative humidity [%]			-9.9	-6.2	-7.3	-30.1	-8.5	-5.1	-7.7	-33.9	-7.0	-0.2	-2.3	-16.3	-13.3	-9.9	-9.1	-30.4	-15.7
	solar radiation [W (m^2)$^{-1}$]			55.2	21.3	17.8	39.2	70.7	38.4	14.2	34.7	57.0	12.0	16.6	22.0	66.3	25.4	9.0	29.8	32.6
	5cm soil temperature [°C]			3.1	3.4	1.6	2.9	2.6	3.4	1.0	0.5	1.7	1.9	1.0	-0.7	0.7	1.8	0.0	0.3	0.7
	surface temperature [°C]			3.4	3.7	3.1	6.6	3.0	4.3	1.3	5.9	0.5	1.6	0.8	-1.0	1.8	2.4	0.4	3.8	2.1
	mean wind velocity [m s^{-1}]			/	/	/	/	-0.3	0.1	0.2	-0.4	0.0	0.0	0.0	0.0	0.0	0.1	-0.1	-0.1	0.0
	max. wind velocity [m s^{-1}]			/	/	/	/	-1.5	0.1	4.7	-9.2	-1.1	-3.1	-1.1	3.0	-4.9	-4.8	1.4	-2.7	-2.8
b	lapse rate of mean temperature [°C 100m^{-1}]	t	2010	-0.47	-0.45	-0.23	-0.30	-0.83	-0.44	-0.26	-0.36	-0.38	-0.36	-0.09	-0.17	-0.42	-0.42	-0.17	-0.24	-0.31
			2011	-0.39	-0.33	-0.22	0.12	-0.35	-0.32	-0.24	0.07	-0.27	-0.22	-0.01	0.43	-0.30	-0.27	-0.12	0.30	-0.10
	lapse rate of minimum temperature [°C 100m^{-1}]		2010	-0.66	-0.55	-0.44	-0.36	-0.56	-0.51	-0.51	-0.45	-0.57	-0.40	-0.14	0.01	-0.67	-0.49	-0.43	-0.32	-0.48
			2011	-0.46	-0.47	-0.33	0.49	-0.52	-0.43	-0.50	0.49	-0.15	-0.35	-0.05	0.94	-0.38	-0.36	-0.30	0.45	-0.15
c	inversion days [days]	t	2010	8	8	15	12	4	6	4	6	0	5	4	3	8	12	10	11	10
			2011	17	17	18	28	11	14	13	21	3	9	4	10	13	17	17	27	19
	mean inversion altitude [m a.s.l.]		2010	1224	1266	1264	1138	1040	1089	1066	1104	NA	1497	1474	1406	1108	1234	1206	1114	1166
			2011	1216	1251	1241	1247	1062	1086	1140	1149	1473	1437	1544	1462	1147	1179	1323	1287	1234
d	**phenological phase [BBCH]**			**93**	**95**	**96**	**97**	**93**	**95**	**96**	**97**	**93**	**95**	**96**	**97**	**93**	**95**	**96**	**97**	**/**
	phenological rate *Acer pseudoplatanus* [days 100m^{-1}]	t	2010	0.0	-0.3	-0.3	-2.2	-0.2	-1.1	-1.5	-2.2	-0.4	-1.4	-1.3	-2.1	0.6	-0.2	-0.9	-0.9	/
			2011	0.6	1.5	1.7	1.5	0.1	-0.6	-0.8	-1.4	-0.1	-1.5	-1.5	-1.8	0.0	-0.8	-1.2	-1.8	/
	phenological rate *Fagus sylvatica* [days 100m^{-1}]		2010	-0.8	-2.1	-2.6	-3.2	-0.2	-1.5	-1.7	-3.0	-0.5	-2.8	-0.5	-3.2	-0.2	-1.1	-1.0	-1.4	/
			2011	-1.3	-2.1	-2.1	-2.7	-0.9	-2.1	-2.0	-2.4	-1.9	-1.8	-2.1	-1.6	0.8	-1.0	-1.2	-1.1	/

Table 6.1 supplement: Standard deviations for Table 6.1.

	station (s) / transect (t)			**Kramer / KRA_S**				**Kreuzeck / KRE_N**				**Brandwiese / KRE_S**				**Schachen / SCH_N**				**mean**
			month	**8**	**9**	**10**	**11**	**8**	**9**	**10**	**11**	**8**	**9**	**10**	**11**	**8**	**9**	**10**	**11**	
	parameter	**data**	**year**																	
a	air temp.[°C]	s	diff. 2011-2010	4.8	5.3	5.8	5.1	4.9	5.6	6.7	5.0	3.9	3.6	4.1	4.7	4.8	5.6	6.9	5.0	5.6
	rel. humidity [%]			16.3	16.5	22.6	19.0	17.4	18.7	26.1	21.0	10.2	7.9	10.7	10.6	16.6	20.6	27.9	22.0	21.8
	solar radiation [W (m^2)$^{-1}$]			106.8	97.2	87.4	38.9	101.8	113.6	88.6	35.0	90.9	84.5	60.6	21.4	106.1	93.5	83.1	27.8	77.6
	5 cm soil temp. [°C]			3.0	3.1	4.3	1.8	3.2	4.0	4.3	2.2	1.6	1.6	2.0	2.0	1.5	2.3	1.7	1.6	1.8
	surface temp. [°C]			5.6	5.2	7.4	5.4	4.8	5.5	6.7	5.1	3.1	2.4	4.7	5.8	3.7	5.7	6.9	6.0	5.6
	mean wind velocity [m s^{-1}]			/	/	/	/	1.2	0.8	1.2	0.8	0.1	0.1	0.2	0.1	0.4	0.3	0.7	0.7	0.5
	max. wind velocity [m s^{-1}]			/	/	/	/	6.4	NA	6.5	4.8	2.3	1.6	2.5	2.1	4.8	3.3	5.9	8.3	5.6
b	lapse rate mean temperature [°C 100m^{-1}]	t	2010	0.065	0.052	0.086	0.098	0.063	0.049	0.082	0.094	0.098	0.079	0.130	0.140	0.061	0.049	0.081	0.091	0.07
			2011	0.073	0.062	0.08	0.065	0.069	0.058	0.078	0.06	0.110	0.095	0.12	0.093	0.068	0.058	0.075	0.064	0.07
	lapse rate minimum temperature [°C 100m^{-1}]		2010	0.036	0.032	0.071	0.099	0.018	0.022	0.052	0.081	0.031	0.052	0.065	0.068	0.041	0.019	0.066	0.086	0.05
			2011	0.055	0.046	0.074	0.15	0.051	0.048	0.057	0.160	0.093	0.057	0.078	0.190	0.09	0.038	0.046	0.190	0.09
c	inversion days [days]	t	2010	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	0
			2011	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	0
	inversion altitude [m a.s.l.]		2010	52	49	172	166	39	17	267	191	NA	58	75	261	33	195	233	159	155
			2011	57	107	111	98	38	59	139	148	23	126	34	38	139	151	225	201	179
d	**phenological phase [BBCH]**			**93**	**95**	**96**	**97**	**93**	**95**	**96**	**97**	**93**	**95**	**96**	**97**	**93**	**95**	**96**	**97**	**/**
	phenological rate *Acer pseudoplatanus* [days 100m^{-1}]	t	2010	0.5	0.4	0.7	2.2	0.4	0.2	0.3	0.4	0.1	0.2	0.3	0.5	0.5	0.2	0.2	0.4	/
			2011	0.6	0.4	0.2	0.7	0.6	0.3	0.7	1.1	0.3	0.2	0.5	0.8	0.6	0.6	0.6	0.6	/
	phenological rate *Fagus sylvatica* [days 100m^{-1}]		2010	0.3	0.4	0.3	0.7	0.2	0.2	0.2	0.4	0.4	0.7	0.5	1.0	0.6	0.4	0.6	1.3	/
			2011	1.0	0.6	0.6	1.0	0.5	0.2	0.4	0.8	0.8	0.5	0.9	0.4	0.7	0.5	0.5	1.0	/

Monthly temperature lapse rates at the four altitudinal transects calculated on the daily mean and minimum temperature measured at the 42 loggers are summarized in Table 6.1b. All lapse rates in 2011 were shallower (i.e. less strong vertical temperature differences) compared to 2010. In November 2011, the monthly temperature lapse rates were even positive at all transects. Shallower or positive lapse rates are hints to inversions, thus in 2011 the number of inversion days also increased.

Figure 6.4 displays the altitudinal distribution of monthly minimum temperatures for 2010 and 2011 at the four transects (note: the four first months in 2010 are missing). In 2010, the month May, June, August and September and in 2011 the month June, July and September were hardly affected by inversions. The extraordinary situation in November 2011 led to a distinct difference between the minimum temperatures in the valley and the mountain sites. The high altitude of the inversion layer indicates thick and stable cold-air pools in the valleys.

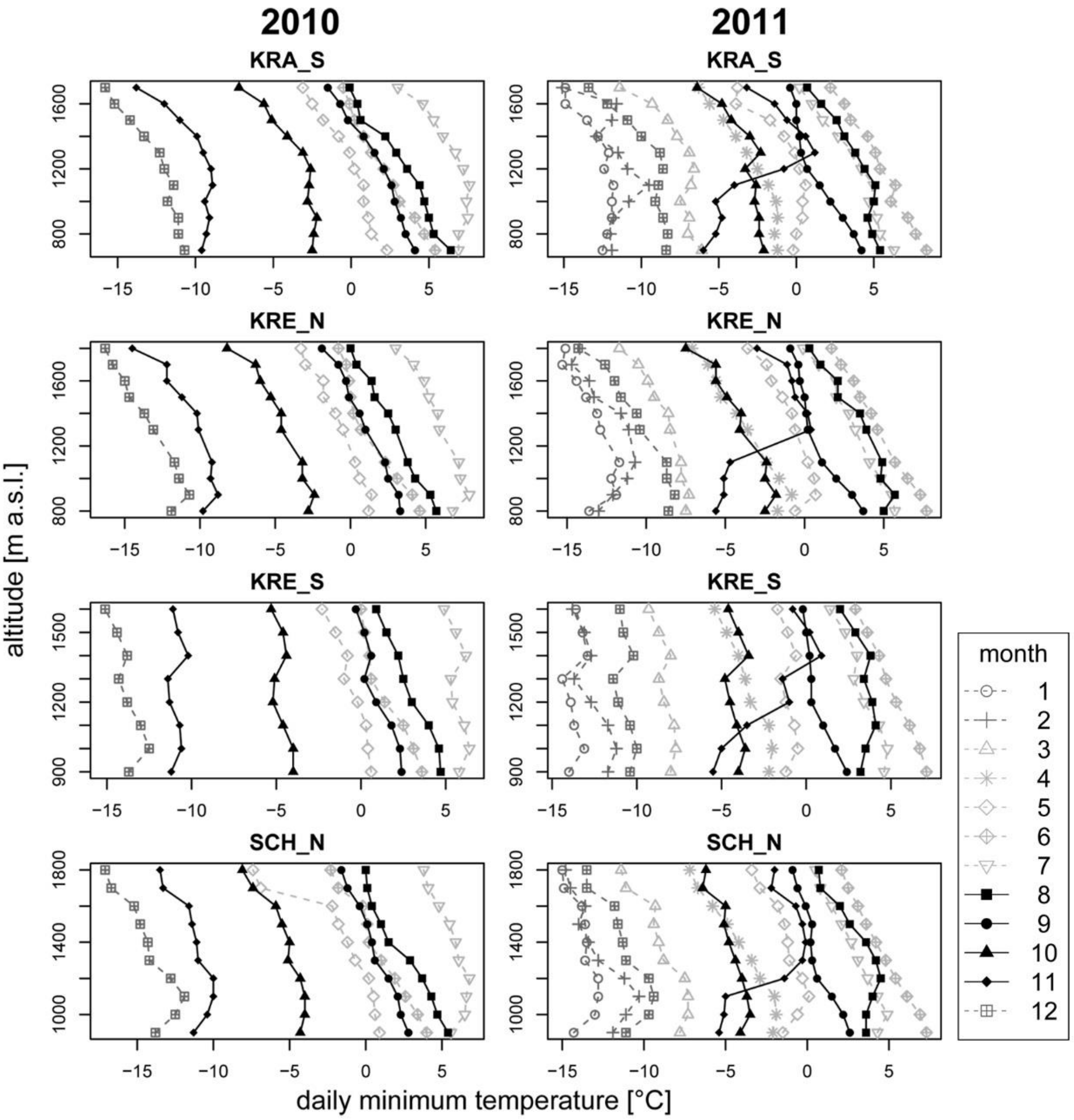

Figure 6.4 Mean monthly minimum temperatures at the four transects in 2010 and 2011. Fall months (August to November) are given in black. Winter months (December to February) are in dark grey, spring and early summer months (March to July) in light grey.

Inversion frequencies (number of days per month with positive temperature lapse rate in lower elevations) and altitudes (m a.s.l., intersection point of both regressions) at the single transects are summarized in Table 6.1c. This demonstrates an approximately doubled frequency of inversions in fall 2011 compared to 2010 and an overall mean inversion altitude of 1251 ± 137 m a.s.l. In fall 2011 (August to November) almost every second day was an inversion day (58 days out of 122).

The distribution of inversion heights (elevation of the valley ground subtracted from the calculated inversion altitude) at the four transects is illustrated by the histograms in Figure 6.5 for both observation years (August to November). Mean inversion heights are similar between the years, but generally about 220 m higher at southern slopes (app. 550 m) than at northern slopes (app. 330 m). At northern slopes, inversion heights peak about 330 m and 720 m. In 2010 and 2011, the high inversions occurred predominantly at the end of October and in November and only sporadically in September (see Table 6.1c). In 2011 the high inversions at northern sites were obviously more frequent than in 2010.

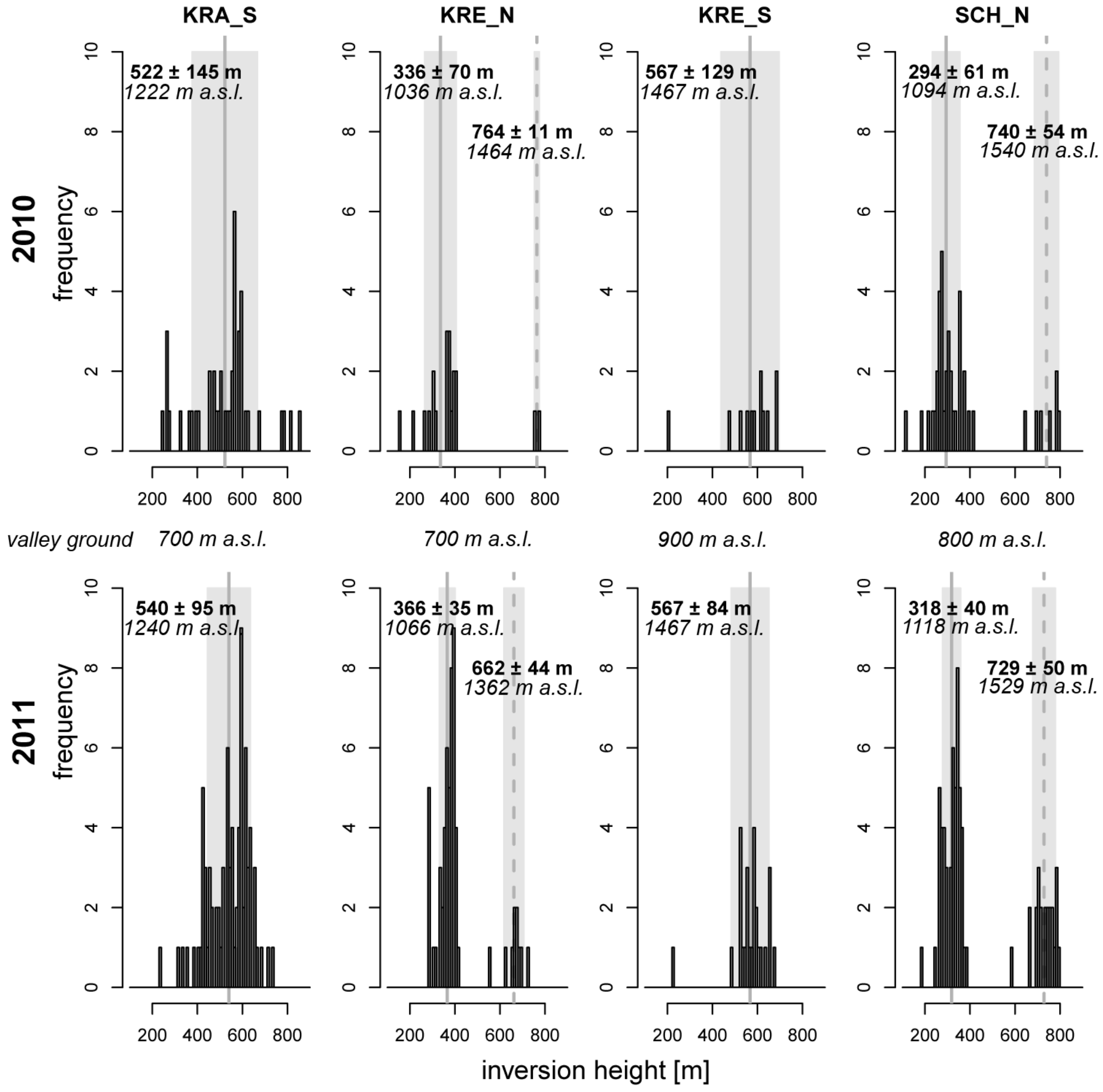

Figure 6.5 Distribution of the inversion heights at the four transects in 2010 and 2011 (August to November) with mean inversion height (dark grey line) and standard deviation (light grey shaded area). For the northern slopes, two means were calculated for inversion heights < 450 m (grey line) and > 450 m (dashed grey line) for the two peaks. Inversion heights are in bold with standard deviation, inversion altitudes (inversion height plus valley ground elevation) in italics.

Responses of Deciduous Tree Senescence

Onset dates of the beginning of leaf coloration (BBCH 93) varied between 28th August (day of year 240) and 15th October (day of year 288), when day length in Garmisch-Partenkirchen (47.49° latitude) was 13.7 and 11.0 hours respectively. This wide range of 48 days is predominantly due to the altitudinal difference of 1000 m between the observation sites. In contrast, there was only a variation of a few days between the two species (0-3 days) and the two years (3-6 days) for the first tree with colored leaves. However, mean onset of *A. pseudoplatanus* leaf coloration in both years was about 10 days earlier than that for *F. sylvatica*.

In the warmer fall of 2011, all senescence onset dates were observed later than in 2010. The altitudinal rates of the phenological senescence phases (BBCH 93 to 97) for both species decreased in 2011 compared to 2010 (except BBCH 93 for *F. sylvatica*), which hints to earlier onset dates in the valleys and/or later onset dates in higher elevations (Table 6.1d).

Averaged over transects, the mean phenological altitudinal rates reveal that in 2010 with few inversion days, only *A. pseudoplatanus* was affected by earlier leaf fall (BBCH 97) below the inversion layer (+1.6 days 100 m^{-1}). In 2011 with about twice as many inversion days, both species responded: *F. sylvatica* with a gradient of +0.7 days100 m^{-1} and *A. pseudoplatanus* with a stronger gradient of +3.5 days 100 m^{-1} in the inversion layer. For *A. pseudoplatanus*, a doubled frequency of inversion days in 2011 seems to have approximately doubled the response rate below the inversion layer compared to 2010. However, two years of observations are too few to validate this statement.

The number of inversion days which potentially influence leaf senescence increased with time of the year. Therefore, the impacts of cold temperatures in lower elevations during inversions are more pronounced on later senescence phenophases. Figure 6.6 displays the onset dates of BBCH 97 (end of leaf fall) for both species and years against altitude and the related linear regression lines for each transect together with the mean inversion altitude (Table 6.1c). *A. pseudoplatanus* responded to cold-air pools in the valley at all gradients and in both years. For *F. sylvatica*, however, this response was weaker or could not even be determined.

