INtra-seasonal **T**ree growth along **E**levational **GRA**dients in the European A**L**ps **(INTEGRAL)**

1. Summary

While considerable uncertainties are associated with the understanding of the earth's climate system, General Circulation Models (GCMs) commonly predict future widespread temperature increases into the next century (Stott et al. 2006), thereby continuing the warming known from instrumental observations and proxy records (Frank et al. 2007a). Impacts of the recent warming have been recognized for both abiotic (e.g., permafrost melting) and biotic (e.g., spring greening) systems. Forests represent an important biosphere component, as they contain about 90% of the living terrestrial biomass, significantly regulate the land-atmosphere flux of water vapor, and are of considerable economic importance to society. However, even without consideration of feedbacks, warming impacts on ecosystem functioning in general and forests in particular, are difficult to predict due to their great complexity.

In the proposed project, we aim to study the influence of a warming climate on tree-growth. To reach this objective, we have selected a study location (Lötschental Valley in the Central Swiss Alps) that offers a 1000 meter elevational gradient within a confined geographical region. The Lötschental offers both north and south facing slopes that are forested from the valley bottom (~1300 m asl) to treeline (~2300 m asl) with inter-mixed evergreen spruce (*Picea abies*) and deciduous larch (*Larix decidua*) trees. The temperature change along this transect (~ 4°C) roughly corresponds with that projected for the year 2100 based on GCMs driven by reasonable emission scenarios (IPCC 2007). As effects from warming may involve non-linear and subtle shifts in growing season length and cellular activity, significant emphasis will be placed on temporally highly-resolved (intra-seasonal) field measurements including:

i) weekly collection of microcore samples,
ii) hourly dendrometer measurements,
iii) weekly phenological observations, and
iv) in-situ meteorological measurements.

Details about the timing and duration of tracheid growth for different growing seasons (2007 – 2010) and as a function of elevation, will allow determination of climatic influences upon growing season length and growth rates. These high-resolution data will be extended by increment cores to retrospectively assess radial growth and density (Frank and Esper 2005a), and wood anatomical characteristics (Fonti et al. 2008c) over the past couple hundred years. As relative growth influences may change over time (e.g., as a function of mean temperature) and are additionally intercorrelated, we propose to use a cambial growth model as an objective framework for investigating climatic forcing (Anchukaitis et al. 2006). In a two-way process, this model will be parameterized/verified by the intra-seasonal measurements, and will then be used to hindcast the growth variations over the past 100+ years. Regionally available long instrumental temperature, precipitation, and radiation series (Auer et al. 2007, Frank et al. 2008b) will be employed for both empirical and modeling assessments. Cambial modeling activities will allow discrimination of the multiple climatic influences that simultaneously drive tree-growth, and in turn will be improved by the intra-annual measurements for improved predictions of future growth with GCM ensembles.

The proposed project will, for the first time, integrate intra-annual observations, long-term measurements, and modeling runs of tree growth along an elevational transect, thereby providing new data and insights of species specific responses to temperature change.

Key words: cambial growth model, climate change impacts, dendroclimatology, forest productivity, global warming, intra-annual growth variations, Swiss Alps, temperature gradient, xylogenesis

2. Proposed Research

2.1. State of knowledge

Significant progress has been made in understanding local, regional, and continental-scale European climate variability over the past 150 to about 500 years through studies of long observational station records (Brohan et al. 2006, Auer et al. 2007), documentary archives (Brazdil et al. 2005), tree-ring chronologies (Frank and Esper 2005b, Büntgen et al. 2006b, Wilson et al. 2005a,b), multi-proxy compilations (Luterbacher et al. 2004, Xoplaki et al. 2005), and modeling efforts (Raible et al. 2006). These European wide studies, along with most of those for other regions and hemispheric scales (IPCC 2007), show consistent evidence for unprecedented warmth in recent decades (**Fig. 1**). Results from GCMs, in concert with observational and reconstructed temperature data, have led to the conclusion that anthropogenic forcing has been at least partly responsible for the observed temperature increases. While considerable uncertainty for the magnitude still exists, all projections indicate future warming.

