Intra-annual tree growth along an altitudinal gradient in the Lötschental, Switzerland

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Lea Moser

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Leiter der Arbeit:

PD Dr. Jan Esper
PD Dr. Jürg Luterbacher
Geographisches Institut
Universität Bern

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Abstract

Intra-annual growth variations of larch and spruce along an altitudinal transect (1350–2150 m asl) in the Lötschental, Switzerland, were studied during 2007. Such elevational gradients offer the valuable and unique opportunity to examine tree growth under comparable meteorological conditions. They also allow "space for time" experiments, i.e. observations along an elevational gradient (=space) should represent long-term measurements (=time). The main focus was therefore on differences in temperatures and growth patterns due to altitude as well as owing to exposure. Additionally, the relationship between temperature measurements and 2007 growth variations was analyzed.

For this purpose, temperature measurements, phenological observations as well as microcore sampling were weekly conducted at four different altitudes on the north and the south facing slopes in the Lötschental. The collected wood microcores were prepared as microsections and analyzed by counting the number of cells in different growing stages. To find possible differences in the timing of growth patterns as a function of altitude or exposure, the Wilcoxon-Mann-Whitney rank-sum test was applied. If particular growing stages revealed such differences, linear regression was used to assess a trend with elevation. These gradients were then linked to growing season mean temperatures with regard to altitudinal differences.

The results showed statistically significant differences between the lowest and the highest sites in the timing of growth patterns, i.e. needle appearance, the onset of cell enlargement, cell wall thickening and cell maturation as well as the maximum of cell enlargement. For these growing stages, altitudinal gradients of 4 to 7 days/100 m were estimated and thereafter related to mean stem and soil temperature gradients which declined by 0.36 and 0.46 °C/100 m, respectively. Connecting these elevational gradients, a change of 13 days/°C in mainly the onset of different growth patterns could be derived. However, no other (environmental) factors, e.g. soil condition or pollution, were considered.

The present thesis shows that there are altitudinal differences in the timing — particulary in the onset — of ring formation but none due to exposure. The comparison of long-term studies, e.g. of needle appearance in spring, with short-term shifts along the elevational transect revealed that "space for time" experiments work rather well. Combined with the predicted temperature increase of approximately 2.7 °C in summer for 2050 compared to 1990 in Switzerland, the mean onset of the growing period of larch in the Lötschental would start about 35 days earlier by 2050!

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Chapter 1

Introduction

Many recent studies have focused on the response of the terrestrial ecosystem to a changing climate (e.g. Theurillat and Guisan 2001). Owing to rising emissions of — mainly — carbon dioxide from 280 (preindustrial) to 379 ppm (in 2005) the radiative forcing and consequently global temperatures have been increasing, e.g. during the last fifty years a linear warming trend of approximately 0.65 °C was observed (IPCC 2007). To put into perspective the recent temperature rise and to get an idea of the future range of such a warming, climatologists try to reconstruct past climatic conditions. This information helps to estimate future temperature scenarios predicting an increase of 0.6 to 4.0 °C for 2090–2099 compared to 1980–1999 on global scale (IPCC 2007). It stands to reason that biologists are concerned how the change in carbon dioxide and temperatures affects the biomass, especially stationary living organisms. A central position in the stationary terrestrial ecosystem belongs to forests and trees, respectively. Due to their wide distribution (30% of the Earth's surface) and their high proportion of living global terrestrial biomass carbon (close to 90 %) trees are important as biosphere component, sources of necessary products, ameliorators of climate and protection against wind, flooding and erosion. Therefore, it is of great scientific interest to monitor how trees respond to increased carbon dioxide and to a warming climate. At this interface of atmosphere and biosphere two scientific fields are touched: Meteorology/climatology and biology.

On the one hand, **dendroclimatologists** focus on the **abiotic** forcing on trees. There are many different environmental factors, e.g. temperature, water supply, soil conditions, or snow cover, influencing trees and their growth (Figure 1.1). In return, tree rings can contain such environmental signals and are therefore used as indirect climate indicators (so-called "proxy") with the objective of reconstructing past climate variability and change. The measurements of annual ring widths (e.g. Esper et al. 2007, Fritts et al. 1971),

Figure 1.1: *Influence of environmental and congenital factors on tree growth (adapted from Pallardy (2007)).*

maximum latewood densities (e.g. Briffa et al. 1992, D'Arrigo et al. 2004) or stable isotopes (e.g. Leavitt 2002, Schleser et al. 1999) have provided seasonally to annually resolved information on past temperatures, precipitation and drought. Similar methods were also adopted in studies conducted in the Lötschental and in the adjacent Rhône valley. For instance, Affolter et al. (2008) investigated the sensitivity of conifers to climate with an emphasis on anomalous dry conditions, Büntgen et al. (2006a) mapped the settlement and building history of the Lötschental, Neuwirth et al. (2004) analyzed the climatic response of spruce pointer years, Treydte et al. (2001) assessed the climatic significance of delta C-13 in subalpine spruces and Weber et al. (2007) studied growth response to drought of pine and oak. Some of these data were used to develop larger scale climatological networks for the European Alps (e.g. Büntgen et al. 2005, Frank and Esper 2005).

A systematic selection of the trees for dendroclimatology is thereby essential because mainly those suffering from abiotic stress, i.e. temperature extremes or droughts, contain a strong temperature or precipitation signal. Thus, sampling sites are mostly situated rather at high elevations or in arid areas. Associated with global warming, inter-annual tree ring analysis along altitudinal gradients are also of high interest (e.g. Dittmar and Elling 1999, Fonti et al. 2007, Kienast et al. 1987, Savva et al. 2006, Wilson and Hopfmüeller 2001). Elevational gradients allow "space for time" experiments (Körner 2003), i.e. long-term measurements (=time) can be replaced by those along a gradient (=space). For example, the different temperatures measured along a gradient simulate the long-term climatic change. Growing under comparable climatic conditions, researchers can observe how trees adapt to varying temperatures. Not only temperatures are changing with altitude but also atmospheric pressure and, to a lower extent, solar radiation as well as UV-B radiation. In contrast, precipitation, wind velocity, and seasonality are not related to altitude in general (Körner 2007).

On the other hand, **plant physiologists** concentrate on **biotic** processes inside trees. Trees are not only influenced by environmental but also by congenital factors or as Pallardy (2007) wrote: "The environmental regime determines the extent to which hereditary potential of plants is expressed". The fields of genetics and molecular biology include the examination of hereditary potentialities while plant physiologist are interested in the multifaceted processes inside of trees, e.g. photosynthesis, respiration, absorption and transport of water as well as of mineral nutrients (Figure 1.1). The entirety of physiological processes is aimed at one thing: Growth - which is strongly related to reproduction and consequently also to the preservation of the species. Growth processes can be divided into reproductive and vegetative growth. The phases of initiation of floral primordia, blossoming, pollination, fertilization, growth and ripening of fruits and cones can be summarized as reproductive growth (e.g. Lord and Russell 2002, Owens and Hardev 1990). In contrast, vegetative growth includes the expansion of buds, shoot elongation, the development of the root system, and the increase in diameter of different parts of the tree (e.g. Kozlowski 1971, Larson 1994).

The scientific observation of the aforementioned *external signs of tree growth* is usually conducted by phenologists. Lechowicz (2002) defined phenology as "the study of the seasonal timing of events in nature: when flowers bloom, trees leaf out, birds migrate, animals hibernate, fish spawn, phytoplankton blooms, lakes freeze [...]". Today's definitions of phenology are very broad and include the biotic as well as the abiotic sphere. The more restrictive definition of Schnelle (1955) concentrates only on plant phenology as "the science of growth appearance and the development of plants". In conjunction with global warming, the timing of these external signs of (tree) growth has changed. Particulary in spring and summer, there is strong evidence to an earlier occurrence of different phenophases, e.g. flowering, leaf unfolding, or fruiting, for the whole of Europe (e.g. Menzel et al. 2006) as well as for Switzerland (e.g. Defila and Clot 2005).

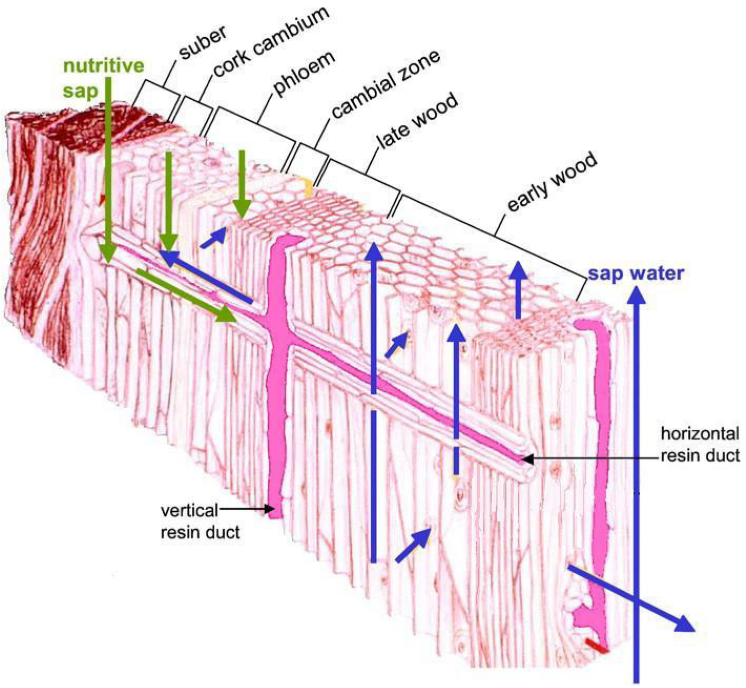

Figure 1.2: *Example of a conifer: Three-dimensional profile of maritime pine wood (Plomion et al. 2001).*

Internal signs of tree growth are detectable when concentrating on cellular level. The meristematic tissues, consisting of apical, primary and secondary (lateral) meristems, are responsible for growth: The undifferentiated cells of the meristematic tissues divide into new cells. Focussing on vegetative growth, e.g. on the increase in tree diameter, the so-called vascular cambium which is part of the secondary meristems induces growth (Figure 1.2). Towards the pith, xylem consisting of earlywood and latewood, is formed. The phloem, cork cambium and suber occur external to the vascular cambium. The sap water ascends via the xylem; while the phloem, composed of still-living cells, is responsible for the transport of the nutritive sap.

Recently, there has been a growing amount of studies linking **the fields of dendroclimatology** and **plant physiology** (e.g. Gindl et al. 2000). Their similarities are the focus on vegetative growth at cellular level as well as on the intra-annual timescale. Following conventional dendroclimatological research, some of these studies related intra-annual cell development to environmental factors. For example, Antonova and Stasova (1997) studied effects of temperature and precipitation on xylem cell production of larch in central Siberia. Deslauriers and Morin (2005) investigated the influence of temperature, precipitation, relative humidity and global radiation on tracheid production of fir in eastern Canada. Mäkinen et al. (2003b) analyzed temperature and xylem formation data in Norway and Rossi et al. (2007) assessed threshold temperatures for xylogenesis in conifers in the Italian Alps. Recent studies with rather physiological background concentrated on processes during tree ring formation. For instance, research into the timing of growth (Deslauriers et al. 2003), the age-dependent duration of xylem differentiation (Rossi et al. 2008) or the comparison of growth variations in different species (Rossi et al. 2006b) in the Italian Alps and eastern Canada placed secondary emphasis on environmental factors. However, most of these recent studies concentrate on a few trees at one or two study sites. Except for Fonti et al. (2007) who linked inter- and intra-annual growth of chestnut along an elevational gradient in the south of the Swiss Alps and Mäkinen et al. (2003a) who analyzed large-scale climatic variability (North Atlantic Oscillation, NAO) and radial increment variations across latitudinal and altitudinal transects in Finland, Norway, and Germany, the examination of intra-annual tree growth along an altitudinal gradient has been broadly ignored.

The uniqueness of seasonal weather fluctuations during any particular year can complicate the year-to-year comparison of intra-annual tree growth. "Space for time" experiments along elevational gradients offer therefore valuable opportunities to investigate intra-annual tree growth under comparable weather conditions.

Accordingly, the main focus of this diploma thesis is on intra-annual growth variations of larch and spruce along an altitudinal transect in the central Swiss Alps during 2007. The primary objectives are a better understanding of tree growth in general as well as of the response of intra-annual growth variations to different meteorological variables. Secondary objectives include the comparison of the increase in stem diameter on cellular level (=internal signs of tree growth) to phenological observations (=external signs of tree growth) and temperature measurements along the elevational transect. Specific research questions are:

(1) What are the differences in temperature and in the duration of the thermal growing season along the altitudinal transect in the Lötschental (1350–2150 m asl)?

(2) Are there any significant differences in tree growth patterns between different elevations or expositions?

(3) Can we detect a connection between the temperature measurements and 2007 growth variations?

Following the introduction, the data and methods used in this study will be explained in chapter 2. The results obtained will be described in chapter 3 and subsequently discussed and interpreted in chapter 4. Finally, chapter 5 will contain conclusions and give an outlook on future activities along the transect.

Chapter 2

Data and Methods

2.1 Geographical setting

2.1.1 Study area

The Swiss canton Valais is located in the southernmost parts of Switzerland. The dry inner-alpine Rhône valley is surrounded by the southern Pennine and the northern Bernese Alps. The study area is situated in the Lötschental which is, with a length of 28 km and an area of about 150 km^2, the largest northern side valley of the alpine Rhône (Figure 2.1).