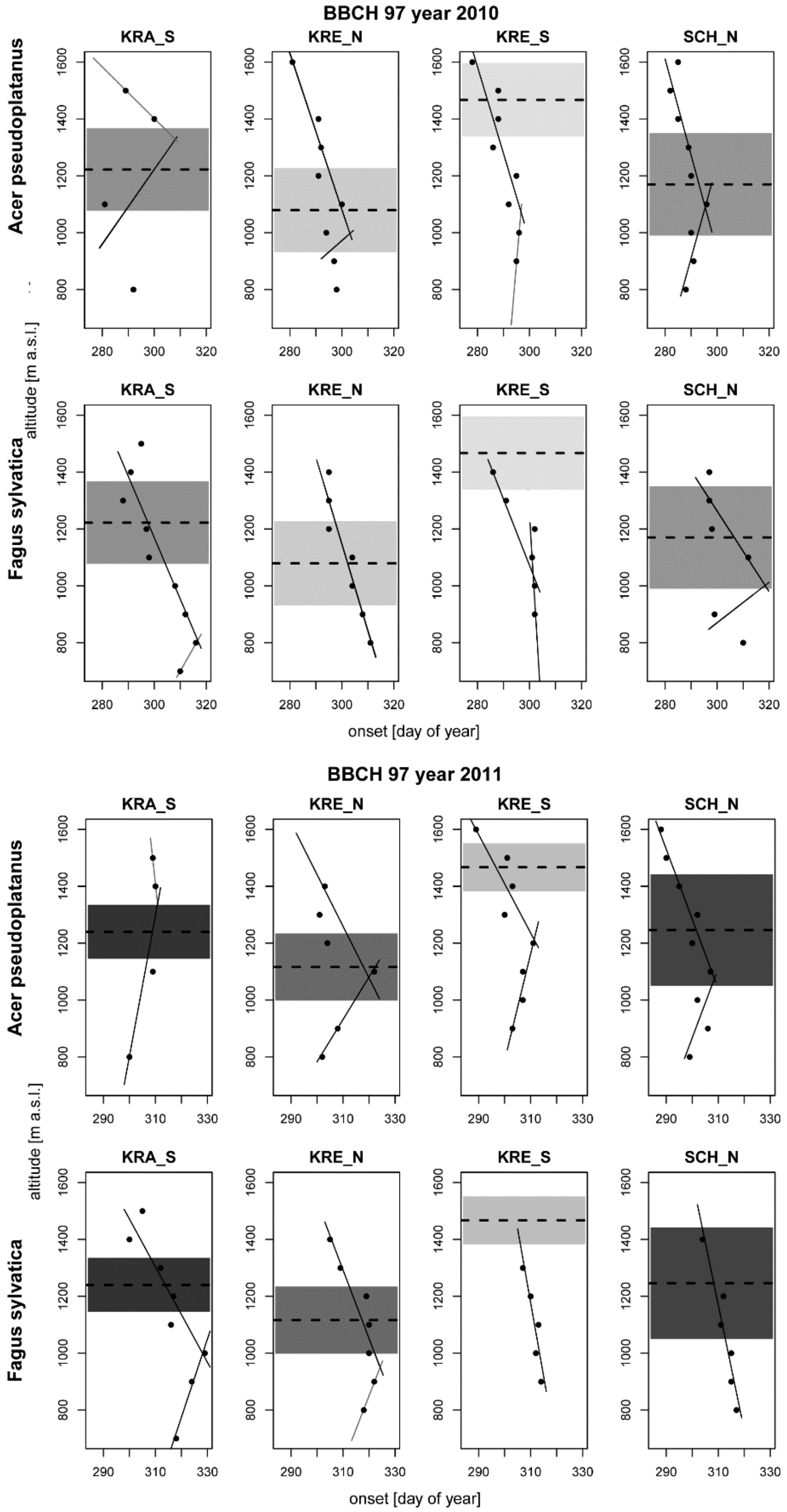

Figure 6.6 Inversion altitude with standard deviation (thick dashed line with grey area, degree of grey shading is related to the number of inversion days, see Table 6.1c) and its effect on phenology (here BBCH 97, end of leaf fall, two regressions on altitude ≥ and ≤ altitude (doy_{max}). Note: altitudinal rates (days $100m^{-1}$) were calculated by separate linear regressions (onset vs. altitude), therefore there are differences between regression lines and given slopes.

Since the initiation of leaf coloration depends probably not only on temperature but also on other factors such as day length, early fall phenophases show less dependency on altitude than later phases. The altitudinal rates of phenophases (all transect mean) in Figure 6.7 display smaller rates for later phenophases in 2011 compared to 2010. This means that all senescence phenophases were cumulatively influenced by cold temperatures in the valleys during inversion periods. The intensity of the effect seems to be directly connected to the accumulated time span in which the trees are exposed to the cold temperatures in the inversion layer, but more observation years are necessary to reinforce this conclusion.

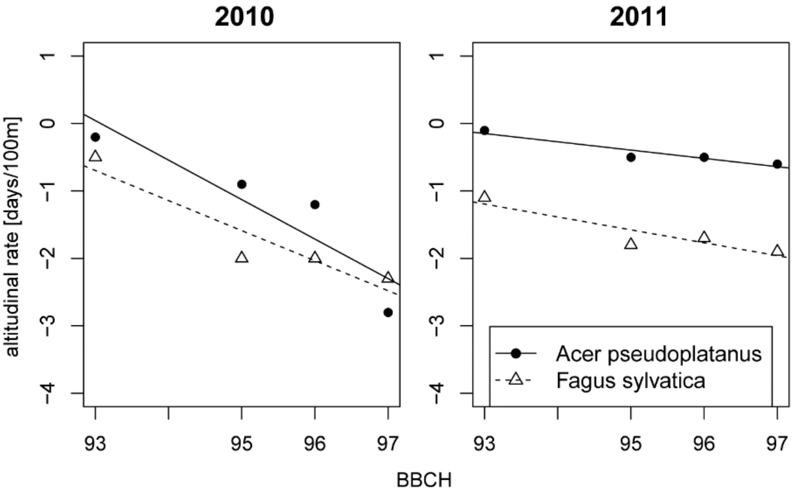

Figure 6.7 Mean altitudinal rates of phenological senescence at all transects, intra-fall seasonal variation in 2011 are reduced due to more frequent cold-air pools in the valley compared to 2010.

In Figure 6.8 the duration of leaf senescence (days from BBCH 93 to BBCH 97) in different altitudes is shown with a fitted GAM. The mean senescence duration for *F. sylvatica* on average was around 2 weeks longer than for *A. pseudoplatanus* (12 days longer in 2010, 17 days longer in 2011). The duration of leaf senescence was similar on north and south facing slopes, but longer in 2011 (10 days longer for *A. pseudoplatanus*, 15 days longer for *F. sylvatica*), when fall was 3°C warmer than in 2010.

Shortened senescence duration in the valley compared to mid elevations can be seen in both years for *A. pseudoplatanus*, but only in 2011 for *F. sylvatica*. This also suggests that *A. pseudoplatanus* is more sensitive to temperatures and thus to cold-air pools.

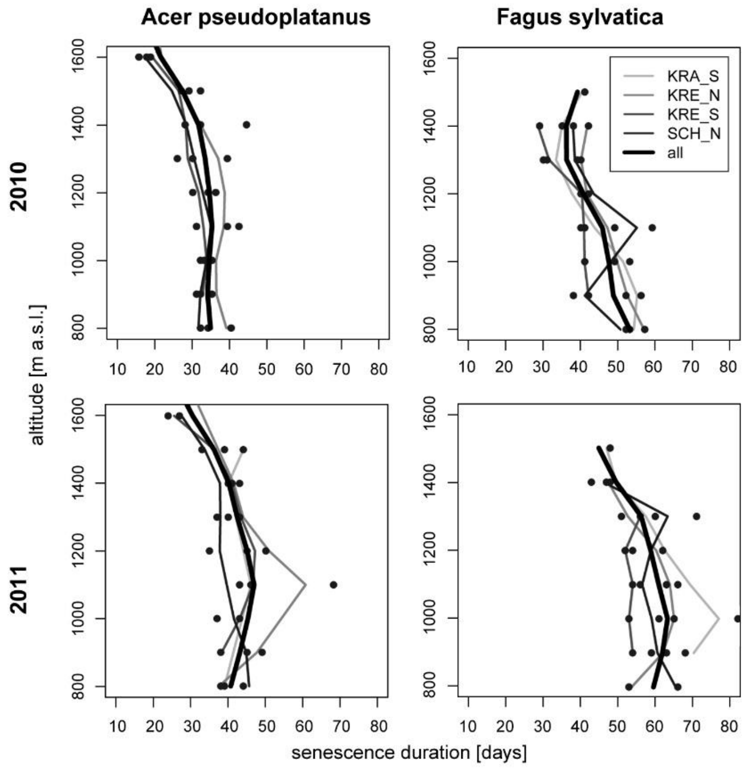

Figure 6.8 Leaf senescence duration (onset$_{BBCH\ 97}$ minus onset$_{BBCH\ 93}$) with GAM for both species and years. The thick black line includes all transect data, grey lines show each transect separately.

6.5 Discussion

General Fall Phenology

Our results confirm that in years with warmer fall, senescence phenophases occur later, leading to a lengthening of the vegetation period and a longer leaf senescence duration, e.g. as seen in 2011. These findings are consistent with previous studies (Menzel & Fabian 1999, Chmielewski & Rötzer 2001, Menzel & Fabian 2001, Sparks & Menzel 2002, Estrella & Menzel 2006, Dittmar & Elling 2006, Cleland et al. 2007, Vitasse et al. 2009b, Archetti 2013). On the other hand, Archetti et al. (2013), in agreement with Estrella & Menzel (2006), reported earlier leaf coloration associated with warm spring temperatures.

Another key factor inducing senescence and dormancy in temperate trees is a short photoperiod (Wareing 1956). Leaf coloration in our study occurred at day lengths between 13.7 and 11.0 hours, with almost no difference between tree species and years. To confirm that leaf coloring occurs when day length drops under a critical day length, our study covering a limited area with a homogenous photoperiodic regime and a dataset of only two years is not adequate. Photoperiod might be of much more importance in high latitudes because of rapid changes in day length (Fracheboud et al. 2009). At different altitudes at given latitude, temperature is considered to be more important in the control of senescence (Richardson et al. 2006). Other studies similarly identified temperature as the main driver of senescence in *F. sylvatica* and *A. pseudoplatanus* (Estrella & Menzel 2006, Delpierre et al. 2009, Vitasse et al. 2011, Archetti et al. 2013) on the basis of the co-variability of senescence and temperature on a given site over several years, as confirmed through bioclimatic modelling. Thus, in our study, we consider temperature as the first factor controlling senescence and therefore onset dates of phases, accompanied by a high variance between individuals (Baumgartner 1962, Estrella & Menzel 2006).

Inversions

Inversion altitudes were about 200 m higher at southern slopes than on northern slopes. This is due to the earlier and higher insolation on southern slopes which builds up a shallow upwind zone and ascends the air layers. For all transects, the respective valley elevation was included in the calculation of inversion heights. Furthermore, slope characteristics and ridge-top / width-depth ratios of valleys influence the vertical temperature distribution (Bader & McKee 1985, Kirchner et al. 2012). In our study, the valleys in the Wetterstein Mountains are narrower than the Loisach valley. Consequently, the upper border of cold-air pools could rise due to the smaller volume of the valley. However, inversion heights at transects in the narrow valleys (KRE_S and SCH_N) did not differ from the others.

At northern slopes, there is a second peak (at about 1400-1500 m a.s.l.) of inversion heights at about 400 m above the regular peak (at about 1000-1100 m a.s.l., Figure 6.5). On southern slopes, these two peaks might be interfused since here air masses warm up and rise faster due to higher insolation. We assume that the two peaks are connected to different weather situations. Occurrence of the higher inversions mostly concentrates at the end of October and in November and in large-scale weather patterns with southern circulation (stable high pressure conditions over Europe and air masses from east to southeast). Since the upper limit (m a.s.l.) of these high inversions exceeds the altitudinal distribution of *A. pseudoplatanus* and *F. sylvatica* we conclude that in these cases the phenology at all observation sites is affected by cold air pools in the valleys similarly. Therefore, these high inversions cannot be linked to the observed pattern of latest senescence in mid elevations.

Phenological Response

The literature suggests that many biochemical and phenological processes are sensitive to low temperatures (Jolly et al. 2005, Levitt 1980). In our study, the altitudinal pattern of senescence is linked to inversions since the trees are faced with colder temperatures in the valleys than the trees in mid elevations. The signal is stronger in later phases (such as leaf fall) due to the accumulation of inversion days with time. *A. pseudoplatanus* responded more than *F. sylvatica*, which suggests differences in their temperature sensitivity. *F. sylvatica* showed advanced onset dates in the valley in 2011 but not in 2010. The reasons for this are quite speculative, e.g. perhaps trees need a certain amount of inversion-induced cold temperatures to respond. If so, an increased inversion frequency would also increase the response rate of later senescence phases with altitude below the inversion belt (as observed for *A. pseudoplatanus* in 2010 and 2011). According to the literature, *F. sylvatica* has a lower sensitivity of leaf unfolding to temperature compared to *A. pseudoplatanus*, but often shows a higher temperature response in leaf senescence (Vitasse et al. 2011, Schuster et al. 2013). The minor response of *F. sylvatica* might be induced by a dynamic sensitivity to temperature as described by Delpierre at al. (2009) suggesting that the sensitivity to temperature in *F. sylvatica* declines before the main occurrence of temperature inversions in fall. Moreover, for *F. sylvatica*, the influence of photoperiod plays an important role (Heide 1993, Delpierre at al. 2009, Vitasse et al. 2011) and may be difficult to disentangle from temperature responses.

With longer exposure to cold air, the course of leaf senescence is cumulatively influenced; the signal is more pronounced for later phenological phases. The effect is highly dependent on the timing when inversions occur. We showed that the accumulation of cold temperatures shortens the senescence duration, which matches the results of Archetti et al. (2013) who showed that warmer fall temperatures increase the duration of colored leaves. Moreover, frequent inversions also shorten the vegetation period of the trees in the valley floor. Trees in mid elevation therefore can have approximately the same full leaf period as trees in the valley. Whether this is beneficial or not, also in terms of accumulated carbohydrate reserves for the next year, depends on photosynthesis and respiration rates (Piao et al. 2008, Wu et al. 2012, Archetti et al. 2013).

Other Factors Influencing Senescence

Although in our study we found temperature as the main driver for the course of leaf senescence, since it clearly explain the pattern of advanced phenological senescence phases in the valleys due to inversions, we have to consider other potential influencing factors. Short photoperiod triggers senescence, but not as much as temperature in our restricted area at a given latitude (Richardson et al. 2006, Fracheboud et al. 2009). Inversions often reduce insolation in the valleys by a mostly dense cloud cover, but in literature early leaf coloration is rather caused by high radiation in fall (Seyfert 1970, Estrella & Menzel 2006). Therefore reduced radiation in the inversion layer cannot explain the observed pattern of advanced senescence. Senescence rates furthermore depend on tree age and the location of the leaves within the crown (Baumgartner 1962, Estrella & Menzel 2006, Röthlisberger 2010). These factors as well as light, nutrient and water supply all interact with the species' temperature sensitivity and therefore influence the course of senescence (Smart 1994). In 2011, early snow fall might have been another important factor for leaf fall due to the additional weight of the snow adhering to the leaves (not measured). But snow loads are expected to occur earlier and more often in higher elevations. Mean and maximum wind speeds at all meteorological stations in 2011 were lower (or equal) than in 2010. Thus, neither snow nor wind speed may explain the pattern of early leaf fall dates in the valley compared to later leaf fall in mid elevations.

The phytohormones cytokinin and ethylene play a role in senescence control. Ethylene is essential for fruit ripening and has an advancing effect on leaf senescence (Buchanan-Wollaston et al. 2003). Since 2011 was a mast year for *F. sylvatica* (e.g. Meining et al. 2011, Ziegler 2011) and ethylene is produced by the fruits (e.g. Burg & Burg 1962) a higher yield of fruit in lower elevations could therefore promote earlier leaf senescence. But the production of ethylene also depends on temperature (Burg & Burg 1962) and its role in leaf senescence is species-specific (Buchanan-Wollaston et al. 2003), not well-investigated for temperate trees and does not explain the strong pattern in *A. pseudoplatanus* senescence onset dates in both years.

It may also be possible that the vertical distribution of temperature on the slopes also indirectly influenced leaf senescence via pollutants and pathogens. But it is rather unlikely that the same pathogen affected both *A. pseudoplatanus* and *F. sylvatica* more strongly in 2011 than 2010. A major role of air pollutants is equally unlikely because of relatively low concentrations in the area and the great distance to possible sources (Menzel et al. 2013). Last, but not least, Taylor et al. (2008) concluded that delayed leaf coloration and leaf fall was directly influenced by increased atmospheric CO_2 concentrations. In the stable inversion layer mixing of CO_2 could be restricted, but again this fact would not explain the advanced senescence onset dates. Therefore, the pattern of early leaf fall in the valley is most likely to be directly explained by cold-air pools during inversion situations.

Climate Change and Phenological Modelling

Effects of cold-air pools in mountain regions have been investigated in sinkholes in the calcareous karst regions of the Alps. Here, influences on phenology and even reversions of vegetation zones were reported (Sauberer & Dirmhirn 1954, Wegener 2006).

Baumgartner (1962), who investigated inversion situations at a transect at Grosser Falkenstein, Germany, proved that shortened shoot growth in the valleys is due to inversions, which was most distinct for *A. pseudoplatanus*. This corresponds to our results that *A. pseudoplatanus* showed a stronger response to inversion-induced low temperatures than *F. sylvatica*. The phenological growing season in Baumgartner's study (1962) was 1 to 2 weeks longer at the top of the inversion layer compared to the valley, also due to earlier spring onset. Leaf coloration of *F. sylvatica* occurred about 5 to 7 days later in mid elevations than 200 m below in the valley.

It is unclear if the weather situations involved in the occurrence of inversions will change in the future. In their study in Garmisch-Partenkirchen, Kirchner et al. (2012) showed a high variation in lapse rates but no significant trend in average minimum temperature lapse rates since 1970. Therefore, we expect the phenomenon of advanced leaf senescence due to inversions to be highly variable in time and also in space.

However, our results underline the need for site-specific temperature measurements. With precise temperature data, phenological models such as the cold degree day model (Dufrêne et al. 2005, Delpierre et al. 2009, Vitasse et al. 2011), will produce convincing results. Predicting phenology in a larger area by using temperature data from one single meteorological station will totally neglect the influence of inversions, especially in mountainous regions.

The next step, also to improve phenological modelling of senescence phases, is to systematically test in experiments or modelling studies, whether it is minimum temperature itself (used to determine inversion heights and days) or general reduced mean air temperature (depicted as cold air pools in the inversion layer) that are decisive for the observed pattern of advanced senescence.

6.6 Conclusions

In contrast to spring phenology, various drivers of senescence phases have been broadly discussed in the literature. The only trigger which could be shown to have some relevance and significance was summer/ fall temperature (Estrella & Menzel 2006, Delpierre et al. 2009). We were able to show for the first time that inversions at altitudinal transects in fall influence senescence phenophases (from BBCH 93 to 97), thus confirming earlier results by a totally different approach. Phenological senescence phases are almost consistently reported to be delayed with higher summer/fall temperatures. Advancing onset dates under influence of cold air layers in mountain valleys support the view that temperature is the main driver, since the photoperiodic regime in the area is homogenous. However, other potential factors triggering the beginning of leaf senescence have to be taken into account (e.g. light, drought, pathogens…; Smart 1994), but cannot explain the observed altitudinal senescence pattern in the present study.

Both species (*A. pseudoplatanus* and *F. sylvatica*) responded to inversion induced cold air layers by advanced senescence phenophases in lower altitudes. Since inversion days in fall accumulate with time, the effect was more distinct for later phenophases. Comparing the two deciduous species, *A. pseudoplatanus* responded earlier and stronger and therefore proved to be more sensitive than *F. sylvatica*. In fall 2011, the number of inversion days almost doubled compared to 2010 and also the phenological response rates increased. Once leaf senescence is initiated, the frequency of cold air-pools seems to directly influence the phenological response rates and consequently the length of the vegetation period.

Spring inversions could also influence the timing of bud burst or flowering and therefore pollen distribution, but they are not as frequent or stable compared to inversions in fall and winter (Daubert 1962, Machalek 1974, Kirchner et al. 2012). In the Bavarian Forest with its hilly relief including lots of closed vales, Baumgartner (1962) found delayed bud burst dates in the valleys in spring since descending cold-air accumulates there. In the valleys in the alpine region of Garmisch-Partenkirchen we could not observe this phenomenon in spring. We hypothesize that the cold-air in spring better drained and did not accumulate as much in the wider alpine valleys.

Compared to recent climate change, inversions may play a minor role in changing phenological phases and the vegetation period since they are variable in space and time. But where classical inversions and cold air descending into valleys (such as Baumgartner showed) are common, they should be taken into account for deciduous tree senescence. Cold inversion temperatures might also influence other processes such as stem growth, carbon allocation, build-up of carbohydrate reserves or emissions of biogenic organic compounds. On the other hand, trees with later senescence at the top of the inversion layers may suffer from prolonged respiration or light stress (UV). The clear response of deciduous species to cold-air pools in alpine regions with high inversion frequency helps us to better understand the relationship between climatic drivers and vegetation responses in mountain forest ecosystems.

6.7 Acknowledgments

Our gratitude is directed to the Bavarian State Ministry of the Environment and Public Health for funding the project “Auswirkungen des Klimawandels in den Alpen - Erfassung mittels Höhengradienten” (KLIMAGRAD, Climate Change Impact Monitoring at Altitudinal Gradients) within the “Klimaprogramm Bayern 2020”. The research leading to these results has received funding from the European Research Council under the European Union's Seventh Framework Program (FP7/2007-2013) / ERC grant agreement n° [282250]. The authors furthermore acknowledge the support by the Bavarian State Forest Enterprise and the German Meteorological Service (DWD) for the provision of additional data.

7 Intra-annual Tree Ring Formation of Norway Spruce and European Beech in Relation to Elevation and Phenology

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7.1 Abstract

To investigate the intra-annual process of tree ring formation we observed Norway spruce and European beech along two elevational transects in an alpine forest. We expected differences between species and a strong influence of elevation. Wood samples were taken regularly from May to October 2011 using a trephor tool and the microcore thin section method. The ring width was measured for different cell categories (phloem, xylem, growing/ wall thickening/ lignified cells). Their determined start, peak and end dates were compared to elevation, observed spring and autumn phenology and local air temperature.
For spruce, phloem growth started before, and xylem growth at, bud burst. For beech, phloem growth started with bud burst and xylem growth with leaf unfolding. Ring widths were reduced with elevation for both species, but the timing differed: For beech the growth period was strongly reduced with elevation, but the maximum growth rate increased. In contrast, for spruce, both growth period and maximum growth rate were approximately constant with elevation. Evergreen spruce seemed to have a relatively fixed intra-annual stem growth and phenology development over the elevational, and thus temperature, transect. Stem growth in beech was more variable and seemed to be more adaptive to elevation or temperature.

Key words: microcore, cell growth, cambial activity, Alps, gradients, *Picea abies*, *Fagus sylvatica*

7.2 Introduction

Dendroecological studies on tree rings have proved to be a reliable tool for the characterization of local and regional weather and climate and their variation. Chronologies of tree ring width and density have been used for climate reconstructions prior to the instrumental period (e.g. Hughes et al. 1984, Briffa et al. 1990, Frank & Esper 2005). The capability to reconstruct climate from tree ring formation depends on several factors such as tree species, site characteristics, measured tree-ring parameters, standardization method used, and elevation (Fritts 1976, Schweingruber 1996). In particular, chronologies from trees at high elevations or high latitudes reveal stronger climatic signals since such trees are very sensitive to temperature (Jacoby & D'Arrigo 1989, Briffa et al. 2002, Frank & Esper 2005).