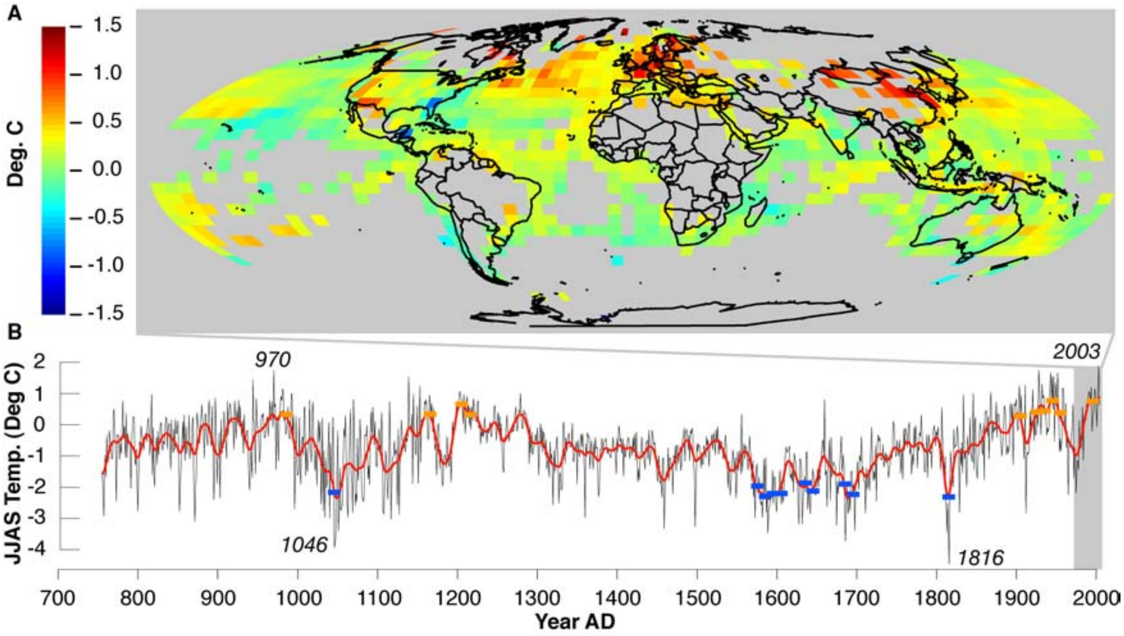

Figure 1. *Recent and reconstructed temperature changes for* ***A)*** *global annual temperature difference between 1977-1991 and 1992-2006 for all locations with complete data coverage (data from Brohan et al. 2006), and* ***B)*** *summer temperature evolution (755-2004 AD) for the greater Alpine region (Büntgen et al. 2006b). The central European area has experienced recent warmth with respect to* ***A)*** *global conditions and* ***B)*** *the past millennium.*

Impacts of the recent warming trend are currently recognized for both abiotic and biotic ecosystems. Ecological changes that have already been attributed to warming include tree-line migration (Esper and Schweingruber 2004), changes in insect outbreak activity (Esper et al. 2007a), trends in boreal forest productivity (Bouriaud et al. 2008), earlier onset of spring (Menzel and Fabian 1999, Rutishauser et al. 2008), and biome (Walther et al. 2002, Penuelas and Filella 2001) and biodiversity shifts (Parmesan and Yohe 2003). Independent of recent temperature trends, impacts of climate variability on plant growth are omnipresent. The similarities between climatic classification and the global distribution of tree species, the ability to use tree-ring chronologies to study past climatic variation, and also the flurry of papers describing the impacts to plant ecosystems following the exceptional summer of 2003 (Ciais et al. 2005, Jolly et al.

2005, Leuzinger et al. 2005) are all examples suggesting strong climate-plant linkages. Of particular relevance to the proposed research, we identify dendrochronological time-series, wood anatomical quantification, intra-seasonal observational measurements, and modeling simulations as important methods and tools to assess climatic impacts on plant growth.

Insights to the longer-term climatic controls on radial tree growth have been derived from empirical analysis of annual rings and climatic variations. Most of these studies have investigated tree-ring width (TRW) (Gindl et al. 2000, Cook et al. 2001, Carrer and Urbinati 2001, Motta and Nola 2001, Frank et al. 2005, Büntgen et al. 2006c, Affolter et al. 2008), or maximum latewood density (MXD) (Schweingruber et al. 1979, Frank and Esper, 2005a, Büntgen et al. 2006b) with inferences about the climatic forcing drawn from response functions or more simple comparisons with meteorological variables. While one of the few prominent sources for long-term assessments of growth-climate response, empirical studies of annual tree-growth, however, may be confounded by the numerous and mixed environmental influences that occur within a particular growing season. Biotic and abiotic disturbances, biological "memory" related to past processes and influences, as well as possible non-linearities of growth responses may also complicate analyses (Fritts 1976, Körner 2003, Frank et al. 2007a).