Figure 2.1: *Location of the Lötschental study area within Switzerland (Atlas of Switzerland 2004).*

From Steg/Gampel (630 m asl[1]), located in the Rhône valley, the Lötschental continues in south-north direction up to Ferden (1,375 m). Therefrom, the direction of the valley, ending at the Lötschenlücke/Lang-glacier (3,178 m), changes to southwest-northeast. Compared to the lower steep part, this upper part is wide and the access is easier. Thus, most of the settlements, i.e. Ferden, Kippel (1,376 m), Wiler (1,419 m), Ried (1,486 m) and Blatten (1,540 m), are situated there. Only Goppenstein (1,216 m) is in the lower part of the valley.

The Lötschental is surrounded by various mountains. The northern range, from the Hockenhorn to the Mittaghorn (about 3,200 m), is the natural limit to the canton Bern. Bordering on the Rhône valley, the southern range, with the Bietschhorn (3,934 m) being the highest peak, is slightly superior. Several glaciers cover the mountainous regions at higher elevations. The study area is drained by the river Lonza and its feeder rivers.

2.1.2 Vegetation

The agriculturally used valley bottom of the upper Lötschental transitions into continuous forest consisting of conifers, i.e. European larch (*Larix decidua*) and Norway spruce (*Picea abies*) at lower elevations, and European larch and occasional Swiss stone pine (*Pinus cembra*) at higher altitudes. Above the timberline, dwarf-shrubs and subalpine grasslands are predominant (Mosimann 1985). Covering large parts of the south and particulary of the north facing slopes, the forests are characterized by creeks, avalanche and debris flow tracks as well as by anthropogenic use. Forest maintenance is thereby crucial because the so-called "Bannwald" should protect the villages against avalanches. Additionally, Alp-pasturing, lumbering, and tourism influence the lateral and altitudinal distribution of the forest (Hörsch 2001). According to Leibundgut (1938), the average timberline of continuous forest is at about 2,230 m on the north facing slope[2], several trees however reach up to 2,290 m (=treeline). The timberline as well as the treeline are lower (2,160 and 2,225 m, respectively) on the south facing slope owing to anthropogenic use (Leibundgut 1938). The position of the timber- and the treeline has not much changed during the past seventy years. In general, climatic factors due to exposure effects do not seem to influence the elevation of the treeline (Paulsen and Körner 2001).

2.1.3 Climate

The Valais is characterized by maritime (Atlantic Ocean, Mediterranean Sea) and continental influences. The Rhône valley is a classic dry inner-alpine valley with the lowest annual precipitation amounts of Switzerland, e.g. Visp has only an annual mean precipi-

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[1] The term "above sea level" is omitted henceforth.

[2] Timberline vs. treeline: Nomenclature after Körner and Paulsen (2004).

tation sum of 521 mm (1961–1990). The Lötschental, situated in the northern part of the canton, is an ”in-between”: Air currents coming from the north or the west bring humid air to the valley, airmasses from the south and east are rather dry. Since the early 1960s MeteoSwiss has been conducting meteorological measurements in the Lötschental. At the beginning the meteorological station was in Kippel (1961–1974), then in Ried (1974–1998) and finally in Blatten (2001–present). The measurements in Ried (1,486 m) represent almost the climatic conditions[3] of the study area. In Ried, the annual mean temperature is approximately 4.8 (± 0.63) °C and the annual mean precipitation sum is about 1110 (± 189) mm. The course of the year shows an increase in temperature from January (-3.5 °C) to July (13.9 °C) and a decrease from July to December (Figure 2.2). Precipitation is rather low from April to September (67–96 mm) and slightly higher in winter (96–121 mm). The meteorological stations surrounding the study area are Adelboden (1320 m, 1346 mm, 5.4 °C) in the north and Zermatt (1638 m, 611 mm, 3.5 °C) in the south. Both stations confirm the intermediate character of the Lötschental. Located in a southern side valley of the inner-alpine Rhône, Zermatt has as little precipitation as measured at the bottom of the Rhône valley (e.g. Visp). The small differences in annual mean temperature can probably be ascribed to altitudinal and topographical differences.

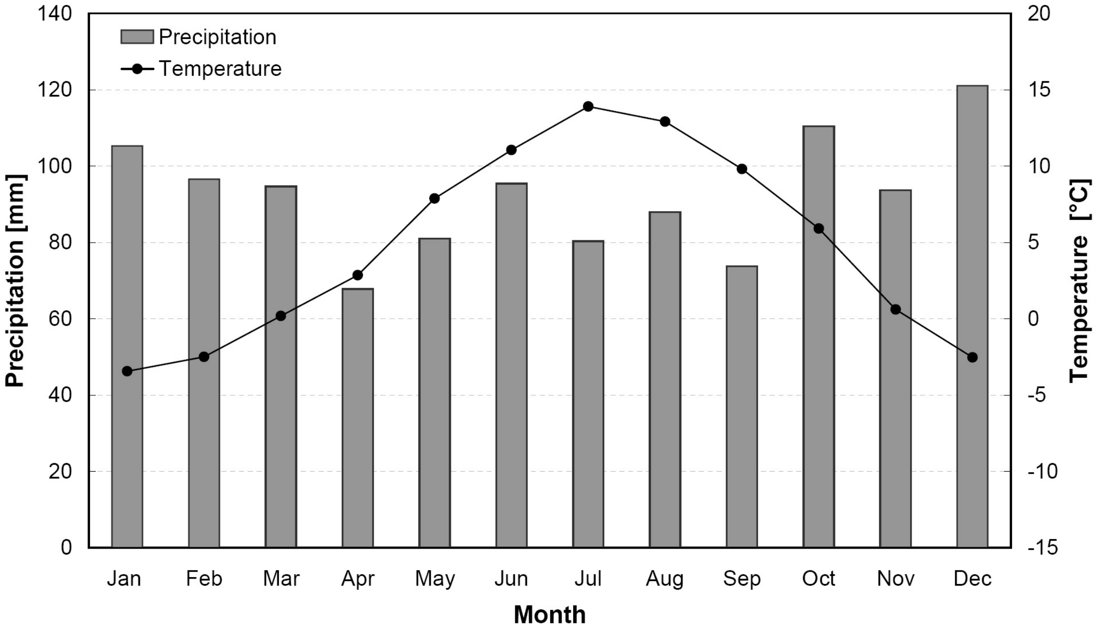

Figure 2.2: *Monthly mean temperature and total monthly precipitation averaged for 1974–1998 from Ried, Lötschental (Data from MeteoSwiss).*

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[3] Climate is defined as ”integral weather conditions” over 30 years (WMO).

2.2 The altitudinal transect

In the present study tree growth variations along an altitudinal transect in the Lötschental are investigated. This transect is close to the village Ferden which is located at the westernmost part of the upper Lötschental. The lowest study site at the bottom of the valley is at 1,350 m (Figure 2.3). The other six study sites are located on the southeast and northwest facing slopes at approximately 1,600 m, 1,900 m and 2,150 m. For xylem sampling twenty-eight European larches (*Larix decidua*) and ten Norway spruces (*Picea abies*) were selected. At each study site four larches and two spruces were chosen with the exception of the two study sites above 2100 m where only larches were available. Ten other spruces were marked to increase the number of trees for phenological observations (Table 2.1). Additionally, stem and soil temperature measurements were conducted along the transect. The temperature data measured at site 1b and 5c were not collected at exactly the same place as the remaining data. To simplify the nomenclature, the terms "site 1" and "site 5" are used instead of "site 1a/b" and "site 5a/b/c", respectively.

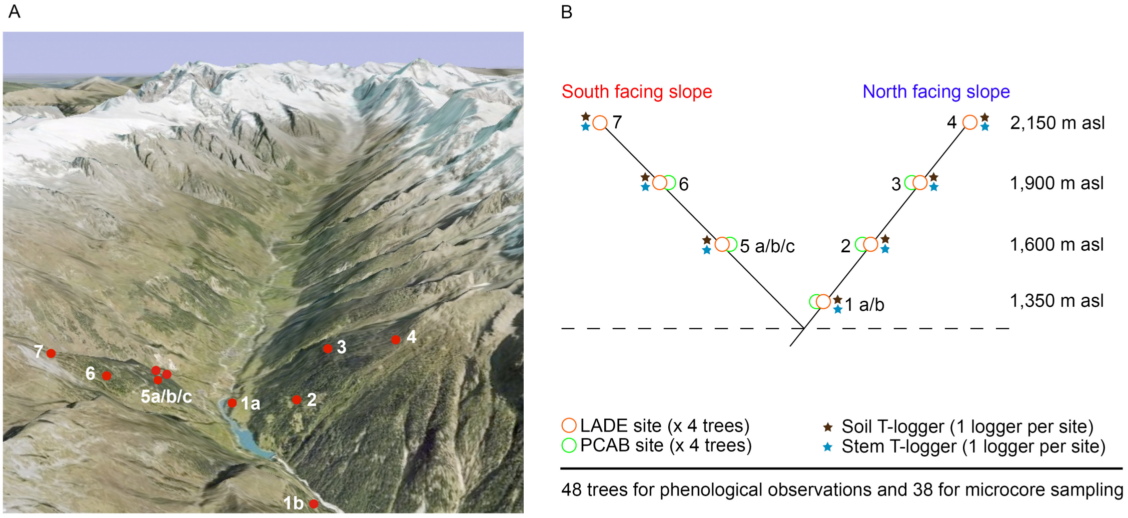

Figure 2.3: *Illustration of the altitudinal transect. (A) Map (GoogleEarth) and (B) schematic diagram of the seven study sites at approximately 1,350 m, 1,600 m, 1,900 m and 2,150 m. LADE indicates larch, PCAB spruce trees. Phenological observations (28 LADE, 20 PCAB), microcore sampling (28 LADE, 10 PCAB) as well as stem and soil temperature measurements were conducted along the Lötschental transect.*

Table 2.1: *Detailed information on the study sites, the selected trees and the measurements. (T: Temperature, P: Phenology, M: Microcores, (+ 2): Additional spruces for phenological observations).*

Site	Latitude/Longitude (N/E)	Altitude (m asl)	Species (Larch/Spruce)	Measurements
Valley				
1a	46°23.500/7°45.688	1365	4/2 (+ 2)	P, M
1b	46°22.799/7°45.203	1315		T(air/soil)
North facing slope				
2	46°23.101/7°45.799	1615	4/2 (+ 2)	T(air/soil), P, M
3	46°23.171/7°46.389	1915	4/2 (+ 2)	T(air/soil), P, M
4	46°22.861/7°46.370	2180	4/0	T(air/soil), P, M
South facing slope				
5a	46°23.790/7°45.269	1645	2/1 (+ 1)	P, M
5b	46°23.834/7°45.337	1645	2/1 (+ 1)	P, M
5c	46°23.946/7°45.301	1615		T(air/soil)
6	46°24.034/7°44.791	1915	4/2 (+ 2)	T(air/soil), P, M
7	46°24.267/7°44.394	2150	4/0	T(air/soil), P, M

2.3 Measurements, observations, monitoring, and analysis

2.3.1 Meteorological measurements

Stem and soil temperatures were measured every 15 minutes and hourly, respectively, from November 2006 to October 2007 at each of the seven sites (Table 2.1). Per site, two StowAway TidbiT temperature-loggers (Long Life for Art, Gottenheim and KS Company, Kremmen, Germany) were installed, with one placed in the soil (-10 cm) and one fixed at the stem (1.5 m above ground). Their measurement range varied from -5 to 37 °C, i.e. temperatures below -5 °C were not recorded. The soil temperature measurements have been continuous for the whole period. Due to expected battery lifetime, the original stem temperature-loggers measured only until mid-September 2007, with replacement loggers placed beside the original at the end of June (Figure 2.4). In addition, the meteorological measurements of the MeteoSwiss weather station at the valley bottom (Blatten) were used for further analysis.

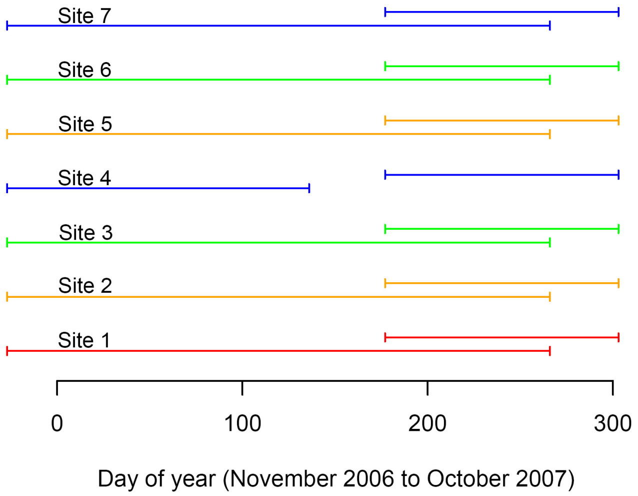

Figure 2.4: *Duration of stem temperature measurements. The interruption at site 4 was caused by a broken logger.*

2.3.2 Phenological observations

Phenological observations were conducted from mid-April to mid-June 2007. The needle appearance of the twenty-eight larch and twenty spruce trees (Table 2.1) was observed weekly following Brügger and Vassella (2003). The phase of needle emergence but prior to needle spreading was defined as a threshold and the percentage of the tree having reached or exceeded this limit was recorded. The date when needles appeared for 50% of the observed crown was listed. Due to only weekly resolution, the 50% phase was missed a few times. In such cases, the date was interpolated linearly. The observations are given as the day of the year (Julian Day or DOY, i.e. 1–365) when the phenological event starts. An example of needle appearance of larch is shown in Figure A.1.