In recent time, attention has also focused on tree ring formation within a year on a cellular level and its relations to environmental conditions (Rossi et al. 2007, Deslauriers et al. 2008, Gričar et al. 2008, Gryc et al. 2012). A few studies also compared secondary stem growth with observed phenology (Lauscher 1988, Čufar et al. 2008, Moser et al. 2010, Michelot et al. 2012), but mostly only bud burst was considered. Henhappl (1965) found that the annual period of stem growth for lowland beech started approximately at the same time as bud burst, but ending at least one month earlier than mid leaf coloring. Merkel (1987) was able to measure e.g. cell lumina of Scots pine (*Pinus sylvestris*); however it was impossible to date the intra annual variations. Thus, for many tree species it is still unknown how intra-annual variation in wood formation is triggered by environmental conditions and phenology. In particular, how these interactions differ with elevation, and thus temperature, has not been satisfactorily investigated (Moser et al. 2010).

With our study of eight sampling sites on two elevational transects from 800 m to 1400 m a.s.l., we aimed to answer some of the questions on intra-annual tree ring development under different temperature regimes. Temperature is likely to be the most important factor controlling intra-annual tree growth and the most important variable changing with elevation (Körner 2007). Therefore, observations along elevational transects are suitable for so called “space-for-time/warming experiments” (Körner 2003). Otherwise extensive long-term studies would be needed to study the response of growth to changing environmental factors. We can use the differences in tree growth under different temperature regimes as a first approximation of future changes under a global warming scenario.

The perennial life of trees is guaranteed by the regular restoration of functional phloem and xylem by cambial activity (Plomion et al. 2001). The process of xylogenesis is controlled by various exogenous (e.g. temperature, photoperiod) and endogenous (e.g. phytohormones) factors and the expression of structural genes (Plomion et al. 2001). For cambium reactivation in spring, temperatures of at least 4.4-8.6 °C are required (Wilcox 1962, Loris 1981, Horáček et al. 1999, Rossi et al. 2007, Deslauriers et al. 2008). Furthermore, sufficient soil water content is important for cambial cell division, since a lack of moisture results in reduced radial width and cell wall thickness (Abe & Nakai et al. 1999, Schweingruber 2007). Antonova & Stasova (1997) reported highest cambial activity for *Larix sibirica* at 20-21 °C mean daily temperature and an optimum of 2 mm day^{-1} precipitation.

Cambium reactivation in spring begins with cell division followed by a differentiation in phloem and xylem (Denne & Dodd 1981, Kozlowski & Pallardy 1997, Larcher 2003), however cell growth starts at the phloem side first (Oribe et al. 2001, 2003; Gričar et al. 2006). Therefore, the onset of cambium reactivation is highly variable between and also among tree species. Nearly 80 years ago, Priestley and Scott (1936) had determined a clear difference in cambium reactivation between diffuse-porous and ring-porous species: The first earlywood vessels are reported to develop when leaves are fully unfolded in diffuse-porous species (e.g. Aloni 1991, Schmitt et al. 2000) and 2-6 weeks before bud burst in ring-porous trees (e.g. Atkinson & Denne 1988, Larson 1994). However, Frankenstein et al. (2005) did not find any difference in the onset of first cambium cell division between ring-porous ash and diffuse-porous maple. After reactivation of the cambium, cell differentiation is passes through different stages: expansion, cell wall deposition, lignification and finally cell death (Plomion et al. 2001, Gryc et al. 2012). Therefore, in our study we used the following xylem growth categories: total xylem, growing cells, cell wall thickening cells and lignified cells. Additionally, the development of phloem was also determined.

Several techniques, tools and methods allow the full survey of stages in this xylogenesis process (Eckstein 1983, Petersen & Eckstein 1988, Rossi et al. 2006a). The expressions “microsampling” for the technique (Deslauriers et al. 2003, Mäkinen et al. 2003) and “microcore” for the wood core (Rossi et al. 2006a) are now commonly used. Compared to classic dendroclimatology, the study of the intra-annual course of tree-ring growth requires repeated microsampling within a year (Gričar et al. 2006, Deslauriers et al. 2003, Rossi et al. 2006a). In our study, we used the trephor tool (Rossi et al. 2006a) and sampled on 17 days over the whole vegetation period.

We chose the deciduous diffuse-porous European beech (*Fagus sylvatica* L.) and the evergreen Norway spruce (*Picea abies* (L.) KARST) because of their wide distribution, longevity, and sensitivity to climate (Bourquin-Mignot & Girardclos 2001, Piovesan et al. 2005, Gryc et al. 2012). Both species therefore have been used extensively for dendroecological studies (e.g. Eckstein & Frisse 1982, Dittmar et al. 2003, Di Filippo et al. 2007) and phenological observations (e.g. Chmura & Rozkowski 2002, Estrella & Menzel 2006, Hänninen et al. 2007, Vitasse et al. 2009b, Čufar et al. 2012, Schuster et al. 2013).

The impact of global warming on tree phenology and the vegetation period was first reported by Menzel and Fabian (1999): spring onset dates were advanced and autumn onset dates were delayed by higher temperatures (Dittmar & Elling 2006, Dose & Menzel 2006, Vitasse et al. 2009b, Schuster et al. 2013). Higher temperatures in spring also advanced the beginning of xylogenesis (Deslauriers et al. 2008). Moreover, the pattern of decreasing ring width with increasing elevation (Burger 1941, Larcher 2001, Kozlowski et al. 1991, Dobbertin & Giuggiola 2006) is considered to be closely linked to the growing season length (White et.al. 1999). For beech, the vegetation period is reported to decrease by 3.4 days 100 m^{-1} (leaf unfolding to leaf coloration; Dittmar & Elling; 2006) up to 7.3 days 100 m^{-1} (bud burst to leaf fall; Schuster et al. 2013). Bud burst of spruce is delayed with elevation by 4.1 days 100 m^{-1} (Schuster et al. 2013), but a visible phenological end of the vegetation period cannot be determined for evergreen species.

Based on our extensive study, including four different elevational levels, two aspects (north and south), two tree species and various cell categories, the following research questions could be examined:

1. Does the intra-annual course of tree ring growth vary with elevation?
2. Are there differences in tree ring growth between northern and southern aspects?
3. Are there differences in the timing (start, peak, end of tree ring growth) among different cell categories (phloem cells, total xylem cells, xylem growing cells, xylem wall thickening cells and xylem lignified cells)?
4. Is the timing of tree ring and cell category growth influenced by leaf phenology, elevation and temperature?
5. What are the main differences in xylogenesis and its dependency on environmental factors between a deciduous and an evergreen species?

Our results may indicate how our selected tree species, which are major tree species in much of Central Europe, could respond to anthropogenic induced warming.

7.3 Material and Methods

Study Site

Our study site was situated in the Bavarian Wetterstein Mountain range (northern calcareous Alps) comprising two elevational transects (one northern and one southern aspect; Figure 7.1a). The highest mountain in Germany, the Zugspitze, is situated here (2962 m a.s.l., 47°25′ N, 10°59′ E) above the Loisach valley and the city of Garmisch-Partenkirchen (708 m a.s.l., 47°30′ N, 11°5′ E). Mean annual precipitation and mean annual temperature is 1363 mm and 6.5°C at Garmisch and 2003 mm and -4.8°C at the Zugspitze (German Meteorological Service data 1961-90).

Mixed forests cover the sub-montane to sub-alpine slopes from the valley floor up to tree line at 1700-1800 m a.s.l. European beech (*Fagus sylvatica* L.) is the most abundant deciduous and Norway Spruce (*Picea abies* (L.) KARST.) the most common evergreen tree species, accompanied *inter alia* by *Acer pseudoplatanus*, *Abies alba* and *Pinus sylvestris*. At higher elevations *Pinus mugo*, *Larix decidua* and *Pinus cembra* are present. European beech and Norway spruce are dominant tree species over a wide vertical range at both the northern and southern slopes which were chosen for microcore sampling. Their upper elevational limits are at about 1500 m a.s.l. for beech and at about 1700 m a.s.l. for spruce.

On the two transects Garmisch-Partenkirchen – Kramer pass (southern aspect, KRA_S) and Garmisch-Partenkirchen – Kreuzeck (northern aspect, KRE_N), sample sites were located at 800 m a.s.l., 1000 m a.s.l., 1200 m a.s.l. and 1400 m a.s.l. (Figure 7.1b). Thus, the study is based on eight sites at each of which were taken temperature measurements, microcore samples and phenological observations.

Meteorological Measurements

At each site, a temperature/humidity logger (onset HOBO® PRO V2 in a radiation shield fixed at the top of a 2 m pole) was measuring temperature and relative humidity at 30 min intervals in 2010 and 2011. Further meteorological information on air-, surface- and soil- temperature, relative humidity, precipitation, solar radiation and wind velocity and direction was measured at our climate stations at Felsenkanzel (1250 m a.s.l. on KRA_S) and Kreuzeck (1600 m a.s.l. on KRE_N).

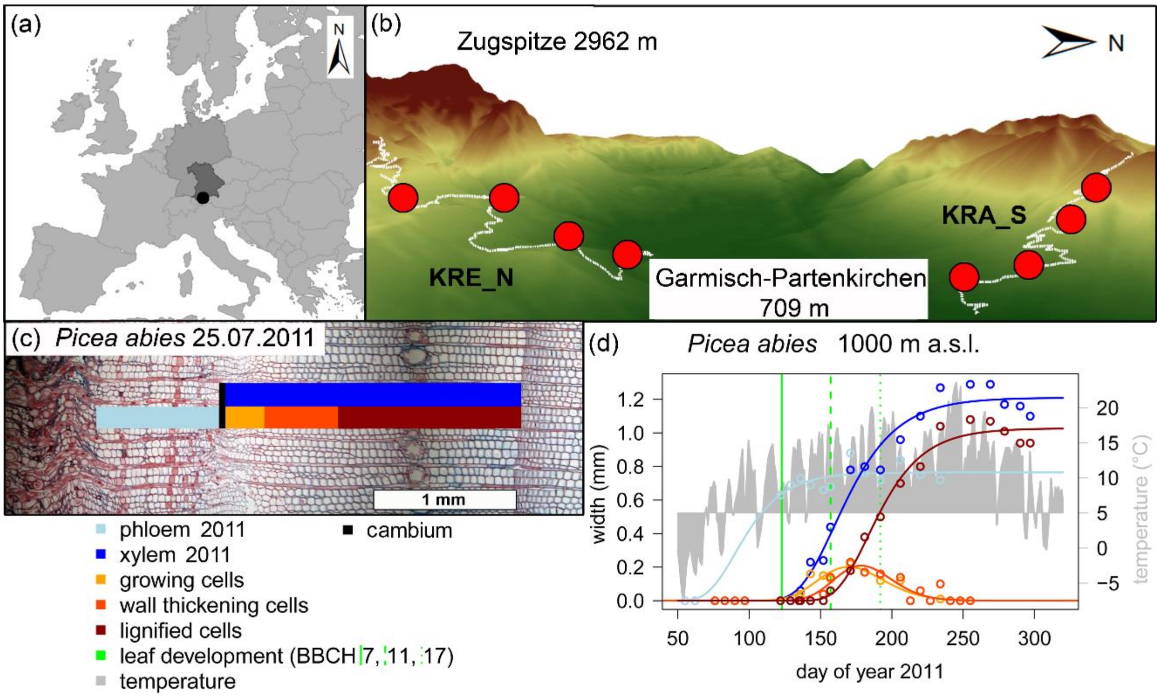

Figure 7.1 ***(a)*** **Location of the study area and** ***(b)*** **the sampling sites on the two transects KRA_S and KRE_N.** ***(c)*** **Different cell categories studied, here thin section of spruce, 25.07.2011.** ***(d)*** **Model fit of annual course of width of cell categories, here spruce at 1000 m a.s.l.: Gompertz growth model for phloem, xylem and lignified cells (light blue, blue, red) and an adjusted Hadwiger model for growing and wall thickening cells (yellow, orange); the course of the mean temperature (grey) and onset dates for the phenological phases BBCH 7, 11 and 17 (green).**

Phenological Observations and Microcore Sampling

Spring phenology was observed weekly on all trees from April to June 2011 following a modified BBCH-Code after Meier (1997). The most advanced development stage found on each tree was noted (see also Schuster et al. 2013). We selected three spring and three autumn phases to relate to tree ring growth:

- BBCH 07: bud burst (first green visible)
- BBCH 11: beginning of leaf unfolding / beginning of shoot growth
- BBCH 17: all leaves fully unfolded / shoot reached final length

Additionally for beech the percentage of green, colored and fallen leaves in autumn was observed and senescence phases defined as following:

- BBCH 93: beginning of leaf coloration (5 % colored)
- BBCH 95: leaf coloration (50 % colored or fallen, 50 % green leaves)
- BBCH 97: end of leaf fall (95 % of leaves fallen)

Based on this observational data, specific onset dates were calculated for each species, phase, and site (see Schuster et al. 2013).

At each site, two individual trees per species were marked. Microcore samples (1.5 cm length, 2 mm diameter) were taken from the beginning of May to the beginning of October 2011 using the Trephor (patented by the University of Padua, Italy, Rossi et al. 2006a). In spring, the initial sampling interval was one week, reducing later to two weeks (exact sampling days of the year: 122 (May 2), 129, 136, 143, 150, 157, 171, 181, 192, 206, 220, 234, 255, 269, 279, 290 and 297 (October 24)). At two sites (800 m on KRA_S and 1400 m on KRE_N) only one beech tree could be investigated. Thus, a total of 510 microcore samples resulted from 30 trees (14 beech, 16 spruce) and 17 sampling dates.

Sampling took place orthogonal to the slope direction at breast height. The microcores (one per sampling date) were taken in rows from left to right with 3-4 cm horizontal and 6-8 cm vertical separation. When necessary, the bark was carefully removed with a small chisel before sampling. Samples were stored in Eppendorf tubes with store-liquid (Ethanol, Glycol, distilled water, 1:1:1).

Preparation of the Samples

In the laboratory, microcore samples were washed and dehydrated in increasing alcohol series (70 %, 80 %, 90 % and 96 %, 2 h each). After pre-infiltration with Technovit 7100 (7-12 h), sample infiltration followed (infiltration solution I and II, 7-12 h each). Finally samples were embedded in Technovit 7100 and dried for about 24 h.

With a Leica RM 2050 rotation microtome, 10 to 15 µm thin sections were cut orthogonal to the fiber direction, in order to obtain transversal cuts of the newest tree rings. Sections were stained (5 min Safranin-O-Astrablau, 1 min acetic acid, 1 min washed in distilled water, 10 min Astrablau, 1 min washed in distilled water) and fixed (alcohol series of 96 %, 100%, Xylol 1 and Xylol 2, 5-10 min each) before covering by a Leica CV Mount.

Completed slices were digitized by photography using the KAPPA Image Base software and camera with 63 × magnification. When more than one photograph was required to display the whole actual tree ring, pictures were composed using Adobe Photoshop. Measuring was done in Adobe Photoshop using the analyzing tools.

Measurements and Analyzes

We defined the cell categories total phloem, total xylem, xylem growing cells, xylem wall thickening cells and xylem lignified cells (Figure 7.1c). Their respective widths were determined as the mean of three measurements in Adobe Photoshop. Growth curves were fitted to the annual course for each of the categories. Wood formation dynamics showed a sigmoidal shape (Schmitt et al. 2004). Therefore, for phloem, xylem and lignified cells, a Gompertz growth curve was fitted (see also e.g. Deslauriers et al. 2003, Gričar et al. 2007, Gryc et al. 2012), since these categories were increasing over the whole vegetation period and had a final maximum plateau (asymptote, Figure 7.1d). For growing cells and wall thickening cells, which display a clear annual maximum, an adjusted three-parametric Hadwiger model was fitted (Formula 1, Figure 7.1d). In total, 150 models were fitted (5 cell categories, 30 trees).

Formula 1

$$d = \frac{a * b * (\frac{c}{doy})^{\frac{3}{2}}}{c} * \; e^{-b^2 * (\frac{c}{doy} + \frac{doy}{c} - 2)}$$

d: predicted ring width
doy: day of the year
a, b, c: variables

The fits of the Gompertz models were all above 0.80 (R^2) and for the Hadwiger model they ranged between 0.59 and 0.92. In two cases for the wall thickening cells, R^2 dropped to 0.42 and 0.49 (Table 7.1). Thus, since the models for the individual tree ring cell categories fitted very well in most cases, they allowed calculation of onset dates with high reliability.

Table 7.1 Model fits (R^2) of Gompertz (G) and Hadwiger (H) functions to model the annual course of width of five cell categories in different elevations.

	phloem	xylem	growing cells	wall thickening cells	lignified cells
model	G	G	H	H	G
			Fagus sylvatica		
800 m	0.94	0.98	0.60	0.85	0.95
1000 m	0.88	0.96	0.88	0.42	0.97
1200 m	0.97	0.96	0.81	0.59	0.99
1400 m	0.94	0.93	0.63	0.74	0.99
			Picea abies		
800 m	0.95	0.98	0.64	0.71	0.80
1000 m	0.98	0.97	0.87	0.80	1.00
1200 m	0.97	0.93	0.73	0.48	0.96
1400 m	0.99	0.96	0.92	0.86	0.99

On the basis of the fitted curve parameters the following onset dates were calculated for all categories: start date of growth (SD, one cell row, approximated by 0.02 mm for beech and 0.05 mm for spruce), end date of growth (ED, when 95 % of the growth limit was reached) and the total growth period (GP). Additional parameters of the Gompertz growth model determined were maximum growth rate (MR, slope at the inflection point in mm day^{-1}), date of maximum growth rate (MD, day of year), and the final (maximum) ring width (MW, mm). Further outputs of the Hadwiger model are the parameters MD and MW: the maximum date and the maximum width. Since sampling only started at the beginning of May, the first phloem cells could not be observed. For model fitting, some zero values were generated for the phloem category for the four weeks before air temperature reached 5 °C, for which no secondary stem growth is assumed (Loris 1981). Thus, the SD of phloem is strongly dependent on this assumption and might be calculated less exactly.

The full set of parameters (SD, ED, GP, MD, MW, MR) for all categories (total phloem, total xylem, xylem growing cells, xylem wall thickening cells and xylem lignified cells) were examined for relationships with elevation and appropriate phenological onset dates. The response to elevation was determined as the slope from a linear regression of mean onset dates per elevation on elevation. Slopes and onset dates of stem growth were compared to slopes and onset dates of phenology. For each tree, the 2010 ring width was determined by averaging nine measurements of the microcore samples. The R software was used for statistical analyzes and figures (R Development Core Team 2010).

7.4 Results

Mean temperatures for the months May to August were 10.8, 12.4, 12.0, 16.1 °C at the Felsenkanzel Station (1250 m a.s.l.) and 8.5, 10.3, 9.8 and 14.5 °C at the Kreuzeck station (1600 m a.s.l.). Daily mean temperature measured by the loggers at the sampling sites also showed a decrease in temperature with elevation, however the lapse rates at the transects varied from day to day (Figure 7.2). Monthly mean lapse rates (May to August) were similar on both transects, -0.47, -0.49, -0.49 and -0.39 °C 100 m^{-1} at KRA_S, and -0.45, -0.47, -0.47 and -0.35 °C 100 m^{-1} at KRE_N, but were slightly stronger at the southern aspect. Less pronounced lapse rates were found for August. Figure 7.2 also shows distinctive temperature drops in all months. After a dry spring (March 84.8 mm, April 73.2 mm), precipitation was higher from May to August (269.2 mm, 232.2 mm, 310.4 mm, 310.0 mm; Felsenkanzel station).

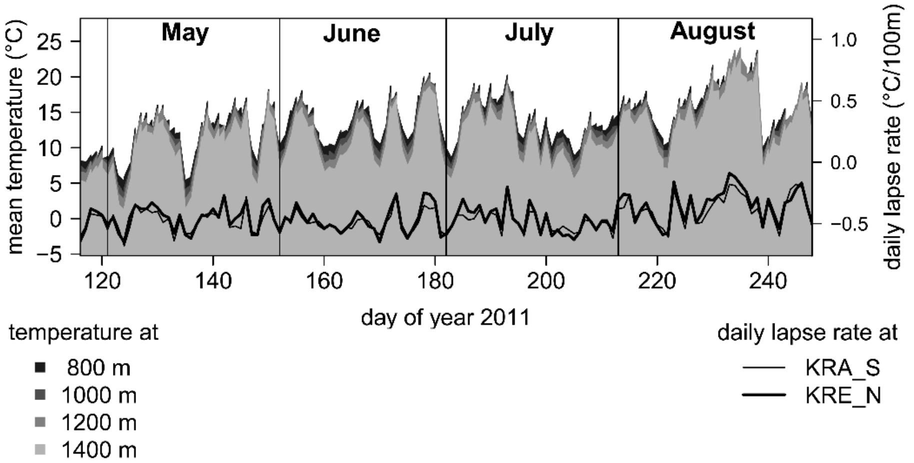

Figure 7.2 Course of the daily mean temperature from May to August 2011 at different elevations (grey curves) and daily lapse rates at the two transects (black curves).