However, in comparison to TRW or even MXD, the basic building blocks of tree-rings in conifers (**Fig. 2**), i.e., the xylem cells, remain much more poorly studied due to technological limitations and the amount of time required for such investigations. These constraints have particularly limited the number of comparative studies seeking to assess intra-annual growth at multiple sites, for multiple species, over longer time periods. Technological and methodological improvements are changing this and long-term records have been developed (Fonti et al. 2008b) and the year-to-year variability in the size of water-conducting cells have been successfully related to climatic records such as monthly temperature and precipitation (Fonti et al. 2007). Clear relationships between climatic conditions and the size of conductive elements have been established for conifers (Panyushkina et al. 2003) and hardwoods (Sass and Eckstein 1995, Fonti and García-González 2004). These empirical efforts contribute to the understanding of which processes control cell production during the growing season and how variations in these processes determine cellular and ring characteristics – thus establishing a link between detailed intra-annual cellular measures and long series of tree-ring data.

Complimenting the statistical growth-climate link derived from classical dendrochronology and novel wood anatomical investigations, observational studies of growth processes and timing have yielded insights into intra-seasonal impacts of climate variability and exactly when particular cells were formed (Ford et al. 1978, Kirdyanov et al. 2003, Deslauriers and Morin 2004, García-González and Fonti 2006). Such studies of ring formation provide concrete information on cellular division and growing season duration and thus may be related to the environmental controls that cumulatively act to form wider or narrower rings.

Due to the uniqueness of temperature, precipitation and radiation variations over a particular growing season and the complex interaction of these factors on tree growth, explicit mechanistic models linking environmental conditions to tree-ring characteristics have been developed (Shashkin and Vaganov 1993, Fritts et al. 1999, Evans et al. 2006, Anchukaitis et al. 2006, Vaganov et al., 2006). These so-called cambial growth models utilize climate information to derive cellular division and enlargement activity during the course of one or more growing seasons – namely the information integrated in tree-rings. These growth models are based on the fundamental hypothesis that climatic influences are associated directly, but potentially nonlinearly, with tree-ring characteristics through controls on the rates and duration of cellular processes (division, growth, and maturation). Such models provide an internally consistent framework to evaluate the relative importance, and changes therein, of the inter-correlated climatic parameters on tree-growth. Cambial growth models have been successfully validated against TRW time-series in Russia and North America (Anchukaitis et al. 2006, Evans et al. 2006).

Of current interest related to global warming and climatic influences on tree growth are studies suggesting the diminishing importance of temperature in controlling growth at high-latitude forests (Briffa et al. 1998, Jacoby et al. 2000, Aykroyd et al. 2001, Wilmking et al. 2004, Wilson et al. 2007, D'Arrigo et al. 2008 and references therein, see also Büntgen et al. 2008a). One hypothesized mechanism for this reduced sensitivity includes temperature-induced drought stress provoked by recent warming trends. Application of a cambial growth model, intra and inter-annual tree-ring data and high-resolution climate data in the "warming experiment" of the proposed elevational transect will allow a better understanding of how growth/climate responses vary as a function of the absolute temperature level. Detailed investigations along the transect will also expose differences in the climate response and drought tolerance of larch and spruce (Frank and Esper 2005a, Büntgen et al. 2006c). While these two tree species often coexist in mixed forests, fundamental differences in their operating and life strategies will likely impart differences in how they will respond to future warming. When needles are present, larch maintain high photosynthetic activity: Larch additionally develop a deep root system which provides water access to the seasonally least variable moisture supply (Tranquillini 1979, Valentini et al. 1994). In contrast, spruce trees are opportunistic and rely more upon internally stored and superficial water supplies and may benefit from photosynthesis before and after the growing season.