2.3.3 Tree growth monitoring

This section first describes the tree sampling strategy as well as the preparation of the wood samples in the laboratory. Analysis of the 2007 tree ring development is then explained.

Microcore sampling and preparation

Weekly xylem sampling started on May 16 and ended on October 31. The twenty-eight larch and ten spruce trees were sampled on the west and east side of the stem. For the present thesis only the former were used (approximately 950 samples). To avoid wound reactions including resin ducts, adjacent samples were taken 3–5 cm apart. Starting at approximately 1.5 m above ground sampling was conducted diagonally downwards in a zone with a width of 0.5–0.7 m (Figure A.2). To collect the outmost stem tissues, i.e. bark, phloem, cambium and the latest tree rings, a Trephor (Centro Studi per l'Ambiente Alpino, San Vito di Cadore, Italy) was used (Rossi et al. 2006a). The tissue samples, the so-called microcores, are 15 mm in length and 2 mm in diameter. After extraction, the microcores were placed in Eppendorf microtubes (Eppendorf AG, Hamburg, Deutschland) which had been filled with a dilution of acetic acid and ethanol (3:1) to prevent the microcores from drying out. After at least 24 hours this dilution was replaced by ethanol. In the laboratory the microcores were cut transversally with a microtome. The so-called microsections (20-30 μm) were stained for ten minutes with a mixture of saffranin and astrablue (1:1). The staining serves to visualize the level of lignification: blue indicates no lignin, red suggests lignin (Figure 2.6). Afterwards, the samples were rinsed with ethanol and xylol. Canada balsam was finally used to preserve the microsections.

During sampling and preparation some of the microcores broke and could not be analyzed. Figure 2.5 shows the number of successful microcores obtained from the twenty-eight larch trees.

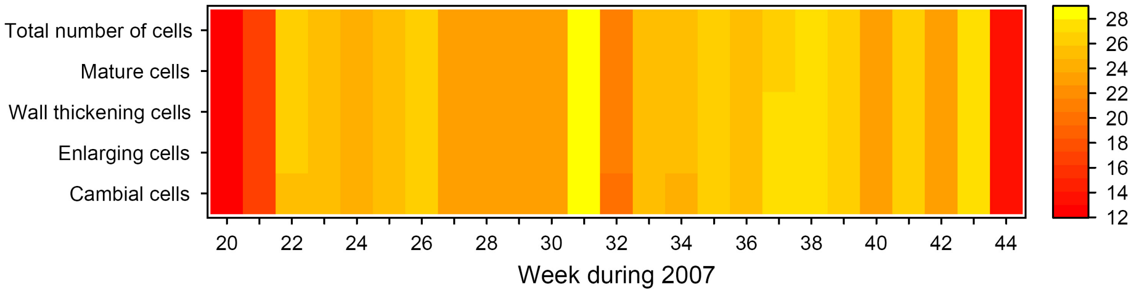

Figure 2.5: *Weekly number of successful microcores obtained from the twenty-eight larch trees. Some of the microcores broke and could not be analyzed. Additionally, in some cases not all the growing stages were visible, e.g. during week 37 cambial, enlarging and wall thickening cells were analyzable 27 times, mature cells as well as the total number of cells only 26 times. At the beginning and at the end of the 2007 growing period the highest study sites were not sampled.*

Microsection analysis

Cell formation can be divided into different stages of development: cell division, cell expansion, cell wall thickening, programmed cell death, and heartwood formation (e.g. Plomion et al. 2001). Microscopic observations with visible and polarized light at a magnification of 400x–600x permit the growing stages to be differentiated. The microsections were analyzed following the criteria established by Abe et al. (1997), Gričar et al. (2005), and Rossi et al. (2007). Accordingly, the developing ring was subdivided into cambial, enlarging, wall thickening and mature cells (Table 2.2). The cells in a particular growing stage were counted along three radial files and the average calculated. The total number of cells (=enlarging + wall thickening + mature cells) was also assessed.

Table 2.2: *Criteria applied for determination of different growing stages during ring formation.*

Cambial cells	Thin cell wall Small radial diameter Not visible under polarized light
Radial enlargement phase	Still thin primary cell wall Radial diameter at least twice that of a cambial cell Not visible under polarized light
Cell wall thickening phase	Cell wall partially red under visible light Glistening under polarized light
Mature cells	Cell wall completely red under visible light

For clarification of the different growing stages of xylem cells, an example of a microsection is shown in Figure 2.6. Following a radial file, in the left-most position there are four phloem cells. Because the phloem belongs to the bark the cells were not counted. The adjacent eleven cambial cells are characterized by very thin cell walls and small radial

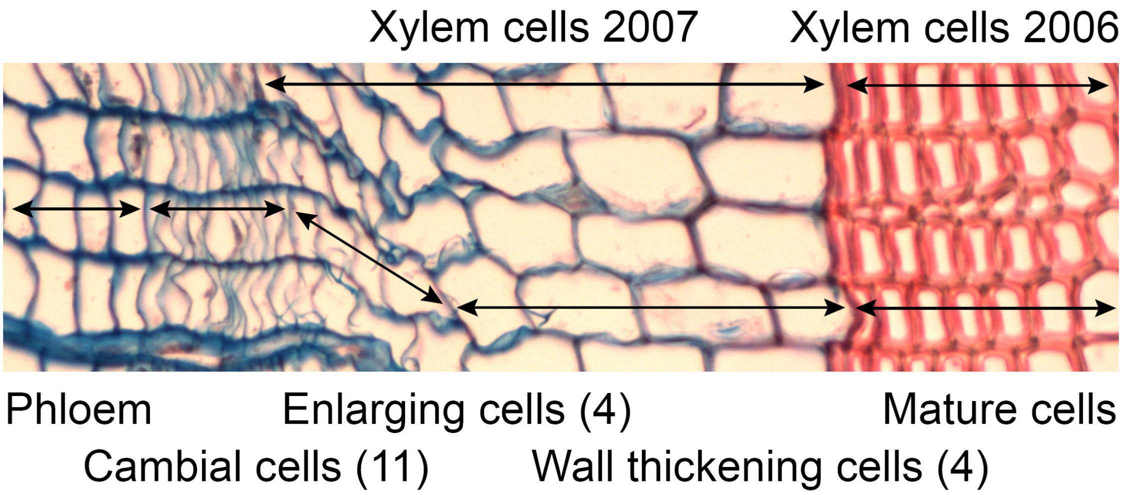

Figure 2.6: *Visualization of different growing stages with the help of a microsection collected on July 24, 2007. The corresponding microcore stems from a larch tree at site 4 (2150 m, north facing slope, see Figure 2.3).*

diameters. The next four cells are in the enlargement phase. Their cell walls are still thin but the radial diameters have to be at least twice that of a cambial cell. The differentiation of enlarging and wall thickening cells (neighboring four cells) is only possible when using polarized light because during the formation of the secondary wall the arrangement of cellulose microfibrils causes a glistening. In summary, the 2007 tree ring collected on July 24 contains eleven cambial, four enlarging and four wall thickening cells but it does not possess any mature cells yet. However, a few fully developed tracheids are visible in the 2006 tree ring. Their cell walls are completely red under visible light, i.e. lignification and thus cell maturation are completely finished.

2.3.4 Data analysis

This section focus on the analysis applied on the meteorological measurements, the phenological observations and the evaluated ring development data.

Meteorological measurements
To limit the period when temperatures are essential for tree growth the duration of the "thermal" growing season was assessed following the definition by Körner and Paulsen (2004): The beginning of the growing season (MAM) is determined when soil temperature exceeds 3.2 °C in spring for the first time. Accordingly, the end of the growing season (SON) is reached when soil temperature is below 3.2 °C in autumn. The duration of the growing season as well as the seasonally average stem and soil temperatures were calculated for each study site. To describe the change in temperature along the altitudinal gradient, simple linear regression was used (Wilks 2006).

Growth variations
Phenology and timing of ring formation
Simple linear regression was applied to assess the altitudinal change in needle appearance, onset and maximum of cell enlargement, the onset of cell wall thickening and maturation. To test if the lowest and highest sites or opposite slopes show statistically significant differences in the timing of different growing stages, the Wilcoxon-Mann-Whitney rank-sum test was applied (Wilks 2006). This nonparametric test was chosen due to the small sample size.

Total number of xylem cells at the end of the growing period
The attempt to estimate the total number of xylem cells at the end of the growing period revealed two main difficulties inherent to the raw tree growth data. The first problem is the high variability of the total number of cells among trees of the same site. The position of the site, the differing influence of various environmental factors, hereditary potentialities, and the age of the trees can effect the amount of cells. To reduce the variability among

trees of the same site the total number of cells of each tree was multiplied by a correction factor (Equation 2.1).

Assuming that tree growth is finished when maturing is completed, i.e. the counted total number of cells thereafter only fluctuates around the ”true” number of cells, the average over the period after maturing is finished should represent the ”true” number of cells. Accordingly, the ”true” number of cells for each site was assessed by calculating the average number of cells of all four trees when maturing was complete. The correction factor consists of the ”true” number of cells of all four trees at site s divided by the ”true” number of cells of tree t at site s. For each site the corrected total number of cells was thereafter averaged - with each tree thus having equal weight in forming the site mean.

$$CorrNC(t,s) = TotalNC(t,s) * \frac{MeanNC(4t,s)}{MeanNC(t,s)} \tag{2.1}$$

CorrNC (t,s) = Corrected total number of cells of tree t at site s
TotalNC (t,s) = Original total number of cells of tree t at site s
MeanNC (4t,s) = Average number of cells of all 4 trees at site s when maturing is completed
MeanNC (t,s) = Average number of cells of tree t at site s when maturing is completed

The second difficulty is the high week-to-week variation of the total number of cells within one tree. As stated earlier adjacent microcores were collected a few centimeters apart. A change in the total number of cells should therefore not only be ascribed to growth but also to this shift in sampling location considering that trees do not build the same amount of cells around the stem. Even within a single microcore not all files contain the same number of cells. As a result, the week-to-week variation within one tree can be large and even negative increments can occur, particulary at the end of the growing period. Dealing with this problem, Camarero et al. (1998) showed that the combined growth of several trees follows a S-shaped curve. To estimate such a S-shaped growth curve nonparametric regression was applied on the corrected total number of cells averaged for each site (Bowman 2006). As an example, Figure 2.7 shows the regression curve for site 6. From this curve, the weekly growth rates (=regressed value of the current week - regressed value of the preceding week) were calculated. It was assumed that the total number of xylem cells at the end of the growing period was reached when weekly growth rates equal zero.

Temperature and growth variations

To explore common growth variations between sites, the differences between the original and the regressed values were assessed (Figure 2.7). These residuals of the seven different sites were correlated with each other to detect a common growth signal (Spearman rank correlation, Wilks 2006). If the correlation was statistically significant ($p < 0.05$) the residuals of the corresponding sites were again averaged. Finally, the "average growth residuals" were correlated with the "average stem and soil temperature residuals", with the temperature residuals determined analogously as for growth.

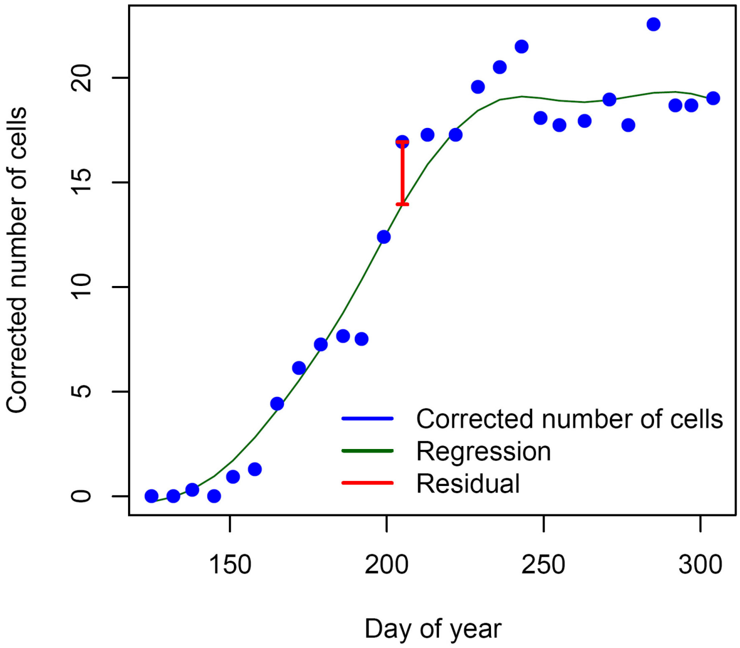

Figure 2.7: *Example of a residual of tree growth (red line). A residual is defined as vertical distance between the regression line and the corrected number of cells.*

Chapter 3

Results

This chapter connects the meteorological measurements to the 2007 tree growth using two different approaches. Firstly, the influence of shifts in average temperatures (Section 3.1) on cell formation (Section 3.2) was evaluated with regard to altitudinal differences. Secondly, an attempt to detect a common pattern in week-to-week changes in tree growth and temperature was made (Section 3.3).