After cambium reactivation the first phloem cells probably began to develop middle/end of March (spruce) and mid-April (beech). Xylogenesis started in the first half of May for both species, thus 6-7 (spruce) and 2-3 weeks (beech) after cambium activation. Xylem growth of both species showed reduced MW with elevation. For beech, MW of the annual tree rings decreased from 3.5 mm at 800 m a.s.l. to 0.7 mm at 1400 m a.s.l.; MW for spruce decreased from 4.1 mm to 1.5 mm over the same elevations. On average, for beech, MW of phloem was about 20 % of that of xylem, but the comparable figure for spruce was about 38%. From 800 m to 1400 m a.s.l., MW of tree rings in 2010 ranged from 2.7 mm to 1.4 mm (beech) and from 6.2 mm to 1.6 mm (spruce). Basal area increment in 2011 was 12.5 % (beech) and 32.1 % (spruce) smaller than in 2010.

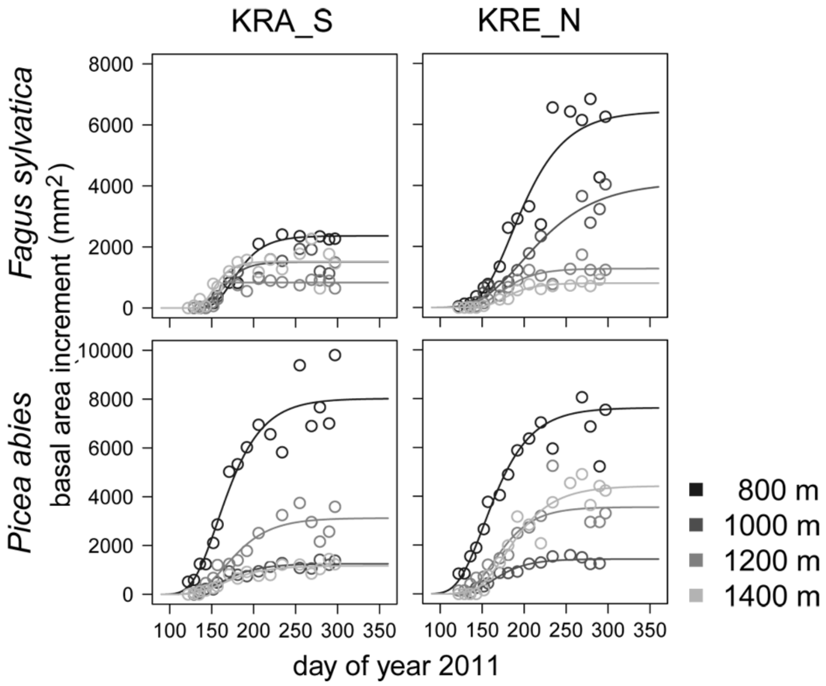

Figure 7.3 Xylem growth in different elevations at the north (KRE_N) and south aspect (KRA_S) transects.

Figure 7.3 displays the 2011 tree ring growth (MW) as basal area increment (mm^2) at different elevations, separately for northern and southern aspects. For spruce we found an unexpected anomaly with an unusually small MW at 1000 m a.s.l. (only 1.2 mm in 2011 and 1.0 mm in 2010). Generally, tree ring growth of beech on the northern slope is greater than at the southern slope, whereas for spruce, surprisingly, almost no differences could be found between aspects.

At first glance, a shorter growth period (GP) at higher elevations (1200 and 1400 m a.s.l.) was detectable for all categories of beech (Figure 7.4). This variation in GP is mainly influenced by a distinct earlier end of xylem growth (ED) at higher elevations. Therefore, ED of xylem growth appeared to be uncoupled from leaf senescence since at high elevations xylem growth stopped several weeks before leaf coloring (BBCH 93), but not at lower elevations (Figure 7.4) where xylem development was still ongoing during leaf coloring.

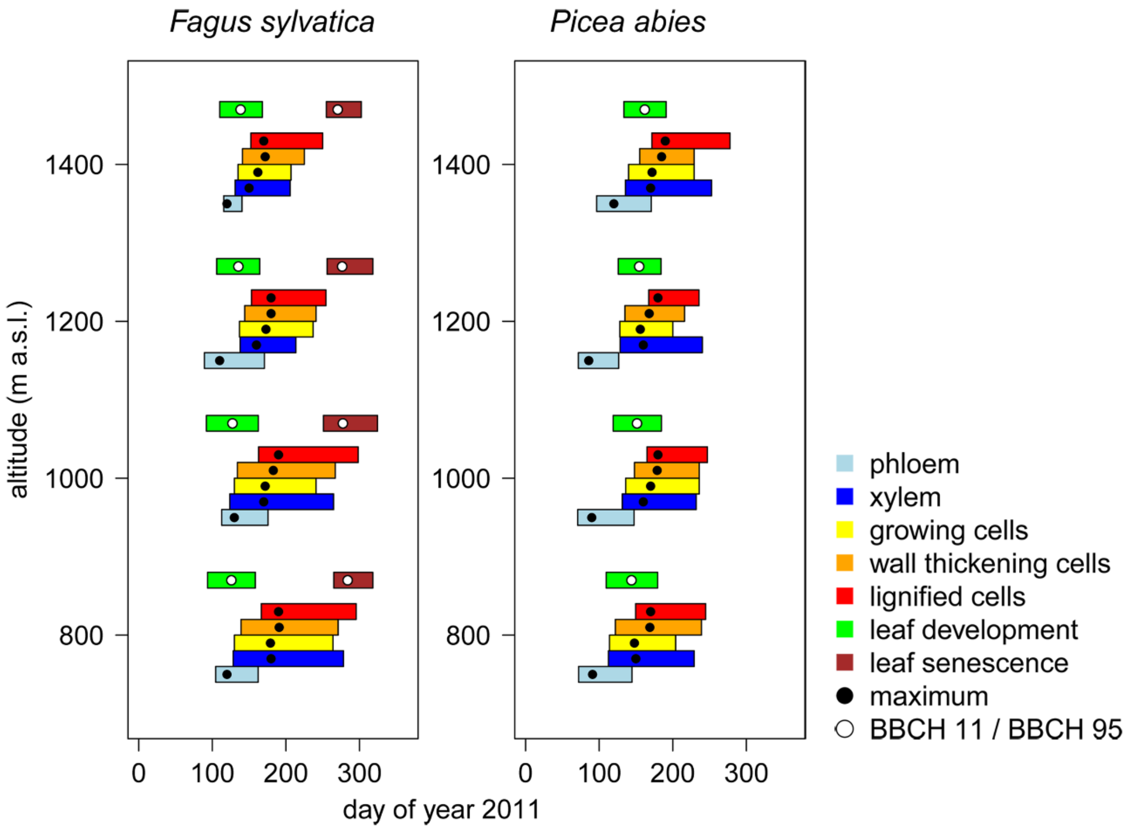

Figure 7.4 Mean phenology and intra-annual tree ring growth according to the different cell categories studied at different elevations (bars ranging from SD to ED, respectively from BBCH 7 to BBCH 17 and from BBCH 93 to BBCH 97). The date of maximum growth (MD, black points) and BBCH 11 (leaf development, white points) and BBCH 95 (leaf senescence, white points) are also indicated.

In contrast, almost all cell categories of spruce showed an approximately constant response to elevation in their SD of about 3-4 days 100 m^{-1}, which was remarkably similar to the elevational response of bud burst (Table 7.2). Equally, ED of total xylem and lignified cells had the same elevational trend. Hence, GP of xylem in spruce of 110 days was approximately constant over transects. ED of growing cells was slightly less dependent on elevation, therefore GP of growing cells decreased with increasing elevation (Table 7.2). Likewise, ED and GP for wall thickening had a negative trend with elevation.

Table 7.2 Response of phenology and intra-annual tree ring growth (different parameters and cell categories) to elevation determined by linear regression of the parameter against elevation with standard error (days 100 m^{-1} for SD, ED, GP and MD; mm 100 m^{-1} for MW and mm day^{-1} 100 m^{-1} for MR); mean with standard deviation (days for SD, ED, GP and MD; mm for MW and mm day^{-1} for MR), significance (p-value), coefficient of determination R^2.

		Fagus sylvatica				*Picea abies*			
	parameter	**slope ± se**	**mean ± sd**	**p**	**R^2**	**slope ± se**	**mean ± sd**	**p**	**R^2**
phloem	**SD**	0.5 ± 3.2	106 ± 12	0.90	0.01	3.7 ± 2.2	78 ± 13	0.23	0.59
	ED	-3.6 ± 3.5	162 ± 16	0.41	0.34	2.9 ± 4.5	147 ± 18	0.59	0.17
	GP	-4.0 ± 5.8	57 ± 24	0.56	0.19	-0.9 ± 2.7	70 ± 10	0.78	0.05
	MR	0.01 ± 0.01	0.09 ± 0.05	0.35	0.43	0.0008 ± 0.0026	0.06 ± 0.01	0.80	0.04
	MD	-1.0 ± 2.1	120 ± 8	0.68	0.10	4.2 ± 3.1	97 ± 16	0.32	0.47
	MW	-0.02 ± 0.01	0.34 ± 0.06	0.15	0.72	-0.023 ± 0.015	0.8 ± 0.1	0.26	0.55
xylem	**SD**	1.1 ± 1.4	130 ± 6	0.52	0.23	3.3 ± 1.5	127 ± 10	0.15	0.72
	ED	-13.0 ± 2.9	241 ± 36	0.044	0.91	4.0 ± 0.8	238 ± 11	0.036	0.93
	GP	-15.0 ± 4.3	110 ± 41	0.078	0.85	0.7 ± 2.1	111 ± 8	0.78	0.05
	MR	0.005 ± 0.002	0.04 ± 0.02	0.097	0.82	-0.0005 ± 0.0005	0.04 ± 0.00	0.44	0.32
	MD	-5.0 ± 0.0	165 ± 13	<0.001	1.00	3.0 ± 0.7	160 ± 8	0.051	0.90
	MW	-0.4 ± 0.1	1.7 ± 1.2	0.075	0.86	-0.36 ± 0.26	2.1 ± 1.3	0.29	0.50
growing cells	**SD**	1.1 ± 0.6	133 ± 4	0.20	0.64	3.5 ± 1.9	130 ± 11	0.21	0.62
	ED	-8.8 ± 1.7	237 ± 23	0.035	0.93	2.0 ± 4.7	217 ± 18	0.72	0.08
	GP	-9.8 ± 1.1	104 ± 26	0.012	0.98	-1.5 ± 3.0	88 ± 12	0.66	0.12
	MD	-2.5 ± 0.8	172 ± 7	0.084	0.84	2.9 ± 2.4	162 ± 11	0.35	0.43
	MW	-0.01 ± 0.01	0.14 ± 0.04	0.11	0.8	-0.03 ± 0.03	0.3 ± 0.1	0.42	0.34
wall thickening cells	**SD**	0.8 ± 1.0	140 ± 4	0.51	0.24	4.3 ± 2.6	140 ± 15	0.24	0.58
	ED	-8.2 ± 1.5	251 ± 22	0.031	0.94	-2.5 ± 2.2	230 ± 10	0.37	0.40
	GP	-9.0 ± 2.4	112 ± 25	0.064	0.88	-6.8 ± 1.9	90 ± 19	0.07	0.86
	MD	-3.0 ± 0.4	182 ± 8	0.014	0.97	1.9 ± 1.8	175 ± 8	0.42	0.34
	MW	-0.03 ± 0.01	0.17 ± 0.08	0.098	0.81	-0.03 ± 0.06	0.5 ± 0.2	0.68	0.11
lignified cells	**SD**	-2.6 ± 0.6	159 ± 7	0.043	0.92	3.4 ± 1.0	163 ± 10	0.08	0.85
	ED	-9.0 ± 3.1	275 ± 26	0.099	0.81	4.4 ± 4.0	251 ± 18	0.38	0.38
	GP	-6.4 ± 2.6	116 ± 19	0.14	0.75	1.0 ± 4.5	88 ± 16	0.85	0.02
	MR	-3.5 ± 0.9	183 ± 10	0.056	0.89	3.0 ± 0.7	180 ± 8	0.051	0.90
	MD	0.002 ± 0.001	0.03 ± 0.01	0.14	0.74	-0.0001 ± 0.0024	0.04 ± 0.01	0.97	0.00
	MW	-0.5 ± 0.1	1.8 ± 1.3	0.062	0.88	-0.36 ± 0.27	2.0 ± 1.4	0.31	0.47

Table 7.2 continued.

		Fagus sylvatica				*Picea abies*			
	parameter	**slope ± se**	**mean ± sd**	**p**	**R^2**	**slope ± se**	**mean ± sd**	**p**	**R^2**
phenology	**BBCH 7**	3.2 ± 1.0	100 ± 9	0.087	0.83	4.0 ± 0.2	122 ± 10	0.0023	1.00
	BBCH 11	2.3 ± 0.4	132 ± 6	0.033	0.94	2.9 ± 0.3	153 ± 7	0.012	0.98
	BBCH 17	1.5 ± 0.1	163 ± 4	0.0072	0.99	1.7 ± 0.5	185 ± 5	0.073	0.86
	BBCH 93	-1.3 ± 1.4	257 ± 6	0.45	0.30				
	BBCH 95	-2.1 ± 0.4	277 ± 6	0.031	0.94				
	BBCH 97	-2.7 ± 1.7	316 ± 9	0.27	0.54				

SD of xylem growth in beech revealed only a small response to elevation, but a distinctive negative response in ED. Consequently, GP of xylem also decreased markedly with elevation (Table 7.2). For both species, MW decreased with elevation, not only for MW of xylem, but for all cell categories (Table 7.2).

MR (maximum growth rate) of xylem in spruce (0.038 ± 0.002 mm day^{-1}) was constant with elevation, as was MD (about five weeks after SD of xylem growth). However, for beech, MR increased with elevation (from 0.031 mm day^{-1} at 800 m and 1000 m a.s.l. to 0.057 mm day^{-1} at 1200 m and 1400 m a.s.l.). MD also varied from about 7 weeks (800 m a.s.l.) to 3 weeks (1400 m a.s.l.) after SD of xylem growth, leading to an advanced MD with elevation.

The sequence and timing between parameters of intra-annual tree ring growth and phenology also differed between the species studied (Figure 7.4). SD of phloem growth in beech occurred approximately concurrently with bud burst (BBCH 7), and SD of xylem growth approximately with leaf unfolding (BBCH 11). SD of wall thickening was about 10 days, and SD of lignification about 29 days, after xylem SD. MR occurred approximately concurrently with the date when leaves were fully unfolded (BBCH 17). ED of xylem growth varied from the end of July (DOY 206) at 1400 m a.s.l. to the beginning of October when leaf coloring had already began (DOY 278) at 800 m a.s.l.
For spruce, as an evergreen species, SD of phloem growth was several weeks before, and SD of xylem growth approximately concurrent, with bud burst (BBCH 7). SD of cell wall thickening was observed 13 days, and SD of lignification 36 days, after xylem SD.
Mean GP was similar for growing, cell wall thickening, lignified and total xylem cells for beech (about 110 days). For spruce, mean xylem GP also was about 110 days, but shorter (about 90 days) for growing, cell wall thickening and lignified cells.

7.5 Discussion

Tree Ring Growth

The Gompertz and Hadwiger functions proved to be suitable to model the annual courses of the different cell parameters studied, except for a few of the wall thickening data. Therefore the reliability of the determined parameters (SD, ED, GP, MR, MD, MW) was high throughout. However, the low number of trees per site could have influenced the results through individual differences, since the period of active cambium depends not only on climate and soil moisture but also on the social position of the tree in the stand (Larson 1994). In contrast to the model fits, the linear regressions of the growth parameters against elevation (Table 7.2) were less significant, especially for spruce where only small effects were found. In particular, the early parameters which were not directly observed (SD phloem) revealed no significant effect of elevation.

It has been known for a long time that tree ring growth is reduced with increasing elevation and latitude (e.g. Burger 1941, Larcher 2001, Kozlowski et al. 1991, Dobbertin & Giuggiola 2006). Here we could show that not only MW of xylem (ring width) but also MW of all cell categories decreased with altitude. Similarly, Gričar and Čufar (2008) reported greater phloem width at a lowland side compared to a higher one.

MW of xylem in spruce decreased with altitude, but was similar at the northern and southern aspects, whereas in beech we found considerable growth reductions on the southern aspect compared to the northern aspect. Contrary to our results, Rossi et al. (2007) reported shorter GP in conifers at northern compared to southern aspects, resulting in smaller tree rings. For beech, the smaller basal area increment at the southern aspect could be caused by less optimal water balance conditions. Beech is known to be significantly limited in tree ring growth by high summer temperatures accompanied by low precipitation (Dittmar et al. 2003, Zang et al. 2011). Although our alpine study area is characterized by high annual precipitation sums, higher insolation and a relatively low soil depth at the southern aspect could have reduced water availability. Jump et al. (2006) suggested that the observed growth decline at the lower distribution margins of European beech caused by droughts could be a widely distributed phenomenon. An additional hampering factor could be reduced nutrient uptake due to the limited soil water availability (Rennenberg et al. 2004).

For spruce our data show an anomaly of unexpectedly low MW at 1000 m a.s.l. This anomaly also reduced the R^2 of the altitudinal rate of MW in Table 7.2. Since there is no indication of large differences in soil water balance at the 1000 m sites compared to other sites that could cause this relative growth suppression of spruce, another factor seems likely. For example, Kirchner et al. (2009) measured high concentrations of organochlorine pesticides in the humus at the Eschenlohe profile of the MONARPOP project, which is only 15 km from Garmisch-Partenkirchen. In general, pesticide concentration in the soil tended to increase with altitude, but at the Eschenlohe profile, a first peak of high concentrations of p,p'-Dichlorodiphenyltrichloroethane (DDT) and dieldrin was observed at 1000 m a.s.l. (Kirchner et al. 2009). Since organochlorine pesticides affect plant health (e.g. Gourounti et al. 2008) it may be possible that equally high concentrations of these chemicals could have caused the unexpected reduction in MW at this elevation.

Cell Differentiation in Norway Spruce

We calculated cambium reactivation and first phloem cells as occurring in mid-March, which was about 7 weeks before xylogenesis and bud burst. Spruce cambium division is more active at the xylem side, and is reported to produce 5-12 times more xylem cells than phloem cells based on cell counts (Gričar & Čufar 2008). Our measurements with about 38 % MW of phloem compared to MW of xylem fit well into this range considering the size difference of phloem and xylem cells. Phloem formation is considered to start before xylem growth (Alfieri & Evert 1968, Oribe et al. 2001, 2003; Antonova & Stasova 2006, Gričar et al. 2006) which corresponds to our results. However, a simultaneous beginning of phloem and xylem growth has also been reported (Gričar & Čufar 2008). Finally, it is apparent from our study that cambium reactivation of spruce, as an evergreen species, does not depend on leaf phenology. The temporal consistency of MR with the beginning of shoot growth, however, implies that the additional photosynthesis products of the new shoots promote secondary stem growth.

If start dates (SD) of all categories respond similarly to elevation (e.g. as found for spruce in our study), this could mean that the differentiation phases in xylogenesis are not independent from each other, a hypothesis also suggested by Rossi et al. (2012). Moreover, our findings imply that the temperature / elevational response of xylogenesis might correspond to that of spring phenology (especially bud burst). We found a slightly reduced GP for growing cells with higher elevation, which explains the reduced MW. However, ED of lignification, and thus of xylem growth, showed the same positive elevational trend as SD of xylem. Uggla et al. (2001) found the formation of the thicker cell wall in spruce latewood to be a result of longer deposition time rather than a higher deposition rate

Other studies reported start dates of cambial activity in spruce much later (mid-May at high elevations above 2000 m a.s.l.; Rossi et al. 2007) than our results indicate (end of March). According to literature, formation of new cells by cambium cell division lasted until the beginning of August (Rossi et al. 2007, Gryc et al. 2012), but the process of enlargement, wall formation and lignification lasted until late in autumn. Rossi et al. (2007) observed the end of tree ring formation in spruce in different years to be between mid-September and mid-October at sites above 2000 m a.s.l., thus about 1-5 weeks later than at our highest site at 1400 m a.s.l. Gričar and Čufar (2008) also reported that cambium division ended at the end of July at a lowland side and mid-August at a sub-alpine site, but xylem formation continued for another 7-9 weeks. A heating experiment in spruce accelerated cell production in the early season, but did not prolong the cambium activity period (Gričar et al. 2007). Moreover, a high cell production in spring by cambial activity resulted in a higher number of developing tracheides (Ford et al. 1978) and therefore led to longer cell maturation in autumn (Gričar et al. 2005). These observations are consistent with our findings that spruce produced numerous cell rows before cell wall thickening and lignification started, that cell differentiation took a long time in autumn, and that the process of cell differentiation in spruce was slower than in beech.

MR of spruce is reported to be in June (Deslauriers et al. 2003, Zang et al. 2011), which matches our dates of MR from the end of May at 800 m a.s.l. to mid-June at 1400 m a.s.l. Gryc et al. (2012) found MR until mid-July. This might be related to the longest period of daylight, i.e. the summer solstice at the end of June which plays an important role in conifers (Rossi et al. 2006b).
GP in the study of Rossi et al. (2007) varied between 100 and 120 days in different years, corresponding well to our mean of 111 ± 8 days for different elevations. This underpins our findings of a later SD and a later ED (including a relatively constant GP) at higher elevations and that cell differentiation phases in spruce are not independent of each other. Another conclusion is that spruce will likely adapt its GP to changing temperatures really slowly (especially compared to beech).

Cell Differentiation in European Beech
Čufar et al. (2008), at their study site at 400 m a.s.l., observed cambial reactivation in mid-April with leaf unfolding and first xylem cells occurring 1 to 2 weeks later. MR was observed at the beginning of June with a rate of 35 µm day^{-1} and cambium activity stopped at the end of July to mid-August, which matches our results at higher elevations. Similar to our results, Michelot et al. (2012) found the beginning of beech growth occurred shortly after bud burst and MR in June when leaves were mature. We can explicitly differentiate phloem and xylem growth: SD of phloem growth corresponds to bud burst (BBCH 7), SD of xylem growth to leaf unfolding (BBCH 11), and MR to young fully unfolded leaves (BBCH 17). Therefore, we could also support the hypothesized timing of phenology and xylogenesis in diffuse-porous species (Priestley & Scott 1936).

Beech showed a strongly reduced xylem GP with elevation and seems to counterbalance this, to a certain degree, by a higher growth rate (MR). However, MR can't fully compensate for the GP effect leading to a final reduction of tree ring width with elevation. This indicates that beech stem growth is highly adaptable to changes in temperatures and may benefit strongly from a prolonged vegetation period. The reduced GP at high elevations could also be interpreted as an adaption to damage by early frost. However, EDs of xylem growth are definitely independent from leaf coloring. The strong decrease of GP can also limit the elevational distribution of beech: Körner (2003) found a distinct reduction in stem growth at the upper tree line which was not linear with decreasing air temperature. He suggested that the conversion of assimilates to structural carbon could be hindered by low temperatures. Dittmar and Elling (1999) reinforced the stronger limitation of tree ring growth at high elevations by thermal and radiation parameters. Since xylem cell differentiation is an energy dissipating process (Oribe et al. 2003), changes in GP could require adapted strategies for usage, storage and allocation of carbon (Moser et al. 2010).

Wood Formation in the Context of Climate Change

One important and previously observed impact of climate change and global warming is the extension of the vegetation period of trees in temperate zones of the northern hemisphere (e.g. Menzel & Fabian 1999, Linderholm 2006). Since the 1990s several studies have reported an increase of secondary stem growth (Pretzsch 1992, Spiecker et al. 1990), which was attributed to higher nitrogen deposition and increasing temperatures (Hasenauer et al. 1999, Dobbertin 2005). Our results for beech and its clear response in GP to elevation, and thus temperature, support those findings. However, we only found a weak elevational response of cambium activity period and no response for the whole xylogenesis process for spruce. Gričar et al. (2007) did not even find a prolonged cambium activity with higher temperatures, only a higher rate of cell production which resulted in wider tree rings. On the other hand, Boulouf Lugo et al. (2012) also found extended xylogenesis duration for Black spruce (*Picea mariana*) based on a 9 year observational study. Dittmar and Elling (1999) showed, in their tree ring study at different elevations, that beech was more sensitive to environmental factors and always showed higher coefficients of determination (R^2) than spruce. Therefore, the authors suggested that wood formation in beech was more strongly controlled by exogenous parameters than in spruce (Dittmar & Elling 1999). This statement is strongly reinforced by the comprehensive results of our study. On the other hand, Geßler et al. (2007) reported that beech competitiveness might be reduced by climate change. Warm and dry summers could lead to a reduced stem growth at lower elevations caused by drought stress, whereas trees at higher elevations could benefit from higher temperatures (Körner & Paulsen 2004, Dobbertin & Giuggiola 2006, Jump et al. 2006, Rossi et al. 2007). Since our study was situated in the upper elevational range of beech distribution, less characterized by summer drought, these contrasting responses could not be observed on our transects.

We conclude that with higher temperatures, beech might be highly adaptive in its secondary stem growth period. Spruce, however, might adapt its growth period only slowly. In the montane forest zone of our study area, beech might therefore gain a competitive advantage compared to spruce. However, our assessment of likely impacts and responses of climate change of Norway spruce and European beech based on elevational transects still remains a preliminary approach. More, and especially more long-term, studies are necessary to verify our conclusions.

7.6 Acknowledgments

Our gratitude is directed to the Bavarian State Ministry of the Environment and Public Health for funding the project “Auswirkungen des Klimawandels in den Alpen - Erfassung mittels Höhengradienten” (KLIMAGRAD) within the “Klimaprogramm Bayern 2020”. The research leading to these results has received funding from the European Research Council under the European Union's Seventh Framework Program (FP7/2007-2013) / ERC grant agreement n° [282250]. With the support of the Technische Universität München – Institute for Advanced Study, funded by the German Excellence Initiative.

8 Further Results in Alpine Phenology

Some additional results, which have not been published so far but are of interest for the thesis, are described below. They should help to enlarge the understanding of relationships between meteorology and phenology illustrated in the publications.

8.1 Comparison with Remote Sensing Phenology

Besides field observations of phenology, a number of studies using satellite remote sensing or near-surface observations by digital cameras have been carried out (Reed et al. 2009, Richardson et al. 2009, Graham et al. 2010, Ide & Oguma 2010, Bater et al. 2011). Remote sensing images mostly have only a coarse spatial resolution (Reed et al. 2009). However, vegetation dynamics can be monitored for larger areas (regional, continental or global) or for various land cover types. The continuous expression of phenological patterns can be captured (Reed et al. 1994, Zhang et al. 2003, Reed et al. 2009, White et al. 2009). Retrieved parameters (among others) are the Normalized Difference Vegetation Index (NDVI), the Fraction of Photosynthetically Active Radiation absorbed by vegetation (FPAR) or the Leaf Area Index (LAI) from remote sensing data, e.g. from the Moderate Resolution Imaging Spectroradiometer (MODIS; Reed et al. 1994, Zhang et al. 2003 Stöckli et al. 2008).

Numerous methods exist to extract phenological onset dates out of recorded satellite and digital camera images (White et al. 2009). These methods are able to identify the annual variability of phenology including the onset, rate and peak of greenness and senescence (Reed et al. 1994). Several studies on satellite images revealed earlier spring green-up of the land surface (Cleland et al. 2007), however, land surface phenology databases have not been satisfactorily validated yet (Reed et al. 2009). Therefore, diagnostic satellite data models can be inaccurate and lack predictive power (Stöckli et al. 2008). For example White et al. (2009) found that used methods to determine average onset dates differed by ±60 days.

The responses of phenological phases determined in our observational field study can be used to interpolate phenological patterns for larger regions. These interpolations can be compared to remote sensing data. A respective study for our research area currently is in preparation in cooperation with Dr. Doris Klein and Carina Kübert (Deutsches Zentrum für Luft- und Raumfahrt e.V.). Deviations between both approaches will be determined and the accuracy of remote sensing onset dates estimated. Moreover, phenological patterns determined by remote sensing eventually could be connected to specific species.

The challenge of validating remote sensing data by field observations is the integration of the large-scale and course-resolution remote sensing data and the small-scale and fine-resolution field observations. Studies comparing different observation methods still are rare (Hufkens et al. 2012). A multi-level validation combining ground observations, dedicated web cameras, and satellite data of different spatial resolution is needed to improve the level of confidence (Reed et al. 2009). Although the coarse spatial resolution and the low validation level, remote sensing determined green-up dates represent important indicators of environmental effects of climate change (Reed et al. 2009).

8.2 Phenology of Generative Phases

Responses in Flowering

The timing of flowering and fruiting of trees determines their reproductive success (Lechowicz 1995). However, studies on generative phases of trees mostly concentrate on first flowering or full flowering onset dates than on flower and fruit development over the whole vegetation period. Moreover, they often handle tree species with usable fruits or trees with spectacular flowering patterns, e.g. apple or cherry trees (e.g. Landsberg 1974, Defila & Clot 2001). Timing of the impressive cherry flower in Japan, which has been recorded since 705 AD at the imperial residence in Kyoto, is one of the most popular long-term flowering data series (Aono & Kazui 2008). Since tree species of mountainous forests mostly neither have spectacular flowers nor fruits interesting for commercial use, phenological studies are rare and mostly focus on leaf phenology. Complicating factors are the difficult observation conditions in the alpine surrounding and the fluctuating amount of flowers and fruits due to mast years. Additionally, according to Chuine et al. (1999), there is no general model that could accurately predict flowering onset dates from environmental data for different tree species. Another estimation of flowering timing and duration is the analysis of pollen amount in the air (Andersen 1991, Chuine et al. 1999, Ziello et al. 2012a,b).

In our study, we included the observation of generative phases (see the BBCH observation scheme, Table 4.4 in Chapter 4.4). However, we were faced with some difficulties which led to incomplete observations. For example observations of *Abies alba* flowers were very rare since flowers on the very top of the large trees often are hardly visible. For *Fagus sylvatica*, there were hardly any flowers in 2010, whereas 2011 was a mast year. For some evergreen species, determination of seed development was difficult since it often requires two or more years for cone ripening. Hence, different phases belonging to different years could be found at one individual.

For the generative phenological phases which hold a sufficient observation dataset, we determined responses on elevation and temperature similar to the leaf development phases in Chapter 5. Phenological response rates (days $°C^{-1}$) were calculated based on observed altitudinal response rates (days 100 m^{-1}) and measured temperature lapse rates (°C 100 m^{-1}, Table 8.1). The timing of flowering and fruit development of the observed trees varied with elevation and temperature. Almost all trees (except *Larix decidua*) advanced in flowering dates with higher temperatures. Hereby, magnitudes and standard errors were highly variable.

The missing altitudinal response in *L. decidua* flowering can be explained because this species is only distributed over few elevation levels close to tree line. Determined phenological responses of generative phases appeared to have no connection to the leaf development response rates. This also was observed by Lechowicz (1995), who only found weakly coupled foliar and reproductive phenology in deciduous trees of the temperate zone.

Table 8.1 Altitudinal response rate (arr, days 100 m^{-1}) with standard error, R^2, flowering month, calculated phenological response rate (prr, days °C^{-1}) based on temperature lapse rate (tlr, °C 100 m^{-1}) in the respective month for generative phases (BBCH 61-89).

species	BBCH	2010/11 arr ± SE	R^2	month	tlr	prr
Acer pseudoplatanus	61	3.0 ± 1.0	0.53	April	-0.45	-6.7
	65	4.0 ± 1.0	0.69	April	-0.45	-8.9
	69	2.0 ± 0.8	0.39	July	-0.44	-4.5
	71	1.0 ± 0.9	0.25	July	-0.44	-2.3
	79	0.9 ± 3.0	0.02	July	-0.44	-2.0
	81	1.0 ± 1.0	0.10	July	-0.44	-2.3
	89	2.0 ± 1.0	0.37	October	-0.17	-11.8
Fagus sylvatica	65	3.0 ± 0.3	0.95	April	-0.45	-6.7
	69	4.0 ± 2.0	0.47	April	-0.45	-8.9
	71	3.0 ± 0.8	0.78	April	-0.45	-6.7
	79	0.4 ± 0.2	0.39	October	-0.17	-2.4
Larix decidua	65	-0.6 ± 0.0	1.00	April	-0.45	1.3
	69	-0.2 ± 0.4	0.15	July	-0.44	0.5
	71	3.0 ± 0.7	0.95	July	-0.44	-6.8
Picea abies	61	0.4 ± 0.3	0.21	April	-0.45	-0.9
	65	2.0 ± 0.1	0.98	April	-0.45	-4.4
	69	3.0 ± 0.3	0.92	April	-0.45	-6.7
	71	3.0 ± 1.0	0.64	July	-0.44	-6.8
	79	0.1 ± 0.1	0.39	October	-0.17	-0.6
Pinus mugo	61	4.0 ± 1.0	0.77	April	-0.45	-8.9
	65	5.0 ± 0.8	0.90	July	-0.44	-11.4
	69	3.0 ± 1.0	0.57	July	-0.44	-6.8
	71	0.3 ± 1.0	0.02	July	-0.44	-0.7
Pinus sylvestris	61	0.6 ± 2.0	0.04	April	-0.45	-1.3
	65	2.0 ± 0.7	0.59	April	-0.45	-4.4
	69	0.5 ± 1.0	0.06	July	-0.44	-1.1
	71	4.0 ± 3.0	0.48	July	-0.44	-9.1

Earlier tree flowering due to warmer temperatures was determined based on long-term time series across Europe, whereas wind-pollinated trees mostly advanced (Sparks et al. 2000, Ziello et al 2012b). The pollen period was also extended and atmospheric pollen amount was increased (Ziello et al. 2012a), which primarily was caused by higher CO_2 concentrations. Flowering in timing and number was also affected by CO_2. Hence, global climate change may disrupt patterns of foliar and reproductive phenology, but the magnitude of these effects will depend on the balance of influencing parameters for respective phenological events (Lechowicz 1995). Moreover, shifts in flowering onset dates could result in plant-pollinator interaction problems (Erhardt & Rusterholz 1997, Rusterholz & Erhardt 1998, Hodkinson & Bird 1998).

Further research is needed e.g. on the parameters involved in tree flowering, on predicting models, and on different responses between species or between male and female flowers. Since it is a matter of human health, especially flowering of species with allergenic pollen are of special interest - even (or in particular) in alpine regions, which are still regarded as recreation areas for people suffering from pollen allergy.

Altitudinal Trends in Beech Seeds' Quantity and Quality

The year 2011 was a mast year for *Fagus sylvatica*. According to Piovesan & Adams (2001), masting in *F. sylvatica* is triggered by climate events in the preceding growing season. They suggest that a moist summer combined with a drought event in the next summer triggers intensified flowering and seed production in the following year. Matthews (1955) found significant correlations between the mast size and previous summer air temperature and sunshine.

We took advantage of the 2011 mast year for seed collections along our observation transects. On the basis of 20 seeds collected from each *F. sylvatica* tree in the phenological observation program on the 20th of October, the variation with elevation of the seed weight and the percentage of hollow seeds was estimated by linear regression (Figure 8.1). The seed weight decreased with elevation by 18.3 ± 0.03 g 100 m^{-1}. The percentage of hollow seeds decreased slightly but not significantly from about 9 % at 800 m a.s.l. to 6 % at 1500 m a.s.l. The time necessary to collect the 20 seeds was stopped and increased by 1.8 ± 0.6 s 100 m^{-1} (R^2: 0.13, not shown). This can serve as a relative estimation of the amount of seeds produced by the trees. Therefore, with increasing elevation the amount of seeds slightly decreased, but was high throughout.

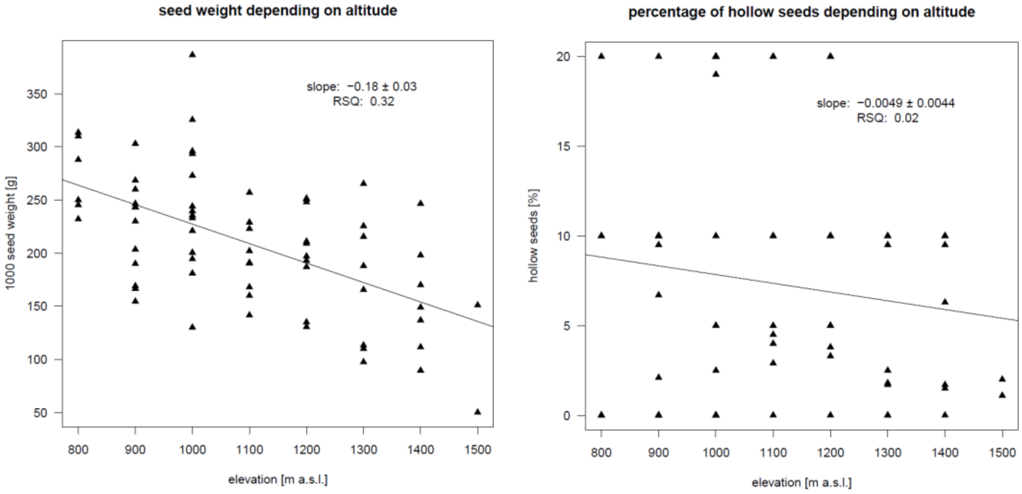

Figure 8.1 Trends in seed weight and percentage of hollow seeds with elevation.

Vitasse et al. (2009c) found the same trend in seed weight for *Quercus petraea* (MATT.) LIEBL with seeds from high elevations being lighter than seeds from low elevations. A consequent conclusion is that temperature change along transects influences the seed weight. Moderate warming is reported to favor some alpine species in seed production and seed size (Wagner & Reichenegger 1997, Erschbamer 1999). Seed size in turn positively affected initial seedling height and leaf longevity of deciduous tree species (Seiwa & Kikuzawa 1991).

To determine the effects of elevation and seed size on phenology and biomass of young seedlings, another more extensive seed collection was done along the gradients on the 4th of October 2011. These seeds were competently stored over winter in the ASP (Bayerisches Amt für forstliche Saat- und Pflanzenzucht) and sown in a greenhouse experiment in spring 2012. Data of phenology observations over the whole vegetation period and finally biomass / leaf area determinations were collected and analysed by our colleague Renée Capdevielle-Vargas. She currently prepares a respective publication (see Publication List), also including seedling samples from the field observation sites.

The success of in-situ seedlings, however, depends on several factors and mostly is lower than for seeds under controlled greenhouse conditions. Besides frost risks, lack in soil nutrients or soil moisture, herbivory reduces plant dispersal potential (e.g. by *Cervus elaphus* L., *Capreolus capreolus* L. in the Alps (Motta 1996, Ammer 1996). Species success moreover is limited by a lack of chilling temperature inhibiting leaf unfolding and flowering under warm and the inability of full seed maturation under cold conditions. Thus, flowering and fruit phenology is a key adaptive trait in shaping species distribution (Chuine 2010). Biodiversity is increasing success and performance of tree seedlings (Manzanedo et al. 2013), therefore species with higher genetic variability are considered to be more adaptable. The importance of flowering and fruit phenology for species distribution and adabtability under climate change conditions could be of high interest in future research.

8.3 Phenological Differences in Associated Classes

Phenological observations in our study were done for three adult and three juvenile trees per site. Observations of adult trees were additionally separated in upper and lower part of the crown. The study design included four gradients with two northern and two southern aspects. We expected distinct differences between classes belonging together (juvenile-adult trees, upper-lower crown, northern-southern aspect). For *P. mugo* as a shrub tree, only northern and southern aspect phenology was considered. Since *P. sylvestris* only was distributed at the Kramer transect there was no comparison of aspects.

Juvenile and Adult Trees

We expected differences between juvenile and adult tree phenology, since phenological avoidance of canopy shading might be an option for juvenile trees to gain carbon (Uemura 1994). This would be achieved by earlier bud burst and later leaf senescence of seedlings and juvenile trees compared to canopy trees (Augspurger & Bartlett 2003). Combined with higher photosynthetic capacity (Bond 2000, Thomas & Winner 2002), larger and thinner leaves and a self-shading avoiding canopy architecture (Gerrish 1994, Kikuzawa et al. 1996) juvenile trees can maximize light acquisition in shaded understories (Gill et al. 1998, Seiwa 1998). However, magnitudes and generalizability of phenological differences between life stages are not well known (Augspurger & Bartlett 2003, Vitasse 2013).

For *A. alba*, *P. abies* and *P. sylvestris*, juvenile trees started bud swelling and bud bust slightly later than adult trees and finished leaf expansion earlier (Figure 8.2). Latter one also was true for *L. decidua*, but juvenile trees started slightly earlier than mature ones. For the deciduous species, no consistent results could be found. Here, year-to-year variations in spring weather conditions could have highly influenced phenology and thus, two years of observations were not sufficient for accurate statements. In comparison, earlier bud burst in juvenile *F. sylvatica* was determined by Estrella et al. (2013). Augspurger & Bartlett (2003) found ealier bud burst of juvenile trees in the majority of 13 studied species. They suggest that the vertical gradient of temperature is explaining this pattern, since temperature sums accumulate in the sheltered undestory. However, they observed later leaf senescence only for the minority of species. Leaf period therefore was longer for young trees of most species, but also the same or shorter leaf period was determined for some species (Augspurger & Bartlett 2003). Juvenile trees either advanced spring phases or delayed autumn phases or did both, dependend on the species (Augspurger & Bartlett 2003, Seiwa 1999).

Vitasse (2013) additionally concluded that advanced spring phases in forests understory rather are related to ontogenetic developments than to temperature. Juvenile trees might moreover have smaller chilling requirements or a less dependency on photoperiod than mature trees (Hänninen et al. 2007, Vitasse 2013). Hence, we could not determine a generalizable trend in phenological patterns between life stages. We conclude that phenological differences in life stages are explicitly species-specific and dependent on more environmental factors and weather patterns than the vertical temperature gradient within forests.

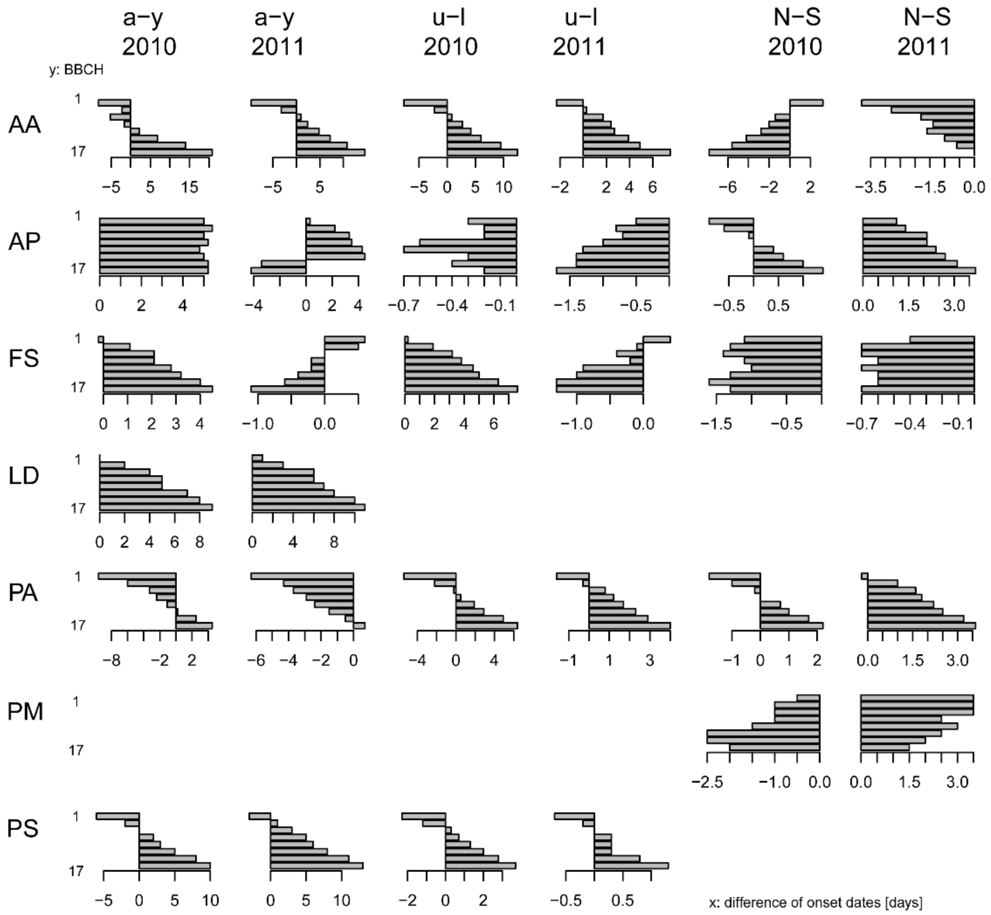

Figure 8.2 Differences of day-of-year onset dates (a-y: adult minus juvenile tree, u-l: upper minus lower part of the crown and n-s: north minus south aspect) for the two observation years.