3.1 Meteorological measurements

Figure 3.1 compares the 2007 temperature and precipitation measurements at Blatten to those of the period 2001 to 2006 (MeteoSwiss). On average, the year 2007 was slightly warmer (4.15 °C vs. 3.63 °C) and rainier (1350 mm vs. 990 mm). Obvious differences occur in January, February, and April with 2007 being considerably warmer (+4–5 °C). On the other hand, post-midyear temperatures were rather below average (about -1 °C). There was more precipitation in May (+200 mm) as well as in January, July, August and December 2007 (+60–90 mm) in comparison with the 2001 to 2006 average.

Temperatures measured along the altitudinal transect are summarized in Figures 3.2 and 3.3. The former figure shows absolute stem and soil temperatures of site 1 at 1350 and site 7 at 2150 m (see Figure 2.3) which represent the largest temperature differences along the transect (Figure 3.2, panel c). At the beginning as well as at the end of the year stem and soil temperatures are close to 0 °C. In early spring stem and soil temperatures increase within several days and remain on this higher level during summer until they decline in October. Generally, if the ground is not frozen or snow-covered, soil temperatures parallel stem temperature variations but in a more smoothed fashion and with little delay. During

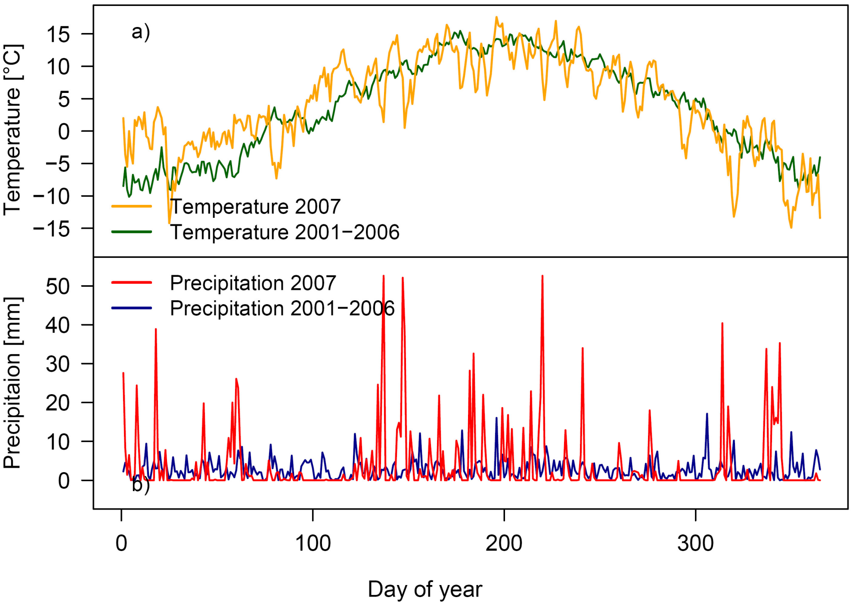

Figure 3.1: *Average 2001–2006 temperature (a) and precipitation (b) measurements at Blatten compared to those of 2007.*

late spring and summer the temperatures at the valley bottom are clearly higher (+2–6 °C) than those at 2150 m.

The second figure (3.3) reveals stem and soil temperature differences due to exposure. In contrast to altitudinal stem temperature differences, those owing to exposition range only from -1 to 1 °C except for the sites at 1900 m revealing larger differences in winter, spring and autumn (Figure 3.3, panel b). Soil temperature differences also vary less (-2–1 °C) in summer and increase during the rest of the year (0–4 °C). The sites at the north facing slope seem to possess higher soil temperatures (Figure 3.3, panel c). However, there is no consistent slope effect detectable, i.e. temperatures are not generally higher on one slope. Compared to others, daily mean stem and soil temperature differences between the lowest and the highest sites as well as between opposing slopes, the altitudinal temperature differences are larger than those owing to exposition.

To quantify the change of stem and soil temperature along the elevational transect, the duration of the thermal growing season (i.e. in spring > 3.2 °C, in autumn < 3.2 °C) and growing season mean temperatures were assessed at each site (Table 3.1). The length of the thermal growing season varies from 154 at 2150 m (Site 4) to 203 days at 1350 m (Site 1), showing a shortening with increasing altitude even if the threshold temperature

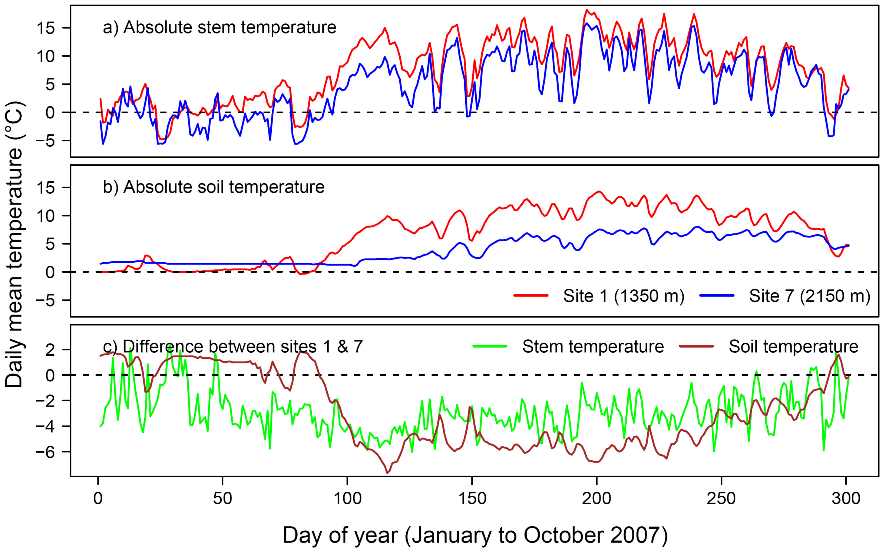

Figure 3.2: *Absolute stem (a) and soil (b) temperatures as well as temperature differences (c) between the lowest (site 1) and the top (site 7, south facing slope) sites (see Figure 2.3 for locations of the sites).*

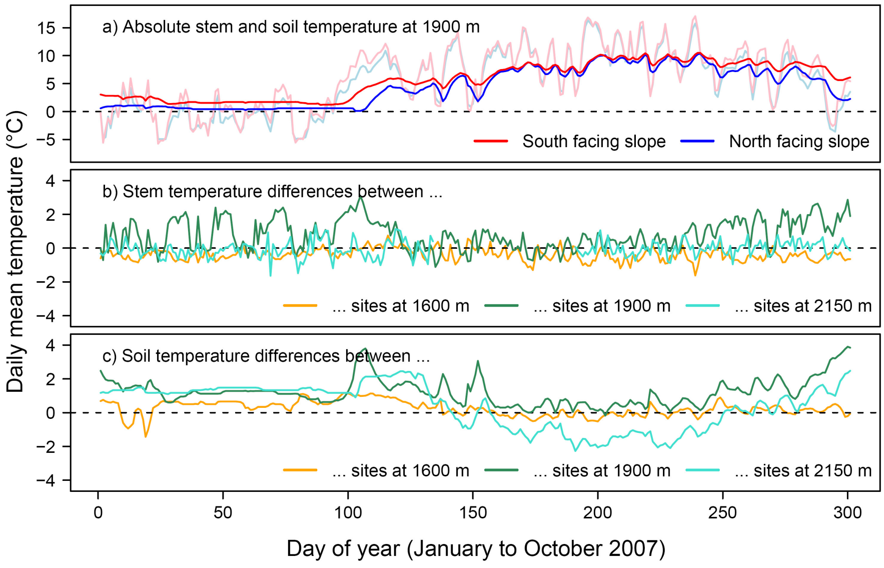

Figure 3.3: *Absolute stem and soil temperature of opposite slopes at 1900 m (a). The stem (b) and soil (c) temperature differences of the sites on the north facing slope to those on the south facing slope are demonstrated in the lower panels.*

Table 3.1: *The duration of the thermal growing season (i.e. in spring > 3.2 °C, in autumn < 3.2 °C) and growing season mean temperatures in 2007. At some study sites the temperature threshold (3.2 °C) was not reached in autumn (+), i.e. the growing season would have lasted a few days longer.*

Site	Stem temperature (°C)	Soil temperature (°C)	Duration of growing season (d)	
Valley				
1	10.8	9.7	203	
North facing slope				
2	9.8	8.4	197	(+)
3	8.5	6.9	181	
4	8.3	6.7	154	
South facing slope				
5	9.4	8.5	200	(+)
6	8.8	7.6	197	(+)
7	7.9	5.9	168	(+)

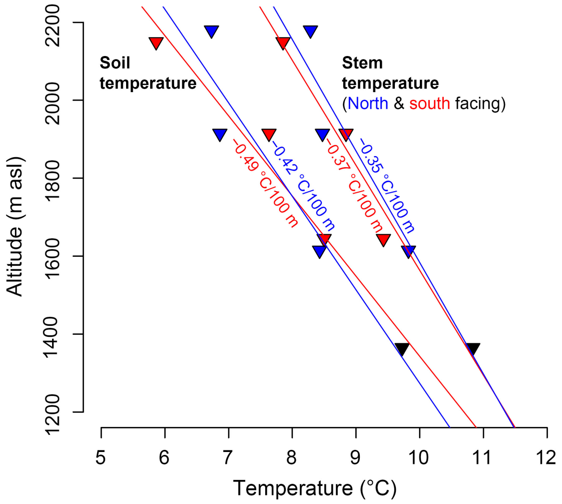

Figure 3.4: *Stem and soil temperature gradients on the north (blue) and the south facing (red) slopes in 2007. The triangles denote the growing season mean temperatures.*

was not reached in autumn at some sites. Growing season average temperatures are close to 10 °C at the lowest site and decrease to 6–8 °C at the highest sites. As stated earlier average altitudinal stem and soil temperature differences (2.9–3.8 °C) exceed those due to exposition (0.4–0.8 °C). To represent temperature changes along the entire transect, linear regression was applied on growing season mean temperatures (Figure 3.4). Stem temperatures decline by 0.35–0.37 °C/100 m with increasing altitude while soil temperatures decrease along a steeper gradient (0.42–0.49 °C/100 m). The differences due to exposure are more distinct in soil temperatures (Figure 3.4).

3.2 Growth variations

Phenology

Phenological observations reveal that needle appearance of larch and spruce differs by more than one month (Figure 3.5). At the valley bottom the needle emergence of larch (spruce) began on April 16 (May 20), at 1600 m it started on April 22 (May 31), at 1900 m the onset was on April 27 (June 10) and at 2150 m on May 7. It is obvious that the needle appearance of larch at a particular altitude is broadly distributed compared to that of spruce, e.g. at 1900 m it lasted from April 27 to May 20 for larch and from June 10 to June 13 for spruce. Therefore, the needle appearance of larch along the transect happened within 35 days, that of spruce within only 25 days.

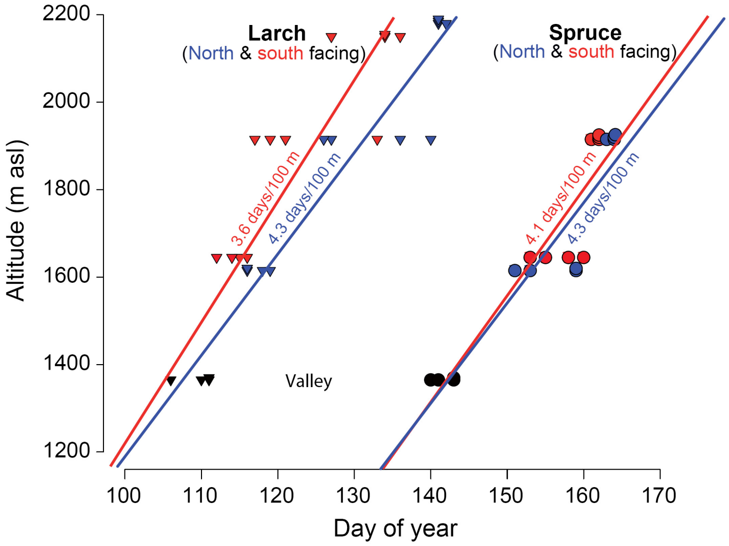

Figure 3.5: *Needle appearance of larch and spruce on the north (blue) and the south facing (red) slopes. The triangles indicate larch, the circles imply spruce. At each study site four larches and four spruces were chosen with the exception of the two study sites above 2100 m where only larches were available.*

The Wilcoxon-Mann-Whitney rank-sum test shows statistically significant differences ($p < 0.05$) in needle appearance not only between the two species but also between the lowest and highest (larch: 1 vs. 4/7, spruce: 1 vs. 3/6) as well as between the two highest opposing sites (larch: 4 vs. 7, spruce: 3 vs. 6). No statistically significant differences were detected when testing the lower opposing sites (larch: 1600 and 1900 m, spruce: 1600 m) as well as the composite south and north facing slopes. Applying simple linear regression, the delay of needle appearance with increasing altitude is similar for both species (about 4 days/100 m). Concerning exposure larch reveals greater differences rising with elevation.

Ring formation

The evolution of ring formation for larch and spruce is demonstrated in Figures 3.6 (larch) and A.3 (spruce). The weekly number of cells per growing stage (enlargement, wall thickening and maturation) was averaged for each site. Both graphs overview the available data and give an idea of the timing of ring formation at different altitudes as well as of the total number of xylem cells at the end of the growing period (see below).