Upper and Lower Part of the Crown

Studies about differences between upper and lower crown are rare and mostly focus on leaf area or leaf nutrient concentration instead of phenological onset dates. For conifers, foliage formed in low light (e.g. in the lower crown) had a lower net photosynthetic rate, a higher specific leaf area (SLA) and low leaf nitrogen concentration compared to foliage developed under full light conditions (Shelton & Switzer 1984, Cregg et al. 1993, Stenberg et al. 1998, Jose et al. 2003, McGarvey et al. 2004). Similar to juvenile trees, leaves in the lower crown could avoid shading by earlier leaf-out, supported by warmer temperatures in the sheltered lower canopy (Augspurger & Bartlett 2003). However, light conditions are an additional important factor triggering bud phenology and even might be a better predictor than chilling and forcing temperatures (especially in boreal trees; Häkkinen et al. 1998). Hence, buds in the upper part could break earlier because of a higher acquired amount of light.

In our study, we found a similar picture in the results for upper and lower crown as for the comparison of juvenile and adult trees (Figure 8.2). For the evergreen species, leaf development in the upper part of the crown started earlier than in the lower part. But this was compensated with time and the upper part finished later in leaf development than the lower one. Again, for deciduous trees there were no regular or even opposite trends in the two years.

It is not easy to differentiate between interacting factors influencing budburst. Light conditions might promote early bud burst in the upper crown; warmer temperature sums in the sub-canopy might promote early bud burst in the lower crown. We conclude that for deciduous species, both factors might highly interact causing the irregular patterns within and between years. The homogenous pattern of earlier bud burst in the upper crown for evergreen species, however, implies that for them light conditions might have a higher influence.

Northern and Southern Aspect

Different exposition leads to variances in radiation and temperature budget (Rutishauser & Jeanneret 2009) and therefore changes phenological conditions (Defila & Clot 2005, Ziello et al. 2009). Leaf unfolding and flowering is advanced on sunny (southern) and delayed on shaded (northern) slopes (Gensler 1946, Chen 1994, Jochner et al. 2012b). Additionally, surface and soil temperatures can have noticeable effect on phenology (Scherrer et al. 2011).

Leaf development at our northern and southern aspects was very different between species (Figure 8.2). *A. alba* showed opposite behavior in 2010 and 2011. For *A. pseudoplatanus*, the difference between aspects increased with later phenological phases, which means that at southern slopes, the development was finished faster. However, beginning of leaf development not necessarily was earlier at southern slopes. The same pattern was found for *P. abies*. However, *F. sylvatica* started and finished leaf development earlier at southern aspects with some variations, but showed no trend between the phases. The development of *P. mugo* phenology surprisingly was faster at northern slopes, but onset timing also showed different trends in the two years: Once the trees at northern aspects started first and once those on southern aspects.

The general assumption of earlier phenological onset dates at southern slopes in our observations was only appropriate for *F. sylvatica*. For the other species, the influence of aspect on the phenological onset dates appeared to be superimposed by other environmental factors. For example, micro-topographical characteristics have a high influence (Scherrer et al. 2011, Jochner et al. 2012b). Temperature variance within slopes can be similar or even higher than between slopes, whereas within-slope variations are independent from macro-exposure (Scherrer & Körner 2010, Scherrer et al. 2011). However, this should rather influence herbaceous species than trees (Defila 2007). Another factor is phenotypic plasticity, which enables large shifts in phenology onset dates within one single generation (Vitasse et al. 2010).

Summarizing, the inhomogeneous results imply that two years of observation were not sufficient for clear statements. We can only conclude that phenological differences between the classes clearly differed among species and no general trend could be observed. Meteorological conditions varying from year to year, the course of temperature within the year and the microclimate of sites probably caused different relations between the compared classes, in particular for deciduous species. This finding matches our conclusions of our tree-ring study (Chapter 7), that deciduous trees responded more opportunistic and highly variable to temperature, whereas evergreen species appeared to be more inflexible.

9 General Discussion

9.1 Methodology

Natural Gradients

In the General Introduction (Chapter 2.4) we described the suitability of spatial gradients as "space-for-time warming experiments" following Körner (2003). Since temperature is one of the most important variables changing along natural gradients and influencing phenology (Hickin & Vittum 1976, Castonguay et al. 1984, Hunter & Lechowicz 1992, Larcher 2003, Estrella & Menzel 2006, Körner 2007, Migliavacca et al. 2008, Caffarra & Donnelly 2011), altitudinal gradients are suitable for the estimation of plant phenological responses to temperature. The dependence of phenology and temperature on elevation induces a direct connection between temporal trends of both parameters (Larcher 2006, Menzel et al. 2006) - a feature we utilised in our study.

Along altitudinal gradients temperature decrease is linear with increasing elevation (-0.54 to -0.58 °C 100 m^{-1}, Rolland 2003). Similarly, dependency of phenology on elevation is reported to be linear, even for different phenophases and restricted Alpine regions (Studer et al. 2005, Dittmar & Elling 2006, Larcher 2006, Ziello et al. 2009). These circumstances have been utilized in this study to identify phenological response rates to temperature by combining linear temperature lapse rates and linear phenological response rates to elevation. However, Pope et al. (2013) and Jochner et al. (2013) stated that phenological response to temperature was linear with elevation but became non-linear with changing temperature in time and in very warm or cold environments. Thus, it is still to be proven if phenological responses to long-term climate change are the same or at least comparable to responses determined on changing climate conditions over space. Only then is a space-for-time substitution reasonable (Dunne et al. 2004).

It must be noted that temperature is not the only factor changing with elevation which influences phenology. With increasing elevation land area is reduced, total atmospheric pressure decreases and solar radiation (in particular the percentage of UV-B) increases (Körner 2007, Barry 2008). Hence, temperature is not always sufficient to explain the variability in the timing of plant phenology (Cornelius et al. 2012). As was assessed and discussed earlier in this thesis, there is additionally a high dependency of some species on photoperiod (Heide 1993, Migliavacca et al. 2008, Vitasse et al. 2011) and winter chilling (e.g. Schaber & Badeck 2003, Caffarra & Donnelly 2011). However, photoperiod rarely varies in a small regional study along altitudinal gradients and might play a more important role in latitudinal gradient studies (Fracheboud et al. 2009).

Some authors also suggested that winter chilling can also be neglected in alpine regions since it is easily fulfilled (e.g. Chuine et al. 1999, Van Wijk et al. 2003). More likely, snowmelt is influencing phenological development in alpine and arctic ecosystems, especially of herbs and shrubs (e.g. Galen & Stanton 1995, Pop et al. 2000, Dunne et al. 2003, Aerts et al. 2006, Inouye 2008). Cornelius et al. (2012) suggested snow cover duration to be an important factor explaining differences between herbs and trees in their sensitivity to elevation. Additionally, altitudinal responses of phenophases were greater in northern than in southern parts of the Alps (Larcher 2006, Ziello et al. 2009). Thus, geographical location of the gradients can modify altitudinal trends. Actual studies highlight the importance of other parameters triggering leaf phenology such as nutrients, which were less discussed so far. As was shown by Jochner et al. (2013), higher foliar concentrations of potassium, boron, zinc, and calcium significantly correlated to earlier onset dates.

Alternatives to observational field studies along altitudinal gradients are manipulative field studies and laboratory experiments. All methods are useful to assess plant responses to climate change, but all have their advantages and disadvantages. Field observations and field experiments mostly cover only small areas (Shaver et al. 2000), and climate factors cannot be controlled. In most studies, recorded responses cannot clearly be attributed to one ecological condition without also considering the influences of other non-observed or unknown factors.

In laboratory experiments environmental conditions can be controlled and can be applied with different levels of treatment (Dunne et al. 2004, Wolkovich et al. 2012). When historical observations are missing or offer no comparison opportunity, responses to climate change conditions can be simulated in a short time. However, warming experiments are shown to underpredict advances in the timing of flowering and leafing compared to observational studies (Wolkovich et al. 2012).

Field studies often require expensive equipment, high running costs and considerable efforts by the researchers (e.g. the newly installed meteorological station/ logger network and 3000 meters in elevation to walk weekly in our field work). Therefore, they mostly are executed only over a relatively short period of time (Dunne et al. 2004, Leuzinger et al. 2011). However, trends in short-term studies can disappear or flatten if a longer time scale is considered (Leuzinger et al. 2011). Short-term studies reflect plastic responses to changing environment conditions, but often only show parts of the potential dynamic of an ecosystem (Shaver et al. 2000, Dunne et al. 2004). On the other hand, long-term studies are able to demonstrate genotypic or community composition changes. In general, plant responses to natural gradients are considered to correspond to long-term dynamics, whereas manipulative experiments show short-term reactions (Dunne et al. 2004). However, Cornelius et al. (2013) found similar plant responses to temperature in both experimental and natural gradient studies.

Summarizing, spatial (in particular altitudinal) gradient studies are among the most powerful “natural experiments” for assessing plant ecological responses to temperature (Körner 2007). Thus, we consider the determined phenological response rates of this study as reliable approximations to real temporal change rates we have to expect in the future.

Phenological Observations

The BBCH Code used in this work was primarily developed for agricultural plant science, but in recent times also has found use in ecosystem studies. The advantage of the BBCH scale is the standardized definition of plant development phases which allows direct comprehension and comparability of phenological phases (e.g. phase “7” always is bud burst). However, only a few studies have investigated the whole life cycle of wild species based on the BBCH Code. Not all phases which were defined for agricultural crop plants are applicable to all wildlife species. Thus, there is an inevitable need to select a subset of existing BBCH phases which are suitable for observation. Therefore, we developed observation keys for the species observed in our study.

The standardized description of the phases is in contrast to the lack of a standardized observation method and a common method for calculating onset dates from BBCH recordings. Cornelius et al. (2011) described and compared four different methods to determine phenological onset dates from BBCH datasets (Weighted Plant Development, Pooled Stage Development, Cumulative Stage Development and Ordinal Logistic Regression). Which method to use is dependent on the structure and quality of the dataset, e.g. a frequency distribution of observed BBCH phases is sometimes required, which in turn requires more recording time.

Since in our study we had a high number of observation sites over a wide range of elevation, we chose an easy and quick observation method by always noting the most forward development stage of an individual. We chose the relatively easy determination of onset dates from logistic regressions on the observation data, since in that way gaps in the dataset could be filled.

Data gaps resulted from the great effort needed for observation in this alpine area (we only were able to visit the sites once a week). Moreover, during field observation we were faced with some problems, in particular the harsh climatic conditions in alpine regions. Extreme weather events such as storm, heavy rain or snowfall during the study period led to gaps in the observation dataset, which we could largely compensate. Light conditions or rain could have affected the estimation of phenological phases, especially in autumn leaf coloration. However, Cornelius et al. (2011) showed that onset dates estimated from data of lower sampling frequency only slightly diverged from data collected at higher sampling frequency. This means, for remote areas such as our alpine study area, that BBCH recordings at an interval of one week appear feasible to determine accurate onset dates.

Although several studies have determined temperature as the main trigger of tree phenology and stem growth (e.g. Chmielewski & Rötzer 2001, Fitter & Fitter 2002, Sparks & Menzel 2002, Menzel 2005, Menzel et al. 2006, Estrella & Menzel 2006, Delpierre et al. 2009, Vitasse et al. 2011, Archetti et al. 2013), we have to keep in mind other environmental factors influencing tree phenology (light, water availability, CO_2, nutrients…). Moreover, the number of individual plants included in a study influences the quality of results since the impact of outliers can be reduced using higher individual numbers. We chose six individuals per site and species in this study (resulting in 571 individuals) which was a compromise between number of individuals per site and the need to keep the observations manageable at a weekly interval at the 42 observation sites.

Observation quality of this thesis was ensured since all the field work was done by the same person (the author). Good coefficients of determination throughout the phenological results (R^2 mostly ≥ 0.8, see e.g. Chapter 5) confirm the reliability of our observation datasets and used statistical methods.

Microsampling

The focus on intra-annual tree ring formation at the cellular level using the microsampling method is a relatively new development in dendroecological research (Rossi et al. 2007, Deslauriers et al. 2008, Gričar et al. 2008, Gryc et al. 2012). With time, different methods in sampling and thin cutting preparations were tried and used in different studies. Which method to use for microcore sampling or preparation (e.g. for cutting or staining) depends on several factors such as site characteristics, tree species, wood characteristics and measured tree-ring parameters (see also Fritts 1976, Schweingruber 1996).

Since comparative studies are rare (Moser et al. 2010), in particular for the species studied here, our sampling and sample preparation methods (described in Chapter 7.3) were carried out based on existing methods and our field and laboratory experience to obtain high quality results. However, similar to our phenological study, we had to face some problems occurring in field and laboratory work. Some samples were lost or broke during the preparation process or only resulted in average-quality cuttings, which complicated the exact determination of measured parameters. Since, in the tree-ring study, only two individuals per site and species were included, individual variance could have highly influenced the results. Like for the phenological observations, we had to find a balance between the sampling size (in terms of individuals included) and the considerable effort.

Since sampling started beginning of May, phloem development in *P. abies* at the lower sites already begun. Therefore, our results for phloem onset dates can only be considered as approximations influenced by the model fitted on the data. However, we achieved good results, especially for xylem growth and xylem differentiation phases. Determined onset dates of the stem growth onset dates of our study are an excellent database, in particular in combination with our extensive phenological observations and temperature measurements on the sites.

9.2 Key Findings

This thesis has intensively focused on a critical part in the interaction between climate and vegetation. There are numerous studies on climate change impacts in the Alps, including investigations on the effects of elevation on phenological phases and their temporal trends in different zones of the alpine region (e.g. Defila & Clot 2001, Studer et al. 2005, Dittmar & Elling 2006, Larcher 2006, Vitasse 2011, Jochner et al. 2012a, Cornelius et al. 2013). Although the Alps probably are the most studied mountainous area in the world, there is still much uncertainty on future changes and their biological and economic consequences (Theurillat & Guisan 2001).

Referring to our initial research aims specified in Chapter 3.2, in the following the most important key findings of this thesis are summarized and discussed. They are compared to other studies and their relevance to climate change impacts in forest ecosystems is evaluated.

Alpine Forest Phenology

The first central question of the thesis was:

- **What is the magnitude of tree phenological response to a wide range of elevation and thus temperature regimes?**

We could determine species-specific and phase-specific response rates to elevation and temperature of the seven observed alpine tree species. The magnitude of phenological responses varied greatly between species, indicating differences in their sensitivity and reaction to temperature changes. However, all species showed a homogenous trend: Phenological spring events were advanced and autumn events (for deciduous trees) were delayed with increasing temperature. Trends and magnitudes of determined response rates fit to rates reported in the literature (e.g. Schnelle 1955, König & Mayer 1988, Menzel 1997, Vitasse et al. 2009b, Davi et al. 2011, Pellerin et al. 2012). Comparing the species, we identified *A. pseudoplatanus*, *L. decidua* and *P. abies* response rates as highest (8.4-9.4 days °C^{-1} for bud burst), surprisingly closely followed by *F. sylvatica* (7.9 days °C^{-1}). *A. alba* and the two *Pinus* species had smaller rates of 4.1-5.9 days °C^{-1}.

Other studies reported shifts of spring events by 1 to 4 days 100 m^{-1} (Schnelle 1955, König & Mayer 1988, Menzel 1997, Cornelius et al. 2012, Pellerin et al. 2012), which matches the findings of Vitasse et al. (1.9 to 6.6 days °C^{-1}; 2009b) converted by an average lapse rate of 0.6 °C 100 m^{-1}. Using the same lapse rate conversion, Davi et al. (2011) determined responses between 4.6 and 7.3 days °C^{-1} for leaf unfolding of *A. alba* and *Pinus* species. In our study, *F. sylvatica*, which is reported to be less sensitive to temperature (Vitasse et al. 2009a, Čufar 2012), showed relatively high responses in spring onset dates to temperature. However, the high response rates of *A. pseudoplatanus*, *L. decidua* and *F. sylvatica* can be explained since these are the species forming new leaves every year. Thus, they have to react opportunistic to temperature. Likewise, the lower rates in the *Pinus* species and *A. alba* are understandable since as evergreen species they have no need to take every opportunity of warm temperatures. Thus, in two aspects our findings do not match the mainstream: the high response of *F. sylvatica* as a climax species and the high response of *P. abies* compared to the other evergreen species.

In autumn, responses of leaf coloring to temperature were stronger for *F. sylvatica* (3.7 days °C^{-1}) than for *A. pseudoplatanus* (0.7 days °C^{-1}, not significant). Response of leaf fall was high for both species (8.0 and 7.7 days °C^{-1} respectively). For comparison, Vitasse et al. (2009b) found delayed senescence of 0.0 to 5.6 days °C^{-1} for deciduous trees. These values match our rates of peak of autumn leaf coloration. It is obvious that temperature responses in autumn highly vary between species, single years and phenological phases, which makes it difficult to compare magnitudes of responses between studies.

In the course of the vegetation period, we were able to determine responses from a large set of phenological phases (from bud burst to end of leaf fall) and to quantify differences between them. As expected, response rates differed between phenological phases but showed a homogenous pattern: Spring response rates decreased and autumn response rates increased again with later phases. Thus, the dependency on temperature was high for early spring and late autumn phases and was consistently lower for phenological phases occurring in the middle of the vegetation period (see also Estrella et al. 2009). We suppose that the more explicit altitudinal temperature gradients in spring and autumn caused the more explicit phenological gradients. Moreover, after bud burst later in the year in high elevations, temperature sums increased faster and thus could have accelerated phenological development. Thus, phenological differences in altitudes were less distinct in summer. The finding that elevation and temperature sensitivity strongly depends on the observed phase emphasizes the need of clearly defined phenological phases for better comparability between studies.

Similar to the onset of leaf unfolding, the onset of flowering of most species in our study (except of *L. decidua*) also was advanced by higher temperatures. This trend induced by climate change has been observed for trees across Europe (e.g. Chmielewski & Rötzer 2001, Cayan et al. 2001, Parmesan 2006). Moreover, an increase in atmospheric pollen amount and an extended pollen period is reported (Spieksma et al. 1995, Frei & Gassner 1998, Rasmussen 2002, Teranishi et al. 2000, Ziska et al. 2003, Jochner et al. 2011, Ziello et al. 2012a), which could make people suffer from longer allergenic pollen release – even in the Alps which were considered as climatic health resorts.

Between species groups (montane deciduous, montane evergreen and high elevation species), onset dates were similar between montane evergreen and high elevation species and about four weeks earlier for montane deciduous species. Response rates for montane deciduous and high elevation species were large for bud burst, but varied from bud burst to end of leaf unfolding. In contrast, rates for montane evergreen species were smaller and remained relatively unchanged during leaf development. We explain these findings with the need of montane deciduous and high elevation species to be more opportunistic and more flexible in reacting to temperature since they are forced to adapt their leaf development to given environmental conditions.

As a consequence of shifted spring and autumn onset dates, the vegetation period of observed tree species was lengthened by higher temperatures. This trend of an extended vegetation period with ongoing global warming has been reported in several studies (e.g. Schnelle 1955, König & Mayer 1988, Menzel 1997, Menzel & Fabian 1999, Dittmar & Elling 2006, Estrella & Menzel 2006, Vitasse et al. 2009b, Röthlisberger 2010, Davi et al. 2011, Pellerin et al. 2012). Based on the deciduous species included in our elevational transect research (*A. pseudoplatanus* and *F. sylvatica*), we calculated a lengthening of the vegetation period by about two weeks (13.7 days) per degree warming. This magnitude initially appears to be very high, but only slightly differed between the two approaches used in our study (lapse rate and temperature sum method). However, the extraordinary warm autumn 2011 could have influenced the dimension of this value.

For comparison, Menzel & Fabian (1999) found an extention of the vegetation period by 10.8 days since the 1960s analyzing long-term observations of the International Phenological Gardens. In the same period, mean annual temperature of the northern hemisphere increased by 0.5-0.6 °C (Houghton et al. 1992). Combining both values, an even higher extension of the vegetation period per degree can be estimated. Values similar to our increase of 13.7 days$°C^{-1}$ were reported by Myneni et al. (1997, 12 days for northern latitudes) and Defila & Clot (2005, 13.3 days within 50 years in Switzerland). Montgomery et al. (2012) determined a lengthening of the vegetation period by 10-20 days under experimental warming of +1.8 to +3.6 °C. Hence, even regarding the influence of the warm autumn 2011, our resulting extension of the vegetation period in the Alps of about two weeks per degree warming is in the range of already reported temperature responses.

Regarding the contribution of advanced spring and delayed autumn phases in lengthening the vegetation period, Davi et al. (2006) reported a 55 % contribution of spring and 45 % contribution of autumn onset date shifts, which fits almost perfectly to the advanced bud burst and delayed leaf fall dates we found for our deciduous species. In detail, we sometimes found the same or even a stronger influence of delayed autumn phases, which we explain by the strong influence of highly increased temperatures in autumn 2011 (+ 3 °C), whereas spring temperatures only were <1 °C warmer compared to the year before. Based on this finding, we conclude that the season which experiences higher warming will mainly influence the lengthening of the vegetation period.