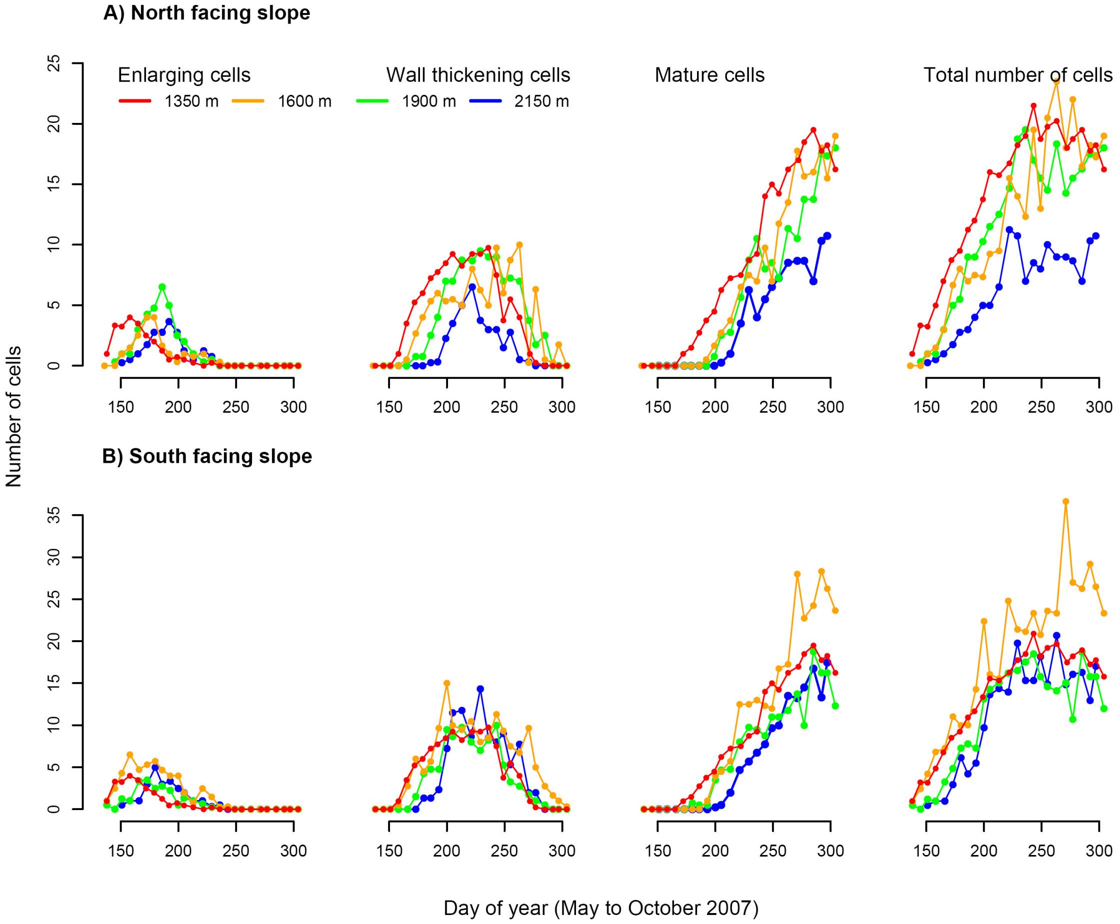

Figure 3.6: *Evolution of ring formation of larch on the north (A) and the south facing (B) slopes. The points indicate the weekly number of cells in a certain growing stage averaged per study site, the colors denote the different altitudes.*

However, they also show the high variability; especially the larch trees at 1600 m and spruces at almost every site reveal week-to-week variations of up to ten or even twenty cells. The higher variability of the spruce results in part from having only two trees per site in comparison to four. These sample sizes are not large enough to average out measurement errors, variability due to sample location, individual tree variation, etc. The data collected from larch are thus more reliable and therefore spruce will be excluded from further analysis.

Timing of ring formation

The timing of ring formation can be characterized by focusing on the onset, maximum and ending of cell enlargement and cell wall thickening as well as on the beginning of cell maturation (Figure 3.7). The two most important development stages are the onset of cell enlargement and the ending of cell wall thickening because they denote the beginning and the end of cellular growth, respectively.

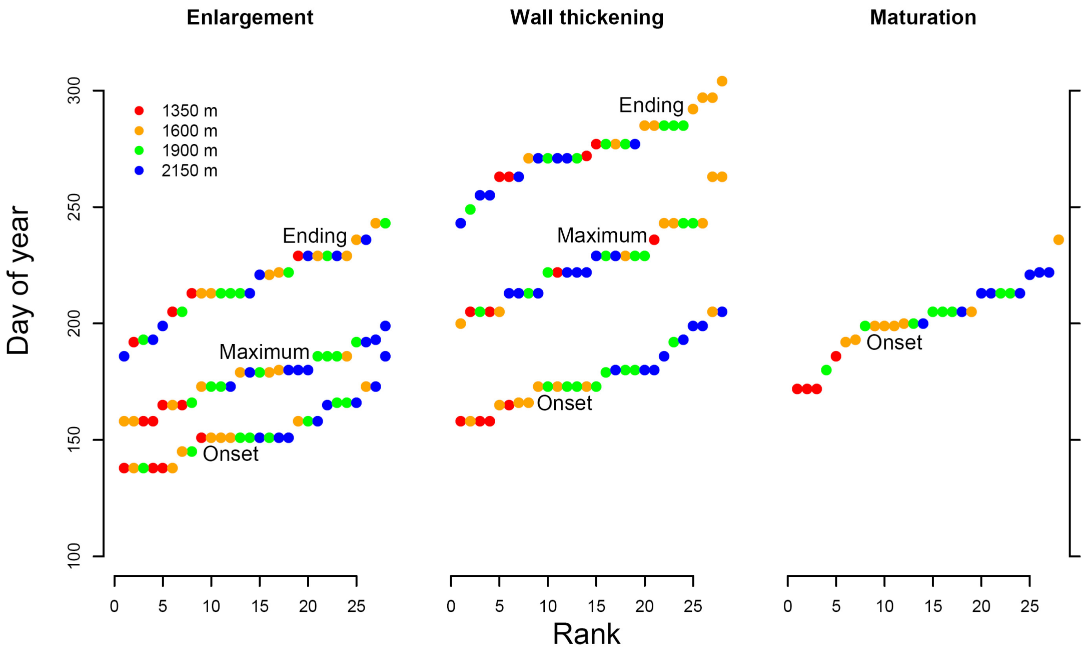

Figure 3.7: *Timing of ring formation: Onset, maximum and ending of cell enlargement and of cell wall thickening as well as initiation of cell maturation. The colors indicate the altitude of a particular tree. No differentiation was made due to exposure. The ranks imply that e.g. the first tree reaching the ending of cell enlargement has rank 1.*

Following cell division, the earliest observed onset of *cell enlargement* started on May 16 (Figure 3.7). Because of methodological changes and likely the exceptionally warm spring, the real onset of some trees at the valley bottom and on the south facing slope was missed. Their microsections revealed already one or two cells on May 16, which leads to the assumption that the real onset was about one or two weeks earlier. In this case the initiation of cell enlargement along the transect would have lasted approximately two months (until July 5) — considering that the trees at the lower sites started earlier than those at the top sites. The same pattern, i.e. trees at lower sites reached the maximum earlier than those at top sites, was also noticed for the maximum of cell enlargement observed between June 7 and July 18, i.e. all trees along the transect achieved their maximal growth within 6 weeks during June and the first half of July. The ending of the cell enlargement process began on July 5 and ceased on August 31 with the influence of the altitude being marginal. The whole enlarging process along the transect lasted about four months (May–August).

The beginning of the *wall thickening* growing stage was between June 7 and July 24 (Figure 3.7). Tendencies to an earlier onset at the lower sites are again revealed. In contrast, the maximum as well as the ending of cell wall thickening do not show any considerable differences due to elevation. These development phases lasted from July 19 to September 20 and from August 31 to October 31, respectively. The entire cell wall thickening proceeded also during approximately four months (June–October). Moreover, the termination of the maximum and ending of cell enlargement phases ceased in the same week when the corresponding development phases of the cell wall thickening began.

The onset of *cell maturation* began on June 21 and was completed by August 24 (Figure 3.7). The trend towards an earlier beginning at lower sites was also observed in this development phase.

The assumption of a particular pattern, e.g. trees at lower sites reach different development phases earlier than those at top sites (see Figure 3.7), was confirmed by applying the Wilcoxon-Mann-Whitney rank-sum test. Statistically significant differences ($p < 0.05$) between the lowest and highest sites (Sites 1 vs. 4/7) were detected for the onset and maximum of cell enlargement as well as for the beginning of the wall thickening and maturing phases. Other elevational differences, e.g. sites at 1600 vs. those at 1900 m, were not tested. The remaining development phases (i.e. the ending of cell enlargement, the maximum and ending of cell wall thickening) did not reveal any statistically significant differences due to altitude. No statistically significant differences were found when testing opposing sites (2 vs. 5, 3 vs. 6, 4 vs. 7) and opposing slopes (sites 2+3+4 vs. sites 5+6+7).

Simple linear regression was applied to quantify the change in needle appearance, in onset and maximum of cell enlargement, in onset of cell wall thickening and cell maturation, i.e. of those development phases showing statistically significant differences between the lowest and the top sites (Figure 3.8). On the south facing slope, the gradients vary from 3.6 to 9.9 days/100 m. Gradients seem to be steeper as the growing period progresses. Some trend calculated for the south facing slope, especially for the onset of cell maturation (Figure 3.8), appears to poorly fit the observations. Except for phenology, the coefficients of determination on the south facing slope are relatively small, i.e. linear regression is probably not the appropriate method because even not the half of the variation of the dependent variable is thereby described. The gradients on the north facing slope range between 4.3 and 6.9 days/100 m and are thus smaller than on the south facing slope (Figure 3.8). Even though there are no statistically significant differences due to exposure, the north facing slope shows a more reliable pattern (=higher coefficients of determination). Hence, we estimate that the shift in growing stages is about 4 to 7 days/100 m. The higher gradients on the south facing slope, i.e. the onset of cell wall thickening and maturation, are excluded due to poor fit.

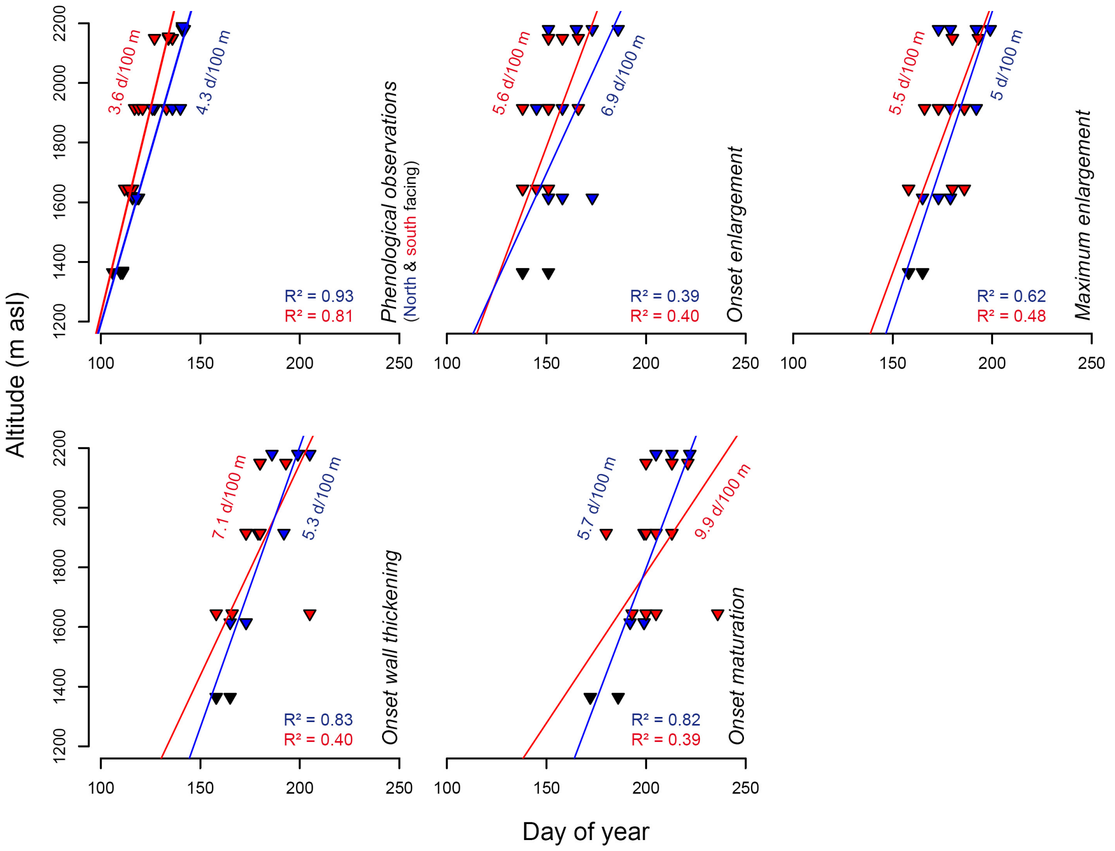

Figure 3.8: *Elevational changes in needle appearance, onset and maximum of cell enlargement, onset of cell wall thickening and cell maturation on the north (blue) and the south facing (red) slopes.*

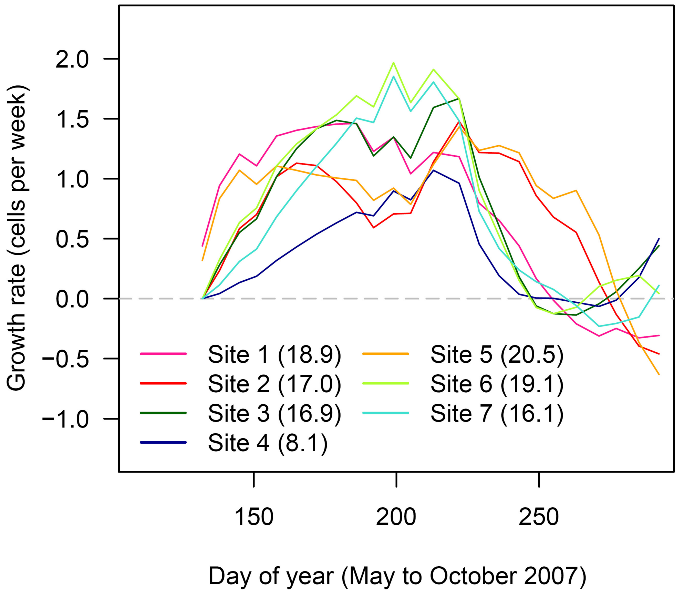

Figure 3.9: *Growth rates during 2007: Colors indicate growth rates at different sites, values in brackets denote the total number of xylem cells at the end of the growing period.*

Total number of xylem cells at the end of the growing period

The weekly growth rates calculated from the nonparametric regression curve (see Figure 2.7) are compared in Figure 3.9. Weekly increments were assessed by subtracting the total number of cells of the preceding week from the total number of cells of the current week. As already observed in Figures 3.6 and A.3 and discussed above, the week-to-week variations in the raw data are considerable with negative increments occurring. A part of the variability could be removed by smoothing via the nonparametric regression. Additionally, the negative increments were nearly eliminated - except for the end of the growing season. Nevertheless no meaningful differences due to altitude or exposure can be detected. The total number of xylem cells at the end of the growing period (Figure 3.9, values in brackets) shows rather higher values at the valley bottom (19 xylem cells) as well as on the south facing slope (16–20 xylem cells) compared to the north facing slope (8–17 xylem cells). A consistent slope effect is detectable, i.e. the 2007 tree rings on the south facing slope contain more cells than those on the north facing slope. There is also a slight decrease of the total number of xylem cells with elevation but the differences between the sites are rather small.

3.3 Temperature and growth variations

As already mentioned in the introduction of this chapter, the change in average temperatures and shifts in development stages are linked with regard to altitudinal differences (see Figures 3.4 and 3.8). The needle appearance, the onset of cell enlargement, the maximum of cell enlargement, the onset of cell wall thickening and the onset of cell maturation showed statistically significant differences due to elevation. Their gradients varied from 4 to 7 days/100 m. Combined with the altitudinal stem and soil temperature differences of 0.35 to 0.49 °C/100 m the average shift per °C is about 13 days!

A first attempt to find common inter-week variations in temperature and 2007 tree growth is summarized in Figure 3.10 for the whole growing period. Applying the same time interval as determined by the weekly sampling, the daily mean stem and soil temperatures were

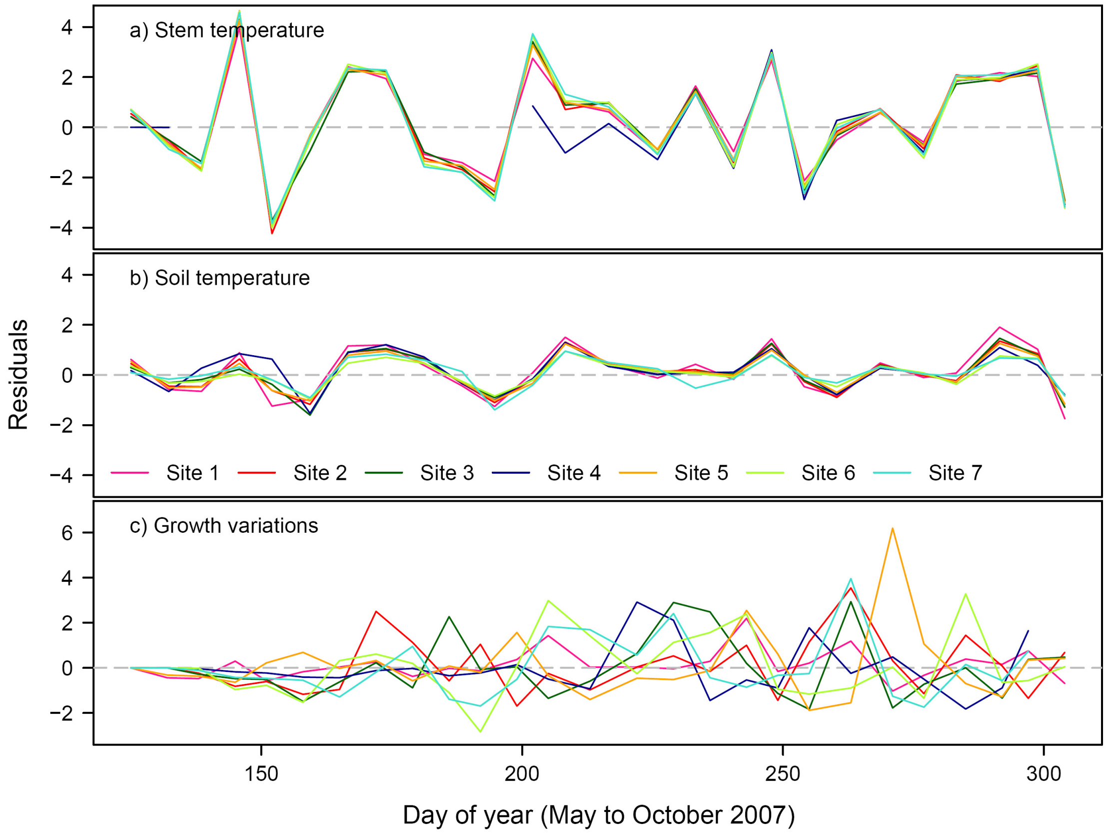

Figure 3.10: *Residuals of stem temperatures (a), soil temperatures (b) and tree growth (c). Residuals are the differences of the original to the regressed values. Different colors denote the 7 study sites.*

averaged and prepared identically to the tree growth data, i.e. nonparametric regression was used to assess the residuals. The stem and soil temperature residuals range from -4 to 4 and -2 to 2 °C, respectively (Figure 2.7). There are almost no differences related to elevation or exposure, i.e. the temperatures of different sites show a similar course during the vegetation period (see also Figures 3.2 and 3.3). In contrast, the residuals of tree growth differ much from site to site, and hardly any common signal can be detected. The Spearman rank correlation matrix ($r_{rank} \leq 0.4$) confirms this observation.

In a second attempt the May-June-July (MJJ) and the June-July-August (JJA) period was focused on because inter-annual studies indicate the importance of early summer and summer temperatures on tree growth. Statistically significant correlation coefficients ($p < 0.05$) among growth residuals of different sites were detected (MJJ: 3/4, 6/7; JJA: 1/6, 6/7). The average growth residuals as well as the average stem and soil temperature residuals of these particular study sites were calculated and correlated with each other (see Figure A.4 and A.5). However, interpreting the two graphs hardly any coherent conclusion can be drawn. The data seems to be too noisy for this type of weekly analysis.

Chapter 4

Discussion

In this chapter the findings are discussed and interpreted. Adopting the same structure as in the result's section, the focus is first on the meteorological measurements. Subsequently, growth variations are discussed and finally connected to temperature.

4.1 Meteorological measurements

The main purpose of the corresponding result's section was to assess the length of the thermal growing season and to describe the temperature differences along the altitudinal transect. The results revealed that the duration of the growing season ranges from 154 (Site 4, 2150 m) to 203 days (Site 1, 1350 m) (Table 3.1). Stem and soil temperature differences due to exposure (0.4–0.8 °C) are considerably smaller than those due to elevation (2.9–3.8 °C) (Figures 3.2 and 3.3). Moreover, stem temperatures decrease less (0.35 and 0.37 °C/100 m) with altitude than soil temperatures (0.42 and 0.49 °C/100 m) (Figure 3.4).

The presented findings need to be discussed in relation to some *limitations* caused by the data collection and analysis. Temperature measurements are relatively simple to conduct except that the exposure to solar radiation has to be avoided. Following Körner and Paulsen (2004), the soil temperature-loggers were placed 10 cm below soil surface under closed forest tree canopy. Stem temperature-loggers were fixed at the north or northeast side of the stem underneath a protective box. As already noted in the results, stem temperatures in winter, spring and autumn seems to be influenced by the lower position of the sun causing an elevated heating-up of the stem (see Figure 3.3). To quantify the temperature differences only growing season mean temperatures were used, i.e. the problematic data were excluded to a large extent. This applies also to errors due to restricted measurement range of the loggers. Because temperatures below -5 °C emerged mainly during winter and early spring this shortcoming did not influence the results. Further difficulties in data collection appeared owing to the broken stem temperature-logger at site 4 (2150 m) (see Figure 2.4). No stem temperature measurements were available at this site from May 17 to June 27. This lack of data results in greater uncertainty of growing season mean temperatures (stem: 8.3 °C, soil: 6.7 °C). Compared to the close-by site 3 (stem: 8.5 °C, soil: 6.9 °C) at 1900 m stem and soil temperatures differ both by 0.2 °C. This indicates that growing season mean stem temperatures at site 4 are nevertheless useable.

With the collected data, the duration of the growing season was assessed by using a threshold soil temperature of 3.2 °C (Körner and Paulsen 2004). For this, soil temperatures were selected because they reveal a relatively sharp increase after snow melt and only dampened day-to-day variations compared to stem or canopy temperatures. Körner and Paulsen (2004) calculated a linear regression of 7-day-means of canopy temperatures and 7-day-means of soil temperatures at the treeline (2050 ± 20 m) of Mount Patscherkofel, Austria. They discovered that soil temperatures corresponded to 3.2 °C when canopy temperatures were 0 °C. The same procedure was applied on the data of the two highest sites in the Lötschental but the correlation between stem and soil temperatures was rather poor. Hence, the threshold soil temperature of Körner and Paulsen (2004) was adopted. A further difficulty appeared when estimating the length of the growing season. The temperature measurements were only available from November 2006 to October 2007 at each site and therefore the threshold temperature in late autumn was not reached at some sites (2, 5, 6, 7). Considering that soil temperature response is delayed with respect to changes in air temperature, the growing season should have been finished within several days. The influence on growing season mean temperatures is therefore rather insignificant.

Even though there are — as shown above — some limitations concerning data collection and analysis, several studies have obtained similar results. Compared to the *mean growing season soil temperatures* of 6.3 to 7.7 °C for five sites (1900–2370 m) in the Swiss Alps (Körner and Paulsen 2004) the present results of 5.9 and 6.7 °C for the highest sites in the Lötschental seem to be reasonable (see Table 3.1). For the same sites, Körner and Paulsen (2004) also showed that the *thermal growing season* lasted between 117 and 152 days (1996–2001). The duration of the growing season (154 and 168 days) at the top sites in Lötschental is slightly longer probably due to the fact that our sites are situated rather lower as well as because of the exceptionally warm spring (see also Rutishauser et al. 2008). There are other studies assessing the length of the growing season but most of them are based on phenological or satellite data sets (Linderholm 2006). For climatological (or thermal) growing seasons, Carter (1998) emphasized that the growing "season" and the growing "period" should definitely be distinguished. The former term implies that plant growth is theoretically possible, the latter circumscribes the period when plants really grow. Even if a few studies estimated the long-term change in the duration of the thermal growing season (for Europe: Carter 1998, Hasenauer et al. 1999, and Menzel et al. 2003) a comparison remains challenging due to differences in the definition. For instance, applying the frost-free criterion Menzel et al. (2003) discovered a lengthening of 0.5 days/year over the 1951 to 2000 time period for Austria and Switzerland. Combined with a rise of annual temperatures of approximately 1.1 °C during the last fifty years in Switzerland (Rebetez and Reinhard 2007), the prolongation is about 25 days/1.1 °C. In the present thesis the duration of the growing season shows a shortening of about 50 days/800 m altitude. Associated with the mean stem temperature gradient of -2.8 °C/800 m, the shift is roughly 20 days/1.1 °C. As aforementioned, altitudinal gradients should allow "space for time" experiments. Here, the long-term change in days per °C is indeed almost similar to short-term shifts along the altitudinal transect. The small discrepancy can probably be ascribed to slightly differing definitions concerning the limitation of the thermal growing season or to differences in the location of the study area. Menzel et al. (2003) mentioned also that the trend of 0.5 days/year appeared to weaken at sites above 950 m.

The findings concerning the small *temperature differences due to exposure* and the lack of consistent slope effects (see Figure 3.3) agree with the results of Körner and Paulsen (2004). Their analysis of treeline ground temperatures revealed no exposure effects on forested slopes in the European Alps. In addition, Innerebner (1933) also confirmed that air temperatures across seasons, measured in the shade 2 m above ground, were similar on north and south facing slopes in the central Alps.