An altitudinal temperature lapse rate of about -0.54 to -0.58 °C 100 m^{-1} (Rolland 2003) and a warming of one degree would be expected to result in an upward shift of phenological patterns by about 200 m. The lengthening of the vegetation period in high elevations could increase the damage by late spring frosts. However, reduced chilling in winter due to warmer temperatures and shorter photoperiod earlier in the year could counterbalance the advance of spring events (Heide 2003, Migliavacca et al. 2008) and therefore prevent, to some extent, late frost risks.

The two deciduous species (*A. pseudoplatanus* and *F. sylvatica*) in our study had high correlations between chilling days and forcing temperature, which means that shorter chilling would highly increase required temperature sums for bud burst (see also Heide 2003). The relationship between chilling and forcing was less distinct and highly variable for the evergreen species. These findings are understandable since in our study deciduous species on average started bud burst about four weeks earlier than the evergreen species and thus are faced with colder temperatures. So, we suggest that the restricted advance of bud burst by not fulfilled chilling might be more important for the deciduous species, e.g. for preventing late frost damage. Moreover, day length is considered to be another important parameter counterbalancing spring advance (Heide 2003) and also might be more relevant for early leafing-out deciduous trees. As a consequence, the four week gap between average deciduous and evergreen bud burst onset dates might be shortened.

Summarizing, all observed tree species responded explicitly to elevation and temperature in their phenological phases. Different magnitudes in response rates, however, lead to species-specific changes. On average, considering climatic parameters, a lengthening of the vegetation period by approximately two weeks and an upward shift of phenological patterns by 200 m per degree can be expected. However, restrictions of these trends (e.g. by chilling requirements and photoperiod) must be considered.

Phenological Response to Inversion Conditions

Since inversions are common meteorological phenomena in mountainous regions such as our study area and occurred extraordinarily frequently in autumn 2011, the second question this thesis focused on was:

- **Do inversion situations in alpine areas influence leaf senescence phenology?**

In our study, we could describe for the first time in detail that, and how, inversions on altitudinal gradients influence tree leaf senescence phenology in autumn. We detected a pattern of advanced autumn phases from the valley floor up to 1000-1100 m a.s.l., where the top of inversions layers most frequently occurs. Thus, we linked the observed phenological pattern to inversions since the trees in the valleys were faced with colder temperatures compared to the trees at mid elevations.

The observed effect was highly dependent on when and how often inversions occurred. With accumulated exposure to cold air, the course of leaf senescence was cumulatively influenced. Hence, the signal was more pronounced in later phenological phases such as leaf fall. *A. pseudoplatanus* responded earlier and stronger than *F. sylvatica*, which suggests differences in their sensitivity to cold temperatures. Since *F. sylvatica* onset dates in the valley advanced in 2011 but not in 2010 a certain threshold of inversion-induced cold temperatures might be needed to induce a response.

The advanced leaf senescence onset dates in the valleys shortened the senescence duration and consequently the vegetation period. For spring events a similar effect of inversions is conceivable (not observed in our study). As a result, spring onset dates could be delayed. Hence, frequent inversions induce shifts in phenological phases opposite to global warming trends by accumulating cold temperatures. Depending on photosynthesis and respiration rates, this could be beneficial for the trees in the valley floors or for the trees in mid elevations (Piao et al. 2008, Wu et al. 2012, Archetti et al. 2013). Moreover, it is unclear if the occurrence of inversion weather situations is influenced by global change (Kirchner et al. 2012). Therefore, observed phenological patterns related to cold air pools might play minor role in future phenological shifts. Although influences of inversions on phenological patterns are restricted to smaller areas and are highly variable in space and time, we consider them to be relevant in alpine regions where inversion situations are common.

Our findings contribute to the discussion which abiotical factor influences leaf senescence most. Many potential factors influencing onset dates in autumn are discussed in literature. Genetics (which is highly variable between life trait and species), light in terms of day length/ photoperiod and temperature are considered to be the most important abiotic drivers of senescence (Thomas & Stoddart 1980, Estrella & Menzel 2006, Delpierre et al. 2009, Caffarra & Donnelly 2011). Moreover, advanced leaf senescence also can be caused by droughts (Vitasse et al. 2010), what could be possible in the warm and dry autumn 2011. However, photoperiod did not differ between our sites and low water availability would have affected all sites. Thus, the observed pattern of latest senescence onset dates at about 1100 m a.s.l. and earlier senescence in higher and lower elevations cannot be explained by photoperiod or drought. Consequently, we can explicitly link the observed pattern area to lowered temperatures under inversion conditions.

With this finding we were able to prove species-specific responses on changes in the temperature regime by a totally different approach. Moreover, based on this different approach, we could confirm that temperature is most likely to be the main driver of senescence in *F. sylvatica* and *A. pseudoplatanus* (see also Estrella & Menzel 2006, Delpierre et al. 2009, Vitasse et al. 2011, Archetti et al. 2013). This makes our results important for the understanding of forest ecosystem functioning under changing environmental conditions.

Alpine Forest Stem Growth

Besides phenology, the intra-annual tree ring growth of *Picea abies* and *Fagus sylvatica* is another main topic of the present thesis and deals with the research question

- **Is the intra-annual course of tree ring growth and its differentiation phases related to leaf phenology, elevation and temperature?**

Reduced tree ring growth with increasing elevation and latitude has been studied for a long time (e.g. Burger 1941, Larcher 2001, Kozlowski et al. 1991, Dobbertin & Giuggiola 2006). In our study, we now discovered for the two sampled species that not only total xylem ring width but also the maximum extension of all cell categories (phloem, xylem, growing cells, wall thickening cells and lignified cells) was reduced with elevation. Similarly, Gričar and Čufar (2008) reported greater width of phloem in a lowland compared to a high elevation site. An unexpected anomaly of small *P. abies* tree rings at 1000 m a.s.l. could not be explained by measured climate parameters. Possible causes could be the influence of single (sick?) individuals or high concentrations of organochlorine pesticides measured at 1000 m a.s.l in the study area (Kirchner et al. 2009). *P. abies* tree ring growth at northern and southern aspect sites was similar in our study. However, Rossi et al. (2007) found smaller tree rings in conifers at northern aspects. For beech, considerable growth reductions on the southern aspect was observed in our study, which could be caused by less optimal water balance conditions, since beech tree ring growth is significantly limited by high summer temperatures and low precipitation (Dittmar et al. 2003, Jump et al. 2006, Zang et al. 2011).

For both studied species we found tree ring growth onset dates advanced by warmer temperatures. Additionally, we could link stem growth onset dates with certain phenological phases. The linkage between stem growth and leaf phenology emphasizes the likelihood of increased stem growth with lengthened vegetation period caused by global warming. In fact, recent investigations have reported an increase in forest wood production since the 1990s and have suggested a relation to higher temperatures due to climate change (Pretzsch 1992, Spiecker et al. 1990, Hasenauer et al. 1999, Dobbertin 2005).

We consider this trend of advanced stem growth onset dates probably to be pronounced under future global warming. However, the timing of cell categories (phloem, xylem, growing, wall thickening and lignified cells) in relation to leaf phenology, elevation and temperature differed between the deciduous *F. sylvatica* and the evergreen *P. abies*. Hence, we advise not to generalize stem growth responses. In the following, our findings for *P. abies* and *F. sylvatica* are first discussed separately and compared later.

For ***P. abies*** first phloem cells appeared about seven weeks before xylogenesis and bud burst, which matches previous findings (Alfieri & Evert 1968, Atkinson & Denne 1988, Larson 1994, Suzuki et al. 1996, Oribe et al. 2001, Antonova & Stasova 2006, Gričar et al. 2006), meaning that the timing of cambium reactivation does rather depend on temperature than on leaf phenology. Our results show temporal consistency of first xylem cells with bud burst and the maximum growth rate with the beginning of shoot growth. Hence, additional photosynthesis products of the new shoots are likely to intensify secondary stem growth. The differentiation phases appear to be dependent on each other since all start dates showed similar response rates to elevation and temperature (a hypothesis also suggested by Rossi et al. 2012). Our results show that response rates of stem growth match the rate of bud burst, meaning that temperature sensitivity of *P. abies* might be similar in stem growth and leaf phenology. The end of stem growth also showed a similar trend and therefore should be dependent on the other stem growth phases rater than on photoperiod as Leštianska et al. (2013) suggested.

We found a slightly reduced time span when new cells were produced at higher elevation, which explains the reduced final tree ring width. However, the total growing period of *P. abies* only slightly differed with changing elevation and temperature. The growing period from first cells to the end of the lignification seemed to be relatively constant (about 111 ± 8 days). For comparison, Rossi et al. (2007) determined that growing period varied between 100 and 120 days in different years. A constant (Gričar et al. 2007) or, in contrast to our study, a prolonged growing period (Boulouf Lugo et al. 2012) was reported in literature for evergreen species.

Other tree-ring growth investigations showed that *P. mugo*, *P. sylvestris* and *P. abies* growth benefit from warmer temperatures (Camarero et al. 1996, Rolland & Schueller 1995, Gindl 1999). Rolland et al. (1998) showed significantly increased radial tree growth for *P. abies*, *L. decidua*, *P. cembra* and *P. mugo* since the middle of the 19th century, which was linked to warmer climate. Thereby, climate is considered to be the limiting factor for *P. abies* and *A. alba* growth (Desplanque et al. 1999), whereas *P. mugo* growth is limited by hydric stress (Rolland & Schueller 1996). For *P. cembra*, growth is reported to be positively related to the growing period (Kronfuss 1994, Kronfuss & Havranek 1999). On the other side, observed increased tree-ring growth over the last 100 years might be more related to elevated levels of CO_2 than to warmer temperatures (Nicolussi et al. 1995, Körner 1995).

The length of the stem growth period is almost not depending on temperature, just in contrast to the high response in bud burst and leaf unfolding. *P. abies* produced numerous cell rows before cell wall thickening and lignifications started. Hence, the process of cell differentiation was slow (compared to *F. sylvatica*). Accordingly, other studies reported that cell maturation (including the process of enlargement, wall formation and lignification) lasted until late in autumn (Gričar et al. 2005, Rossi et al. 2007, Gryc et al. 2012). This probably could explain the contrast of a reduced period of growing cells and a relatively constant period of tree ring formation with elevation. Reduced temperature with elevation on the one hand reduces the cell formation period (and thus the absolute tree ring width), but might slow down the cell maturation process. Both processes might have different dependencies on temperature, which would explain contrasting results. Summarizing, *P. abies* onset dates strongly advanced with higher temperatures, but the stem growth period hardly showed any response.

For ***F. sylvatica***, stem growth start dates were closely linked to leaf phenology in spring. We were able to differentiate the connections between stem growth and leaf phenology onset dates: start of phloem growth corresponded to bud burst (BBCH 7), start of xylem growth to leaf unfolding (BBCH 11), and the maximum growth rate to young fully unfolded leaves (BBCH 17). These findings match reported cambium reactivation with leaf unfolding and maximum growth rates when leaves are mature (Čufar et al. 2008, Michelot et al. 2012). Thus, the lengthening of the photosynthesis period in spring has also a lengthening effect for the stem growth period.

One relevant result for climate change impacts was the strong dependence of stem growth period on temperature for *F. sylvatica*. Based on solid observational data we demonstrated that the stem growth period was strongly reduced with increasing elevation, thus decreasing temperatures. In particular, a highly advanced end of ring growth in higher elevations resulted in reduced tree ring width. At high elevations, stem growth stopped several weeks before leaf coloring, but not at lower elevations where stem growth did not stop until the beginning of leaf senescence. The responses to temperature differed between leaf senescence phases and the end of stem growth. Thus, the end of stem growth was independent of leaf coloration. With these findings, for *F. sylvatica* we moreover can exclude the dependence of the end of stem growth on the photoperiod (as Leštianska et al. (2013) suggested for *P. abies*). Thus, the end of stem growth probably was influenced by temperature mainly.

For *F. sylvatica* the distinct shorter stem growth period at higher elevations resulted in smaller final ring widths. The explicit reduction of the stem growth period with elevation also might be an adaption to frost damages. Another explanation would be that *F. sylvatica* in the study area reaches its distribution limits (in contrast to *P. abies*). This hypothesis would match the findings of Körner (2003) who detected a distinct reduction in stem growth at the upper tree line which was not linear with decreasing air temperature. Thus, in autumn, several factors play a role in controlling the end (and thus the length) of *F. sylvatica* stem growth. Warmer temperatures, but not necessarily delayed leaf senescence prolong the stem growth period.

We conclude that *F. sylvatica* responses more opportunistic to temperatures and also might benefit more from a prolonged vegetation peripod, including both an increase in the leafy season and in stem growth. Stem growth period of *P. abies*, however, we classify to adapt more slowly, in spite of a relatively high response in spring phenology. Accordingly, Dittmar and Elling (1999) stated that *F. sylvatica* was more sensitive to environmental factors and wood formation was more strongly controlled by exogenous parameters than compared to *P. abies*.

Global change induced high temperatures are reported to be only favorable for trees at mid to higher elevations, whereas at lower elevations drought stress might reduce stem growth (Körner & Paulsen 2004, Dobbertin & Giuggiola 2006, Jump et al. 2006, Rossi et al. 2007). However, in our montane to subalpine forests in the Werdenfelser Land study area (located > 700 m a.s.l.) we expect an increase in stem growth in next future rather than negative effects. When our findings of *P. abies* and *F. sylvatica* stem growth can be applied for other evergreen and deciduous species (which remains to be confirmed), primarily deciduous trees will gain in wood production rather than evergreen species.

9.3 Applicability of the Results

The trends observed and described in this thesis are shifted phenological phases with a lengthening of the vegetation period, including a lengthening of the stem growth period. Since temperature was identified as the main driver, these trends are induced and reinforced by recent climate change. The consequences of these trends are upward shifts of species, vegetation belts, tree line and phenological patterns, including a reduction of vegetation belt area and likely biodiversity.

Primarily, our results are of high importance for closing knowledge gaps in forest ecosystem understanding. They provide new detailed information to be compared with other studies and illustrate a range of further research opportunities. Moreover, our proved linkages between phenological onset dates and stem growth can be applied in remote sensing studies. For example, green-up dates in *F. sylvatica* forests now can be linked not only to bud burst, but also to the beginning of stem growth.

Since forest ecosystems are a dominant land cover type, determined results of tree responses are likely to influence the whole ecosystem, including flora, fauna and environmental conditions. Forest ecosystems as well have considerable feedback effects to atmosphere (radiation balance, CO_2-O_2 exchange, biogenic volatile organic compounds), pedosphere (nutrients, soil development) and hydrosphere (water consumption, respiration).

Alpine species and ecosystems are highly threatened by climate change and an upward shift of vegetation zones will include a reduction of distribution area. Therefore, it is highly important to support existing and establish new alpine protection or conservation areas. Since high ecosystem biodiversity might buffer phenological mismatch and maintain synchrony at the community level (Bartomeus et al. 2013), preservation of species richness is necessary. These efforts should not be restricted to the European Alps, but also should be applied to mountains all over the world.

Since anthropogenic pollution is a significant contributor to global warming, man is one of the factors responsible for these trends. Therefore, mankind should adapt in its activities, behavior and lifestyle to reduce its impacts. This includes the reduction of emissions of greenhouse gases and other pollutants (e.g. nitrogen and volatile organic compounds). Moreover, alpine ecosystems already are stressed by intensive human activities (e.g. skiing and hiking tourism, timber industry, agriculture and grazing, constructions, water withdrawal and hydropower). These disturbances finally strengthen the impacts of climate change in the Alps by restraining natural tolerances. Thus, anthropogenic pressure on the alpine zone should be reduced.

The same applies to the colline and montane alpine forest, which deserves protection and sustainable forest management. Stability and multiple functions of mountainous forest ecosystems can be achieved by appropriate regulation of the forest regeneration. Our results of explicit increased stem growth in *Fagus sylvatica* and other models predicting an increase of *Abies alba* growth (e.g. Bugmann 1999) imply that these two species should be target trees in lower to middle elevations. Since the lowest elevation in the Werdenfelser Land study area is about 700 m a.s.l., it might be still too premature to consider *Quercus* species, *Carpinus betulus* or even *Castanea* species to be admixed in lowland *F. sylvatica* forests. But depending on further global warming trends, this opportunity should be kept in reserve. However, finding the balance between predicted and real environmental conditions, controlled sustainable management, natural change processes and protection strategies is difficult.

9.4 Further Research Opportunities

Phenological Shifts under Climate Change Conditions

Although we found a lot of new and detailed information on how alpine tree leaf phenology is influenced by elevation and temperature, questions for further research opportunities never run out in the wide field of phenology. For example, we could only show first trends of how phenology differed between northern and southern aspects or between adult and juvenile trees. Similarly, our results on flowering and seed production of alpine tree species need to be approved by other studies. Long term observations probably would clarify uncertain trends and relationships in these topics. Furthermore, there are open questions on how the extended vegetation period will change the carbon balance of trees (respiration, secondary stem growth), emission of biogenic volatile organic compounds (e.g. isoprene) or the water balance by changed water consumption and evaporation. The role of other factors, such as nutrients or air humidity, in their role in triggering phenological onset dates is scarcely considered so far.

The fact that we (and other studies) have shown that alpine tree and herb species react differently to temperature raises the question of how different plant migrations in space could lead to new communities and therefore new habitat interactions (e.g. symbiosis, competition…). An upward shift of species distribution in alpine areas has been reported (e.g. Walther et al. 2005, Gehrig-Fasel et al. 2007, Lenoir et al. 2008, Erschbamer et al. 2009) and conditions at the lower boundary might become unsuitable (e.g. Jump et al. 2006). Thus, more studies are needed to tackle future changes in upper and lower boundaries of single (tree) species or whole (forest) ecosystems. Moreover, it is still unclear if and which alpine (tree) species are threatened by extinction due to changed conditions in their habitats (e.g. possible for *Pinus cembra* in our study area, which is only distributed close to tree line).

Another consequence of our finding that temperature response highly varied between species underlines phenological mismatch as a key problem of phenological response to climate change. Hence, it is imperative to reinforce interdisciplinary research and study comparisons on mismatching ecological relationships within ecosystems, e.g. on plant-animal interactions (trophic levels, pollination).

Additionally, more studies on the importance of forest ecosystem changes for human life and health are of special interest. Increased allergenic exposure and changed or restricted anthropogenic usage of forest ecosystems (bee keeping, timber industry, recreation areas) are conceivable. For example, higher temperatures might increase forest-damaging pest outbreaks, which can severely weaken dominant tree species used in timber industry. This was shown for pests on *P. abies* (web-spinning saw-fly), *P. sylvestris* (pine shoot beetles) and *L. decidua* (larchbud-moth; Baltensweiler 1993, Marchisio et al. 1994, Rigling & Cherubini 1999).

Inversion Impacts on Phenology

Compared to the impact of climate change on phenological phases and the vegetation period, inversions may play a minor role since they are highly variable in space and time and often only occur in small-scale areas. However, we proved species-specific responses to changing temperatures by a completely different approach. Knowledge about the influence of inversions improves our understanding of forest ecosystem functionality. Further research could focus on spring inversions influencing the timing of bud burst or flowering and therefore pollen distribution. Frequent spring and autumn inversion changing the leafy period of deciduous trees might also influence the balance of stem growth, carbon allocation, build up of carbohydrate reserves or emissions of biogenic organic compounds. In the field of climatology, it is still unclear if recent climate change has an influence on the frequency of inversion promoting weather patterns.

Intra-annual Tree Ring Growth

Studies in a wide range of elevations and the linkage between detailed phases in leaf phenology and ring growth are still very rare. We could conclude likely impacts and responses of climate change on *P. abies* and *F. sylvatica* tree ring formation, however, a variety of research opportunities remain. Species other than *P. abies*, *F. sylvatica* (this thesis) and *L. decidua* (Moser et al. 2010) could be investigated, especially for the comparison between deciduous and evergreen or ring-porous and diffuse-porous species. In turn, long-term designed studies with more individuals per site could reinforce our findings. Since our study only included one sampling year, which in addition was characterized by an extraordinarily warm autumn, a longer study would demonstrate the variability on tree-ring growth timing and duration in relation to changing weather conditions. In particular the proportions of carbon sinks due to increased wood formation in relation to increased CO_2 are of special interest. Our result of different relationships between growth end dates and the end of the photosynthetic period comparing trees in low and high elevations raises the question if there are elevation-induced strategies of carbohydrate reserve deposition in autumn. This in turn could be a factor for bud burst timing in the next spring. The different characteristics of *P. abies* and *F. sylvatica* tree ring growing period found along elevational transects moreover intensify the researchers' questions on the ability of different species to adapt to climate change. Moreover, the influences of extreme events (such as the warm autumn 2011) should be examined more closely.

Thus, opportunities for research in alpine forest ecosystem processes are far from exploited in both observational and experimental studies. More, and especially more long-term, studies are necessary to bring forward knowledge on interactions between climate and forest ecosystems, and to verify the results and conclusions of this thesis.

9.5 Other Factors influencing Alpine Forests

Besides the effects of higher temperatures investigated in this thesis, there are other global change impacts influencing alpine forest ecosystems, which are likely to occur in our study area although they were not considered in our work.

For example, CO_2 affects plant flowering in timing and number and also nectar quality (Erhardt & Rusterholz 1997, Rusterholz & Erhardt 1998). Elevated CO_2 and nitrogen deposition have been shown to modify the distribution and dominance of the *P. abies* forest understory (Hättenschwiler & Körner 1996, 1997) and to increase the biomass of *A. pseudoplatanus* (Overdieck 1996) and *F. sylvatica* (Egli & Körner 1997, Maurer et al. 1999). Trees also respond to tropospheric ozone (Bungener et al. 1999), which in recent time has become a pollutant of great concern for forests (e.g. Pye 1988, Matyssek & Sandermann 2003). In particular, forests at low elevations in the foothills are negatively affected by ozone: reduced growth, early senescence and death of sensitive species have been observed (Pye 1988, Fuhrer et al. 1997, Cherubini & Moretti 1999).