The commonly used wet adiabatic lapse rate declines by approximately 0.65 °C/100m. The *altitudinal stem and soil temperature gradients* of the present thesis are lower with a range of 0.35 °C/100 m to 0.49 °C/100 m. One possible explanation for this difference could be that even though the stem temperature-loggers were fixed at the north or northeast side of the stem they still benefited from the warming of the bark on the other side of the tree. Because the forest tree canopy was more open at the top sites compared to lower elevations, the bole could profit to a greater extent by the heating-up. Growing season mean stem temperatures of 7.9 and 8.3 °C, observed at the highest sites in the Lötschental (Table 3.1), support this theory as they exceed air temperatures of 5.5 to 7.5 °C at the Swiss treeline (Körner 1998, Körner 2003). The comparison with the wet adiabatic lapse rate as well as with Körner (1998) and Körner (2003) remains challenging. On the one hand, air, stem, and soil temperatures are delicate to compare and on the other hand, there is a difference between single year and long-term means.

4.2 Growth variations

The identification of significant differences in growth patterns along the altitudinal transect was the central objective of the associated result's section. The timing of ring formation as well as the total number of xylem cells at the end of the growing period were assessed. The results indicate statistically significant differences in the timing of ring formation concerning the following growing stages: needle appearance, the onset of cell enlargement, of cell wall thickening and of cell maturation as well as the maximum of cell enlargement (Figure 3.7). Their gradients vary from 4 to 7 days/100 m (Figure 3.8). The total number of xylem cells at the end of the growing period reveals small differences due to altitude as well as owing to exposure. Compared to 8 to 17 xylem cells on the north facing slope, the total number of xylem cells at the valley bottom (19) and on the south facing slope (16–20) is higher (Figure 3.9).

Even though *phenological observations* are commonly used, particular *restrictions* have to be mentioned. In collecting phenological data, the observer plays a decisive role because she/he should be familiar with the trees, the surroundings, and the growing stage of the preceding week (Brügger and Vassella 2003). Therefore, alternating observers should be avoided. Due to the spread of sites different persons were involved in observing the trees along the transect in the Lötschental. However to minimize biases the different observers were trained beforehand to develop a common observational framework. Further difficulties emerged if the view of the crown was limited or during unfavorable weather conditions, e.g. cloudiness, rain or sunset. The illumination of the tree is very important and influences the assessment of the growing stage. Such limitations always occur when working with phenological data but their quantification remains challenging (Brügger and Vassella 2003).

The *sampling of the microcores* is also subject to some *restrictions* influencing the derived results. Due to methodological changes and likely the warm winter/spring, the real onset of the enlargement growing stage was missed at the valley bottom and on the south facing slope. Revealing one to two cells on May 16, the interpretation of the particular microsections lead to the assumption that the real onset was approximately one or two weeks earlier. Associated with the altitudinal gradient, an earlier beginning at the lower sites would probably improve the linear relationship (see Figure 3.8). Moreover, the sampling strategy may also affect the quality and characteristics of the data. Starting at approximately 1.5 m above ground, sampling was done diagonally downwards (0.5–0.7 m) and restarting again at 1.5 m (Figure A.2). We assume that one reason for the variability of the total number of cells within a tree could be caused by this restart at the top of the sampling zone. But not all of the variation is due to the sampling method. Other explanations, e.g. the total number of cells varies even within a microsection, are also important. To collect the microcores a Trephor was used (Rossi et al. 2006a). Non-specific tools such as the surgical bone needle or specially designed instruments, e.g. the increment puncher (Forster et al. 2000) or the increment hammer, would be alternatives. The advantages of the Trephor are its easy manageability in the field and the simple removal of the fragile microcores out of the extracting needle. Thus, compared to the increment puncher newly built cells are not damaged by the removal tool. When collecting microcores wound reaction is a further problem to deal with. According to Forster et al. (2000) traumatic tissues appeared approximately as far as 1 cm around the injury. Therefore, it is quite astonishing that in our case, taking adjacent samples 3 to 5 cm apart, wound reaction, especially resin ducts, could not be completely avoided. All microsections with resin ducts were nevertheless analyzed by counting the cells along files not disturbed.

Our procedure of *preparing the microcores* is very time-consuming and demanding. Much practice is needed to cut the small samples transversally with a microtome. Some of the microcores broke due to the weak connection between bark and xylem (see Figure 2.5). Hence, Rossi et al. (2006a) suggested to embed the microcores in paraffin in order to stabilizing them before cutting. This could probably decrease the number of broken samples but their procedure is even more laborious.

The presented findings are also influenced by some methodical decisions. The *analysis of the tree growth data* was dominated by the difficulties of high week-to-week variations within different trees of the same site as well as within one tree. To solve the former problem a correction factor was applied (see Equation 2.1). There are many possibilities to do such corrections, e.g. Rossi et al. (2003) worked with a circumference adjustment whereas the rings of the preceding three years were included. The second difficulty — variations within one tree — was treated by applying nonparametric regression (Bowman 2006). Most of the other authors working in the field applied the Gompertz function to remove short-term variations (e.g. Mäkinen et al. 2003a, Rossi et al. 2003). The S-shaped growth curve captures well the flattening at the end of the growing period when the raw data show their highest variability. This is probably the greatest shortcoming of the nonparametric regression method: In a few cases the curve does not reflect the ending of the growth in a appropriate way owing to its sensitivity to outliers. However, an advantage of the nonparametric regression is that it does not a prior constrain the shape of growth to an expected model. Hence, nonparametric regression was used to assess the growth curve as well as finally the residuals.

When working with data obtained from trees it is necessary to be aware of the various methodical difficulties as shown above. The comparison with similar studies should help to judge the present findings. Concerning the *phenological observations* Defila (2003) examined needle appearance of larch in the canton of Grisons. At Zizers and Chur (both 600 m) the mean needle appearance was on April 8 (Site 1 at 1350 m: April 19) and at Pontresina (1805 m) on May 28 (Site 3/6 at 1900 m: May 7). The larches in the Lötschental appear to start earlier. Considering that Defila (2003) worked with average values over the period 1951 to 1998 and the spring 2007 was exceptionally warm, the present phenological data could be regarded as ”outliers”. According to Rutishauser et al. (2008), the high temperatures were responsible for an very early beginning of spring phenophases within Switzerland. The altitudinal gradient of about 4 days/100 m derived from the phenological observations in the Lötschental (see Figure 3.5) was confirmed by Defila (2002). He estimated an almost similar gradient of 4.1 days/100m for the Engadin situated also in the canton of Grisons. For the leaf/needle appearance Defila and Clot (2005) discovered an earlier beginning of 16 days in the northern and a delay of 1 day in the southern Alps from 1951 to 2002. Assuming that the Lötschental is rather located in the northern part of the Swiss Alps, a change of 16 days/1.1 °C can be assessed emanating from a warming of 1.1 °C during the last fifty years (Rebetez and Reinhard 2007). The shift in the Lötschental is about 12 days/1.1 °C. It seems that the short-term shifts along the altitudinal transect represent again quite well the long-term trend.

There are some difficulties to link the *timing of ring formation* along an altitudinal transect to other studies. The location (altitude and latitude), the species, the year chosen, and the age of the trees complicate the comparison with related research. Situated relatively close to the Lötschental, similar studies were conducted on the southern side of the Swiss Alps as well as in the southern and eastern Italian Alps. Fonti et al. (2007) examined vessel size of chestnut along an elevational transect (300–900 m) in the south of the Swiss Alps. They discovered that the first vessels appeared in late April and early May in 2005. The initiation of cell enlargement along the Lötschental transect lasted from mid-May to early July. The later onset can potentially be ascribed to the higher altitudes of our sites. The comparison of different species is also influenced by the fundamental differences in physiological processes. At the timberline (2080 m) in the eastern Italian Alps Rossi et al. (2006b) observed similar patterns in xylem formation of larch, pine and spruce during 2003. A bell-shaped curve characterized the cell enlargement and cell wall thickening phase, the cell maturation and consequently the total number of cells followed a S-shaped curve. In the same area identical species were also examined during a longer time period from 2002 to 2004 (Rossi et al. 2007). Larch showed an average onset of radial enlargement varying from May 20 to June 9, the average ending of wall thickening lasted from approximately September 5 to October 15 and the mean duration of the growing period ranged from 90 to 137 days. The present results of the highest study sites (see Figure 3.7) revealed a later average initiation of cell enlargement (June 12) but the mean cessation of wall thickening (September 20) as well as the duration of the growing period

(100 days) confirm the findings of Rossi et al. (2007). Moreover, they referred to the statistically significant differences in the length of the growing period among the three years what was also supported by Deslauriers et al. (2008). Such comparisons are not possible with these data as they (at least at the moment) only represent one single year. Deslauriers et al. (2008), in comparing the growth of pine (*Pinus leucodermis*) at 2100 m in two contrasting years (2003 and 2004), showed statistically significant differences in the duration of the growing period, in the onset and the ending of cell enlargement and in the beginning of the cell wall thickening phase (shifts of about 23 days). No statistically significant differences were observed for the conclusion of cell differentiation. Compared to the Lötschental, the trees in southern Italy revealed an obvious earlier beginning of all the growing stages, particulary during 2003 (Deslauriers et al. 2008). Furthermore, Rossi et al. (2008) discovered that the timing and the duration of xylogenesis are age-dependent. However, using only adult trees the differences found in the timing of ring formation along the Lötschental transect do not appear to be caused by differing ages. To summarize, several factors complicate a comparison with linked studies. The detected gradients could neither be confirmed by short- nor long-term research owing to the absence of similar studies.

To get a rough idea of how many cells were built during 2007, the *the total number of xylem cells at the end of the growing period* per site was calculated. The results revealed higher values at the valley bottom (19 xylem cells) as well as on the south facing slope (16–20 xylem cells) compared to the north facing slope (8–17 xylem cells) (see Figure 3.9). The total number of xylem cells declined slightly with altitude and a consistent slope effect was detectable but the differences between the sites were rather small. This comparison is somewhat difficult because — although we corrected the data — the individual tree growth potential, resulting in a different number of xylem cells, is not sufficiently considered. The finding that the total number of cells differs significantly between years (Rossi et al. 2007) possibly supports our results. But they disagree with those of Deslauriers et al. (2008) who concentrated on two contrasting years with different temperature regimes simulating an elevational gradient. Even though the growth period was considerably shorter in 2004 (88 vs. 110 days in 2003) the findings showed a similar total number of cells during 2003 and 2004 while tree ring widths, caused by larger earlywood cells, were different (see also Zweifel et al. 2006).

4.3 Temperature and growth variations

The aim of the corresponding result's section was firstly to merge average temperatures and growth variations via altitude. Secondly, common inter-week variations in temperature and 2007 tree growth should be detected with the aid of residuals determined as difference between the S-shaped growth curve and the raw data. The first approach revealed an average shift of approximately 13 days per °C (see Figures 3.4 and 3.8). The second approach, on the other hand, showed that the growth residuals did not have any common signal (see Figure 3.10), i.e. there is no evidence for the response of inter-weekly tree growth to temperature during the 2007 growing period.

There are two *restrictive points* which have to be discussed in connection with the available findings. Firstly, the assumption that altitudinal changes in average temperatures as well as in the timing of different growing stages are represented by a linear relationship is delicate (see Figure 3.8). It is a fact that temperatures do not always change along a linear gradient and the same applies probably also to the timing of ring formation. But even if the linear regressions do not represent the "real" shifts with altitude, to the first order they describe tendencies of temperature and timing of ring formation with increasing elevation. The second point concentrates on the residuals (see Figure 3.10). The basic idea of growth residuals was to examine anomalies to "standard" growth following usual treatment in dendroclimatological research. Because no "standard" growth curve exists, nonparametric regression was applied to estimate a "standard" growth curve per site and to calculate thereafter the residuals as differences of the raw data to the S-shaped curve. Hardly any common growth signal between the different sites was detected suggesting that one year of tree growth monitoring with ≤ 4 samples per site is definitely not enough to overcome the high variations.

The *first approach* relating average temperature and growth variations with regard to altitudinal differences revealed an shift of 13 days per °C. Neither short- nor long-term research with a similar setting were found to compare the observed change. The temperature measurements and the phenological observations showed that data collected during only one year along an altitudinal gradient seem to relatively well represent the longtime changes. This approach has an important shortcoming: Other (environmental) factors such as soil conditions, precipitation or pollution were neglected although they certainly influence tree growth. However, Körner (2007) emphasized that mainly temperature varies along an elevational transect.

The *second approach* was chosen to find a relation between current-year temperatures and tree growth. As noted in the introduction, there are studies that succeeded in relating environmental factors and intra-annual growth variations (e.g. Deslauriers and Morin 2005, Mäkinen et al. 2003b) by correlating meteorological variables with weekly/daily growth rates. Applying the same approach, statistically significant correlations were detected at the highest sites in the Lötschental (not shown). But high correlations can not definitely be ascribed to a relation between temperature and growth rates because their curves follow both per se a bell-shaped curve over the course of a growing period.

When focussing on the whole growing period, no common growth signal was detected for the Lötschental. Therefore, the time period was limited to May-June-July (MJJ) and June-July-August (JJA) following Büntgen et al. (2005) and Büntgen et al. (2006b). Though the corresponding results could not be used to detect inter-weekly temperature dependence, the observations revealed that the cell enlargement, which is mainly responsible for the tree ring widths, along the whole transect lasted until August 31. The growing stages revealing significant differences due to altitude ended on August 24. Moreover, the maxima of radial enlargement along the Lötschental transect emerged between June and the first half of July. Hence, a high correlation of tree ring widths with average June-July-August temperatures is broadly understandable based upon the intra-seasonal measurements conducted during this thesis. More direct evidence however will only be possible with measurements spanning several years.

Chapter 5

Conclusion and Outlook

The present thesis has examined the intra-annual tree growth of 2007 along an altitudinal transect in the Lötschental, Switzerland. An improved comprehension of tree growth in general and especially of the response of intra-annual growth variations to meteorological variables were the primary objectives. Secondary aims involved the connection of the increase in stem diameter on cellular level with phenological observations as well as in-situ temperature measurements. The research questions raised in the introduction can be answered as follows:

(1) What are the differences in temperature and in the duration of the thermal growing season along the altitudinal transect in the Lötschental?

The results revealed stem and soil temperature differences of 2.9 to 3.8 °C between the lowest and the top sites. Differences due to exposure were considerably smaller (0.4–0.8 °C). The comparison with other studies confirmed the argument of almost nonexistent differences owing to exposition. The mean stem and soil temperature gradients, calculated on the basis of growing season mean temperatures, declined by 0.36 and 0.46 °C/100 m, respectively. Different limitations during data collection and analysis, e.g. the restricted measurement range of the loggers, the definition of the growing season and finally differences in measuring methods of air, stem, and soil temperatures, have influenced the present findings. Our gradients were possibly therefore smaller than the commonly used wet adiabatic lapse rate (0.65 °C/100m). The duration of the thermal growing season became shorter with increasing elevation (from 203 to 154 days). Its length at the highest sites agrees with the results of Körner and Paulsen (2004). Long-term observations of the duration of the growing season (1950–2000) revealed a prolongation of about 25 days/1.1 °C for Switzerland (derived from Menzel et al. 2003 and Rebetez and Reinhard 2007). Compared to the shift of 20 days/1.1 °C along the Lötschental transect, elevational gradients seem to quite well represent long-term changes in the length of the growing season and therefore allowing "space for time" experiments.

(2) Are there any significant differences in growth patterns (including needle appearance, cell enlargement, cell wall thickening, cell maturation and the total number of xylem cells at the end of the growing period) between different elevations or expositions?

Needle appearance, the onset of cell enlargement, cell wall thickening and cell maturation as well as the maximum of cell enlargement showed statistically significant differences between the lowest and the top sites while none due to exposure were found. Thus, only altitudinal gradients, varying from 4 to 7 days/100 m for the different growth patterns, were assessed. The comparison with Rossi et al. (2007) showed broad similarities for the timing of ring formation at higher altitudes. However, the location, the species, the year chosen, and the age of the trees made such comparisons challenging. Long-term monitoring of leaf/needle appearance (1951–2002) denoted an earlier start of 16 days/1.1 °C for the northern Swiss Alps (derived from Defila and Clot 2005 and Rebetez and Reinhard 2007). The shift in the Lötschental was about 12 days/1.1 °C, i.e. the short-term change along the altitudinal transect represented again quite well the long-term trend (="space for time" experiments).

The total number of xylem cells at the end of the growing period revealed altitudinal differences between the lowest and top sites of approximately ten cells and differences due to exposure of three to eight cells. A consistent slope effect was detectable, i.e. the 2007 tree rings on the south facing slope contained more cells than those on the opposing slope.

(3) Can we detect a connection between the temperature measurements and 2007 growth variations?

The relationship between average temperatures and 2007 tree growth via altitudinal differences revealed a change of about 13 days per °C. Although mainly temperature varies along an elevational gradient (Körner 2007), it is however important to note that other (environmental) factors, e.g. soil conditions, precipitation, and pollution, were neglected. The second approach, using residuals to find a connection between inter-week variations in temperatures and tree growth, failed. One year of only four measurements per site is probably not enough to overcome the high week-to-week variation.

For Switzerland, a further increase in temperature of 0.8 to 3.3 °C in spring and 1.4 to 4.7 °C in summer compared to 1990 is predicted for 2050 (OcCC/ProClim 2007). For the duration of the growing season and the phenological observations (see questions 1 and 2), a good agreement between short-term observations along the transect and long-term measurements (fifty years) was found. Hence, the same approach can also help to estimate future changes in the timing of growth patterns, e.g. the growing period in the Lötschental would start 10 to 60 days earlier in 2050 when combining the temperature scenarios (see above) with the observed shift of about 13 days per °C in 2007. An earlier beginning of the growing period in spring would have an influence on the distribution of different plant communities: Especially those at higher altitudes would be displaced but the characteristic landscape at lower elevations would also change. However, it is still partly unclear how the predicted warming and changes in precipitation could affect growth rates and the related total number of xylem cells at the end of the growing period. Because of the (future) importance of trees as relevant primary products, e.g. for constructions and energy, and sinks for elevated carbon dioxide, the assessment of possible changes in future growth rates is of great relevance.

Therefore, the research activities along the altitudinal transect in the Lötschental will continue until 2010. An additional site, situated at 800 m in the Rhône valley, was chosen to represent warmer climatic conditions. The research activities will include the further observation of intra-annual growth of larch and spruce trees and in-situ climatic data to overcome the deficit of possessing data for only one year. Moreover, the monitoring of isotope cycles will be realized. At the end of the field campaign, the relationship between cambial growth and climate will be expanded back in time using local time-series of radial growth, density, and wood anatomical characteristics. Finally, intra-annual growth will be modeled for a even better understanding of the timing of ring formation and the growth rates.

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Appendix A

Supplementary Figures

Figure A.1: *Needle appearance of larch, spring 2007.*

Figure A.2: *Sampling strategy.*

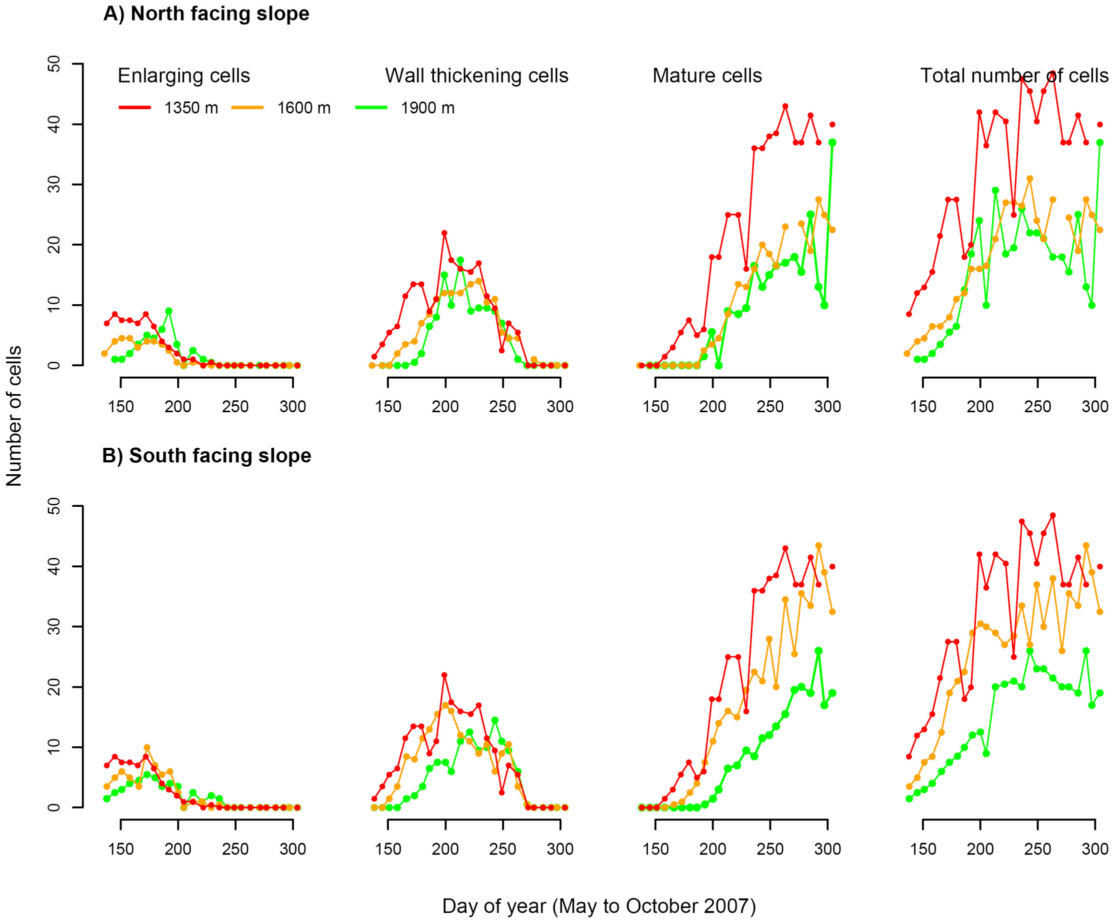

Figure A.3: *Evolution of ring formation of spruce on the north (A) and the south facing (B) slopes. The points indicate the average number of cells in a certain growing stage. The different colors illustrate the altitude.*

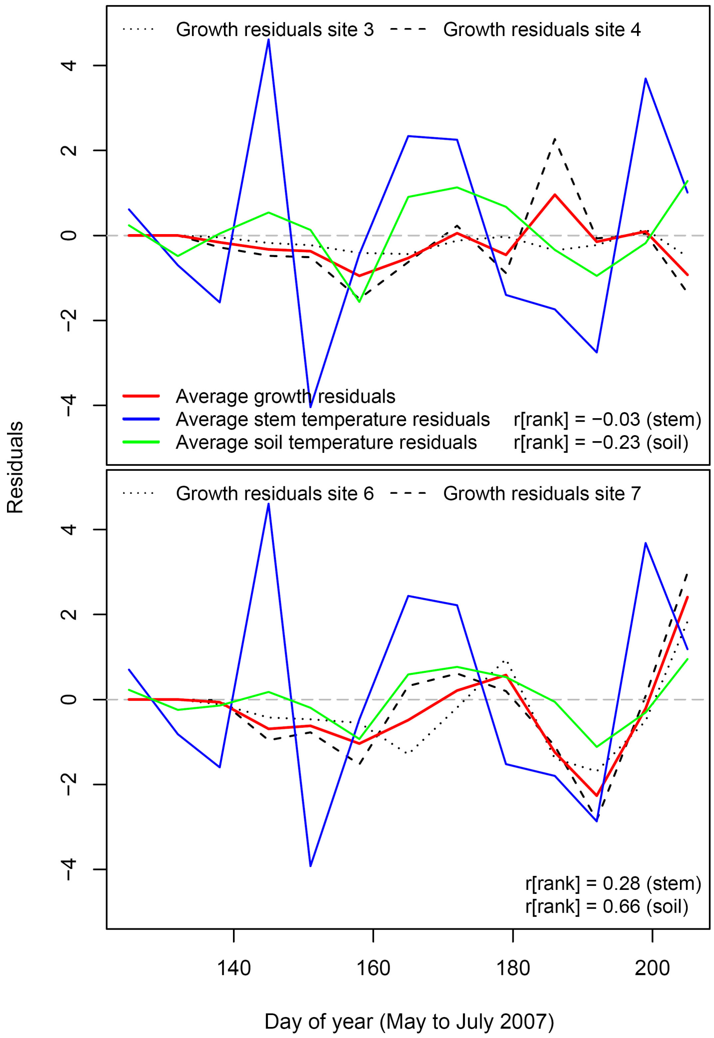

Figure A.4: *Sites 3/4 (top) and 6/7 (bottom): Correlation of "average growth residuals" with "average stem and soil temperature residuals" for May to July 2007.*

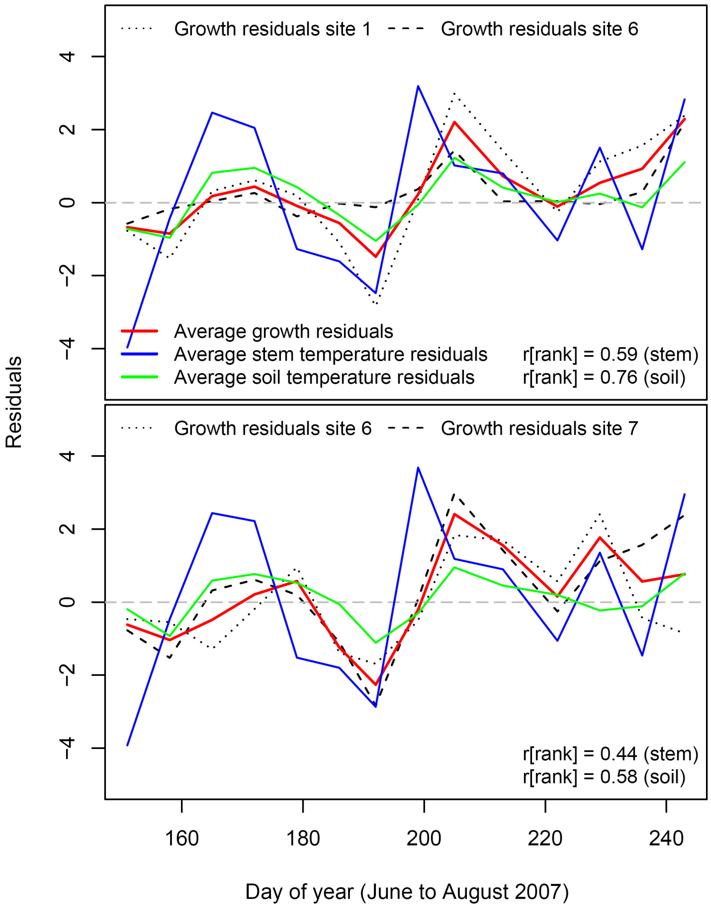

Figure A.5: *Sites 1/6 (top) and 6/7 (bottom): Correlation of "average growth residuals" with "average stem and soil temperature residuals" for June to August 2007.*