Alpine species are considered to react to environmental changes in their habitat by persistence, migration or extinction (Guisan et al. 1995, Bazzaz 1996, Theurillat & Guisan 2001) – responses which are also applicable to the tree species observed in this study. Persistence of species could be possible where permafrost, steep slopes, and unstable rocks and cliffs slow down immigration of new species (Delarze 1994, Urbanska 1995) or for longliving plants (Escaravage et al. 1998, Theurillat & Guisan 2001). It is more likely that alpine species will respond by migration (Huntley 1991). Thus, an upward shift of species or whole vegetation belts along altitudinal or other thermal gradients is a widespread hypothesis (Peters & Darling 1985, Ozenda & Borel 1995, Walther et al. 2005, Lenoir et al. 2008, Erschbamer et al. 2009).

Likewise, the upper tree line is considered to shift upwards with continuous higher temperatures (e.g. Stützer 1999, Gehrig-Fasel et al. 2007, Erdle et al. 2013), since the colline and subalpine tree species at the upper border predominantly are limited by temperature (Sholes 1994, Kollas et al. 2013). Upward shifts in forest ranges previously happened in warm interglacial periods: Pedoanthracological observations of *L. decidua* and *P. cembra* in the south-western Alps proved forest limits have been elevated by 350-700 m during the warmest Holocene periods (Scharfetter 1938, Talon 1997, Carcaillet et al. 1998, Carcaillet & Brun 2000).

Presently, mixed forests cover the mountain slopes in the Werdenfelser Land study area up to the tree line at about 1750 m a.s.l. on southern and 1850 m a.s.l. on northern slopes. In Austria, *P. abies* has colonized the alpine-subalpine ecocline (1850-1950 m a.s.l.) in the last 60 years (Stützer 1999). However, human pressure on the Alps has been exerted for many centuries (grazing, agriculture, forestry), therefore the present vegetation is considered not to be in a natural equilibrium (Theurillat & Guisan 2001). Gehrig-Fasel et al. (2007) identified only 10 % of the new forest areas at high elevations as true tree line upward shifts, whereas 90 % represented ingrowth.

Models predict upward shifts of colline and subalpine forests dominated by montane deciduous trees moving higher and forcing subalpine conifers to migrate into the alpine zone (Fischlin et al. 1995; Kienast et al. 1995, 1996, 1997; Fischlin & Gyalistras 1997; Lischke et al. 1998). *P. cembra* and *L. decidua* dominated forests at the upper tree line appear to be very sensitive to climate change and can experience catastrophic changes in species composition due to climate change (Fischlin et al. 1995, Fischlin & Gyalistras 1997, Lischke et al. 1998). As a pioneer able to settle in stony areas, *L. decidua* is the species most likely to capture new habitats above the current tree line (Röhrlich 2013), followed by *P. cembra* and *P. abies*. In the colline to subalpine zone of the northern Alps models predict an increase of *A. alba* (Bugmann 1999). However, *A. alba* was selectively eliminated by human forestry and pasturing in former times which eventually led to the dominance of *P. abies* (Lingg 1986, Ott et al. 1997, Tinner et al. 1999). In the colline to submontane belt *F. sylvatica* is predicted to be slowly replaced by *Quercus robur* L.*, Q. petraea* (MATT.) LIEBL and *Carpinus betulus* L. (Theurillat & Guisan 2001).

Harsh alpine conditions, high erosion rates and low soil development above tree line are limiting the establishment and growth of immigrating species. High alpine and nival belts are easily reached by pioneer wind-dispersed species (Stöcklin & Bäumler 1996, Erschbamer et al. 1999), whereas other species are often limited by natural barriers (orographical, geomorphical, lithological; Theurillat & Guisan 2001). A slow colonization rate can also be explained by high disturbance of the new habitats and therefore a high mortality of seedlings (e.g. Stöcklin & Bäumler 1996, Erschbamer et al. 1999). A consequence would be a more mosaic structured mixture of vegetation belts: warm and stable areas would allow migration, cold and unstable areas would provide refuges (Theurillat & Guisan 2001, Röhrlich 2013).

Another crux of the matter is the stability of soils, since erosion is high and soils only persist with an intact ground cover root system (Körner 2003). Hence, accumulation of new soil and upward shifts of species are dependent on each other in a fragile balance. Last, but not least, human activity is a central factor responsible for developments and species distribution, especially of trees, in the Alps for millennia (Patzelt 1996). In particular in the last century the alpine region experienced an intensification in human usage (tourism, constructions, water withdrawal) leading to increased pressure and fertilization (Theurillat & Guisan 2001, Körner 2003).

Consequently, the tree line will shift upward only slowly and needs warmer climate for at last 100 years (Holtmeier 1994a,b). Based on observations since the last glaciation, a temperature increase by 1-2 °C would allow an upward shift of the tree line about 100-200 m, but if warming of 2 °C persist over several centuries even more is possible (Theurillat & Guisan 2001). Moreover, migration to higher elevation in mountainous regions means that plant communities will not find equivalent surface areas. Since area decreases with elevation, an upward shift of vegetation belts would mean a reduction of the total ecosystem area, e.g. by -63% of the alpine zone in Switzerland by a warming of 3.3 °C mean air temperature (lower zones would be reduced less; Theurillat & Guisan 2001).

Species migration under warmer and drier climate can locally lead to an increase in species richness (Kienast et al. 1997). However, summits are considered to be homogenized in plant communities by this trend (Jurasinski & Kreyling 2007). Over longer time scales a loss of biodiversity is most likely due to extinction of less competitive species (e.g. Grabherr et al. 1994, Theurillat & Guisan 2001). In particular, alpine species relicts in low mountain ranges are expected to disappear (Röhrlich 2013). In addition, current global warming might proceed too rapidly for the natural migration ability of many species (Rice & Emery 2003, Aitken et al. 2008).

10 Summary and Conclusions

Connections and interactions between climate, plant phenology and dendroecology were, are and will be studied by a wide scientific community from numerous research fields pursuing different objectives. Large datasets of meteorological measurements, observations, experiments, field samples and laboratory preparations are combined, compared and set into context by statistical analyses in order to generate more information on ecosystem functioning and climate change impacts. In this context, our two-year altitudinal transect study in the Werdenfelser Land embedded in the KLIMAGRAD project provides several new contributions to the interactions between meteorological parameters (especially temperature), phenology and intra-annual tree ring growth in alpine forests.

One central issue of the project was the establishment and operation of the meteorological station and logger network. This network provided detailed meteorological information of the study-area. In this way, profound knowledge about the climatic situation in the area and clearly improved climate change impact estimations were ensured.

Since other studies already used the assumption that, in mountainous regions, plant phenology is directly connected to elevation and temperature, the first part of the present thesis focused on the phenological response of seven alpine tree species to elevation and temperature. The most important findings can be summarized as:
Tree leaf phenology was shifted by warmer temperatures (spring events were advanced, autumn events were delayed) whereas responses differed between species. We determined a strong response of *Acer pseudoplatanus*, *Larix decidua* and *Picea abies,* an intermediate response of *Fagus sylvatica* and a weak response of *Abies alba*, *Pinus sylvestris* and *Pinus mugo*. We suggest advanced bud burst to be partly restricted by chilling and day length requirements, in particular for the two deciduous species leafing out early in the year. Moreover, flowering in spring was advanced by higher temperatures at species-specific magnitudes. In total, we calculated a lengthening of the vegetation period by about two weeks (13.7 days) per degree warming.

In autumn 2011, inversions occurred extraordinarily frequently in the study area. Therefore, in a second part, the research project aimed to assess the effects induced by cold air pools on tree phenology in alpine regions. For the first time, we could describe in detail that under inversion conditions cold air in the valleys shifted phenological onset dates in the opposite direction to warming trends. This circumstance we could prove for advanced autumn phases in the valleys of our study area, whereas *Acer pseudoplatanus* responded more strongly than *Fagus sylvatica*. The key finding of this study was that we could determine temperature as the main factor regulating leaf senescence of our two studied species.

To increase knowledge about alpine tree responses to elevation and temperature, in the third part of the thesis, wood formation, intra-annual tree ring growth and cell differentiation of *Fagus sylvatica* and *Picea abies* along the altitudinal transects were studied using the microsampling method. Ring width and maximum occurrence of all cell differentiation phases were reduced with elevation, thus with decreasing temperatures. Similar to leaf phenology, stem growth onset dates of both species were advanced by warmer temperatures. Growing period for *Fagus sylvatica* was clearly lengthened by warmer temperatures and most likely profited by the lengthening of the vegetation period. However, growing period of *Picea abies* proved to change only slowly with changing environmental conditions. The differentiation phases (beginning of phloem and xylem cell growth, wall thickening and lignification) appeared to be dependent on each other for *P. abies*. Moreover, we showed that most start dates (but not end dates) of cell differentiation phases were directly connected to specific leaf phenology phases.

The results of this thesis on observed and determined trends in alpine tree species phenology and stem growth have been discussed and compared to other studies in order to draw a picture of future changes in alpine forest ecosystems. Additionally we described the applicability of our results and highlighted the needs for adaption to recent global warming.

Summarizing, one degree warming will likely lead to a lengthening of the vegetation period by about two weeks and an upward shift of phenological patterns by about 200 m. Based on linear temperature change with elevation, these results are approximations and counteracting factors should be considered. Alpine ecosystems probably could tolerate moderate climate change, but other global change trends such as land-use and eutrophication have already resulted in stress, modification or even destruction of ecosystems all over the world. Therefore, recent climate change just reinforces and intensifies human impacts on ecosystems. Up to now, 1-2 °C warming is being observed in the Alps and warming in the order of about 3 °C is expected.

Hence, it is important to continue studying global warming trends in the European Alps and mountain ecosystems worldwide. Long-term studies to confirm trends determined from short-term projects are still rare. Further research is needed to deepen our understanding of functions and processes in alpine ecosystems and to improve modeling, comprehension and adaption of future developments. Research aims could be species-specific data on persistence, migration or extinction probability, in particular of endemic, keystone or flagship species. Additionally, interdisciplinary studies dealing with mismatches between different trophic levels within an ecosystem are of special interest.

In the end, this thesis presents important results for the understanding of forest ecosystem functioning under changing environmental conditions. Thus, besides the increased fitness of the author, this work is beneficial to the research community by providing detailed relationships between climatic drivers and vegetation responses.

> ***When preparing to climb a mountain – pack a light heart.***
>
> ***Dan May***

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Publication List

Reviewed Publications

Schuster C, Estrella N, Menzel A. 2013. Shifting and extension of phenological periods with increasing temperature along altitudinal transects in southern Bavaria. *Plant Biology*. doi:10.1111/plb.12071.

Schuster C, Kirchner M, Jakobi G, Menzel A. 2013. Frequency of inversions affects senescence phenology of *Acer pseudoplatanus* and *Fagus sylvatica*. *International Journal of Biometeorology*. doi: 10.1007/s00484-013-0709-0.

Submitted Publications

Schuster C, Zang C, Menzel A. Differences in intra-annual tree ring formation of Norway spruce and European beech in relation to elevation and phenology. (Submitted to *OIKOS*, 25.09.2013).

Co-Author Publications

Schunk C, Wastl C, Leuchner M, Schuster C, Menzel A. 2013. Forest fire danger rating in complex topography – results from a case study in the Bavarian Alps in autumn 2011. *NHESS.* doi: 10.5194/nhess-13-2157-2013.

Publications in Preparation

Capdevielle-Vargas R, Schuster C, Estrella, N, Menzel A. Leaf morphology of beech (*Fagus sylvatica* L.) link to environmental conditions depending on the altitudinal origin. (working title).

Kübert C, … , Schuster C, Menzel A, Klein D. *Comparing small scale mountain forest tree phenology of field and remote sensing observations (working title, title not yet defined).*

Oral Presentations

Schuster C, Menzel A. 2010. Phänologische und vegetationskundliche Veränderungen des Klimawandels in der montanen und subalpinen Stufe im Werdenfelser Land. Wissenschaftliche Tagung der Umweltforschungsstation Schneefernerhaus, Iffeldorf, 20.-21.5.2010.

Schuster C, Gröger A, Menzel A. 2011. High elevation phenology in mountain forests and alpine botanical gardens. Tagung des Arbeitskreises Biomonitoring / Global Change der Reinhold-Tüxen-Gesellschaft e.V. Hannover Universitätszentrum Obergurgl, 19.-21.08.2011.

Schuster C, Estrella N, Zang C, Menzel A. 2012. Temperature sensitivity of mountain forest tree species observed by phenology and intra-annual stem growth at altitudinal gradients in the area around Zugspitze. Wissenschaftliche Tagung der Umweltforschungsstation Schneefernerhaus Oberpfaffenhofen, 25.-26.09.2012.

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Schuster C, Estrella N, Gröger A. Menzel A. 2012. Mountain forest tree phenology in the German Alps. Seminar during DAAD-exchange, Laboratório de Fenologia, Depto. de Botânica, UNESP - Rio Claro Brasil, 8.3.2012.

Poster Presentations

Schuster C, Gröger A, Friedmann A, Korch O, Kirchner M, Jakobi G, Menzel A. 2010. KLIMAGRAD – Auswirkungen des Klimawandels in den Alpen – Erfassung mittels Höhengradienten. Postershow Zentrum Wald-Forst-Holz, Freising, 28.1.2010.

Schuster C. Menzel A. 2010. Mountain forest tree phenology along altitudinal gradients in the Werdenfelser Land, Germany. Forum Alpinum 2010, Bayerische Akademie der Wissenschaften, München, 6.-8.10.2010.

Schuster C, Gröger A. Breier M, Menzel A. 2011. High elevation phenology in mountain forests and alpine botanical gardens. European Geosciences Union General Assembly, Wien, 03.-08.04.2011.

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Menzel A, Gröger A, Renner, SS, Friedmann A, Korch O, Kirchner M, Jakobi G, Leuchner M, Ziello C, Lüpke M, Poschinger A, Schuster C. 2012. Forschungsschwerpunkt Biosphäre – Geosphäre, Opening Ceremony of the VAO (Virtuelles Alpen Observatoriums), UFS Schneefernerhaus, Germany, 19.4.2012

Schuster C, Zang C, Menzel A. 2012. Intra-annual cell growth in beech and spruce along altitudinal gradients in the area of Zugspitze connected to climate and phenology. TRACE 2012 Tree Rings in Archaeology, Climatology and Ecology, GFZ Potsdam, 9.-12.5.2012.

Schuster C, Estrella N, Menzel A. 2012. Impact of climate change on leaf phenology in European mountain tree species. 6th International Canopy Conference Oaxaca City, Mexico, 24.-27.10.2012

Schuster C, Zang C, Menzel A. 2013. Wood formation of *Picea abies* and *Fagus sylvatica* and its climatic drivers along altitudinal gradients in the Bavarian Alps. ClimTree 2013, Zürich, Schweiz, 02.-04.09.2013

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Gröger A, Schuster C, Menzel A. 2012. Information panel about the KLIMAGRAD project with actual meteorological data of the Schachen climate station in the Botanical Garden Munich.

Schuster C, Gröger A, Breier M, Menzel A. 2010. KLIMAGRAD - Phänologische und vegetationskundliche Untersuchungen in der montanen und subalpinen Stufe im Wetterstein und am Schachen. UFS - Scientific Results (2009/2010)

Schuster C, Menzel A. 2012. Temperature sensitivity of mountain forest tree species observed by phenology and intra-annual stem growth at altitudinal gradients in the area around Zugspitze. UFS - Scientific Results (2011/2012)

ARTE. 2012. Klimawandel konkret, documentary film, 7.6.2012

Individual Contributions

Schuster C, Estrella N, Menzel A. 2013. Shifting and extension of phenological periods with increasing temperature along altitudinal transects in southern Bavaria. *Plant Biology*. doi:10.1111/plb.12071.

Annette Menzel and Nicole Estrella contributed with suggestions for the development of observation keys, corrections and proof reading. All the fieldwork (site installation, observations, data collecting…), data processing, script programming, statistical analyses, graphic artwork and writing the manuscript was done by myself (90 % contribution).

Schuster C, Kirchner M, Jakobi G, Menzel A. 2013. Frequency of inversions affects senescence phenology of *Acer pseudoplatanus* and *Fagus sylvatica*. *International Journal of Biometeorology*. doi: 10.1007/s00484-013-0709-0.

All the fieldwork (site installation, observations, data collecting…), data processing, script programming, statistical analyses, graphic artwork and writing the manuscript was done by myself (85 % contribution). Manfred Kirchner and Gert Jakobi contributed with their knowledge about inversion situations in the observation area for the manuscript. Manfred Kirchner and Annette Menzel also did the proof reading for the manuscript.

Schuster C, Zang C, Menzel A. Differences in intra-annual tree ring formation of Norway spruce and European beech in relation to elevation and phenology. (Submitted to *OIKOS*, 25.09.2013).

Christian Zang did the programming of the Hadwiger model and corrected/ proof read the manuscript together with Annette Menzel. All the fieldwork (site installation, observations, data collecting…), data processing, script programming, statistical analyses, graphic artwork and writing the manuscript was done by myself (85 % contribution).

Schunk C, Wastl C, Leuchner M, Schuster C, Menzel A. 2013. Forest fire danger rating in complex topography – results from a case study in the Bavarian Alps in autumn 2011. *NHESS*. doi: 10.5194/nhess-13-2157-2013.

I supported this publication by collecting, processing and providing meteorological data for the study area Werdenfelser Land (app. 10 %). The main part of the work has been made by the author and other co-authors.

KLIMAGRAD management

Since the main organization of the project KLIMAGRAD lay on the side of the Chair of Ecoclimatology, my task beside the work directly connected with the thesis, was the coordination of the research partners. This included:

- central communication between project partners and the Bavarian State Ministry of the Environment and Public Health
- creating and demonstrating collective posters and project presentations
- organizing, composing and formatting the project's final reports
- maintenance and repair of the KLIMAGRAD meteorological stations and communication with the providing company
- maintenance, repair and reading out data of the KLIMAGRAD logger network
- data care and provision of the meteorological station and logger network

TUMkolleg

In 2010/11, Lena Trautmann and Christine Heuer from the Otto-von-Taube-Gymnasium Gauting accomplished their seminar works within the framework of TUMkolleg (http://www.edu.tum.de/de/fuer-lehrkraefte/tumkolleg/) at the Chair for Ecoclimatology, attended by Christina Schuster and Raimund Henneken. Both worked on KLIMAGRAD research sites in Garmisch and used the established infrastructure. Their seminar theses „Blattentfaltung von Rotbuche und Bergahorn entlang von Höhengradienten“ (Lena Trautman) and „Phenological observation of tree species by webcam imagery“ (Christine Heuer) were presented at the regional competition Oberbayern „Jugend forscht“ (18.02.2011), where Christine Heuer outstand as winner of the biology section.

CAPES - CGCI PROBRAL Brasil/Alemanha/2010

An additional component of my PhD education was a two-month (06.02.2012-30.03.2012) DAAD exchange program between the Chair for Ecoclimatology and the Departamento de Botânica (UNESP), Rio Claro, Brazil (Prof. Dr. Leonor Patrícia C. Morellato, http://www.rc.unesp.br/ib/botanica/pmorella/). The exchange program provides various opportunities to exchange field work, laboratory work and analysis methods between the participants and enriched the expertise of both sides. Executed works:

- phenological observations, instrument setup and analysis of meteorological data
- GPS-mapping of the tree species *Myrcia guianensis* (AUBL.) DC and *Anadenanthera falcata* (BENTH) Altschul and crating of base maps (ESRI ArcGIS) for phenological space and time analyses
- testing of the microsampling method in the Cerrado forest (tested tree species: *Copaifera langsdorfii* Desf., *Platypodium elegans* Vogel*, Schefflera vinosa* (CHAM. & SCHLTR.) FRODIN &FIASCHI, *Vochysia tucanorum* (SPRENG.) MART., *Xylopia aromatica* (LAM) MART., *Araucaria angustifolia* (BERTOL) KUNTZE and *Podocarpus lambertii* KLOTZSCH; two methods for thin section preparation: with and without embedding in Historesin; support by Prof. Dr. Alessandra Ike Coan)
- assisting in the field work of Cerrado ecosystem recreation research (Parque Estadudal de Porto Ferreira, Prof. Dr. Reinaldo Monteiro)

Graduate School

During the PhD time at Technische Universität München, I participated at the TUM Graduate School program (http://portal.mytum.de/gs/index_html) including disciplinary and interdisciplinary training seminars.

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Eidesstattliche Erklärung

Ich erkläre an Eides statt, dass ich die der Fakultät Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt der Technischen Universität München zur Promotionsprüfung vorgelegten Arbeit mit dem Titel

“Untersuchungen zu Phänologie und intra-annuellem Stammwachstum entlang von Höhengradienten im Werdenfelser Land”

am Fachgebiet für Ökoklimatologie unter der Anleitung und Betreuung durch Prof. Dr. Annette Menzel ohne sonstige Hilfe erstellt und bei der Abfassung nur die gemäß § 6 Abs. 5 angegebenen Hilfsmittel benutzt habe.

Ich habe die Dissertation in keinem anderen Prüfungsverfahren als Prüfungsleistung vorgelegt.

Ich habe den angestrebten Doktorgrad noch nicht erworben und bin nicht in einem früheren Promotionsverfahren für den angestrebten Doktorgrad endgültig gescheitert.

Die Promotionsordnung der Technischen Universität München ist mir bekannt.

Freising, ___________ ____________________________
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Curriculum Vitae

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