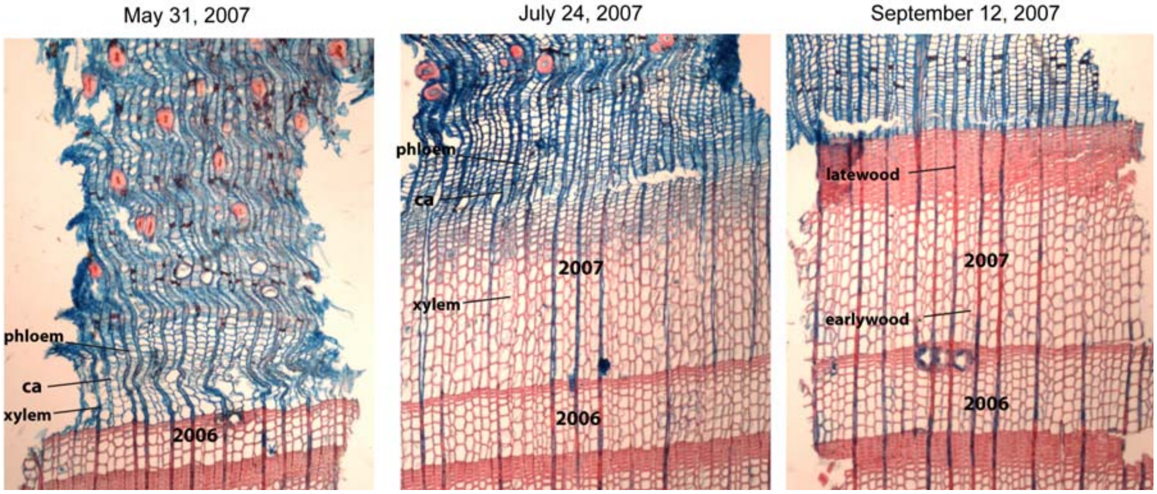

***Figure 2**. Three photomicrographs of samples from a single larch tree growing at 1600 m asl on the north exposed slope of the Lötschental valley. These three samples (from a total of nearly 1000 samples analyzed) were collected approximately 7 weeks apart and show the growth and cellular development throughout the growing season. At the end of May, newly formed xylem cells, the cambial zone (ca), and newly formed phloem cells are clearly visible. Towards the end of July, the radial-growth was nearly complete and the majority of the xylem cells lignified (red color). However, the lignification of latewood cells just started and does not show any evidence for cell wall thickening. By September 12, the 2007 ring on this tree was almost completed with the cell walls mostly, if not fully, thickened and lignified.*

Considering previous research and current questions on climate change impacts, we identify the following three (1-3) research priorities:

1. **Investigate species-specific responses.** Mixed larch and spruce sites allow complicating inter-site effects (soil variations, topography, climate, etc) to be mitigated, thereby allowing characteristics and timing of cambial activity and TRW and MXD formation to be understood.
2. **Integrate intra-seasonal and long-term data.** Knowledge on growth timing and environmental controls gathered from intra-seasonal measurements will be extended back in time based on centennial length tree-ring chronologies and instrumental records. These dual time-scales are also appropriate for parameterization and verification of cambial growth models.
3. **Assess temperature controls on growth timing, rates, and processes.** A ~ 1km elevational gradient offers the possibility to study natural tree growth with all sites undergoing a rather similar evolution of precipitation and radiation variability, but at different mean temperatures.

Synergies arising from coupling i) high resolution growth and climate data, ii) long-term tree-ring and instrumental data, and iii) cambial model output will yield an **INTEGRAL** understanding of climatic impacts upon tree-growth from weekly to centennial time-scales. New data should yield improvements to cambial growth models and hence increase their reliability for future projections. Efforts along a large elevational transects will also allow assessment of how growth characteristics, timing, and rate may depend upon changes in mean temperatures projected for the 21st century.

2.2. Own prior research contribution

The research team has broad competence in tree-ring research, the collection and analysis of environmental data, and their comparison with instrumental measurements with the purpose of understanding the characteristics and consequences of global climate change. Time-series and network analyses are routinely performed to understand the spatial patterns and impacts of climatic variations from seasonal to millennial time-scales. Using data derived from the Lötschental and surrounding regions, we have reconstructed settlement (Büntgen et al. 2006a), insect (Esper et al. 2007a), and temperature (Büntgen et al. 2006b) variations over the past millennium. Scientific interests include quantifying environmental impacts on trees (Frank and Esper 2005a), using tree-rings and other proxies to reconstruct climatic and environmental changes (Esper et al. 2007b, Frank et al. 2007a,b), and studying the interactions between climate and ecological processes (Stige et al. 2007, Esper et al. 2007a, Rutishauser et al. 2008). A wide variety of tree-ring parameters, including TRW, MXD, and isotopic composition in addition to novel quantifiable anatomical cellular features (Fonti and García-González 2004, 2008, Eilmann et al. 2008) have been utilized to achieve research aims. Quantification of processes have been realized via empirical approaches (Frank et al. 2008c) and model simulations (Anchukaitis et al. 2006). Specific areas of competence related to the proposed research include: i) palaeoclimatology, ii) quantitative wood anatomy, iii) cambial growth models, iv) time-series analysis/detection methods, and v) pre-investigations related to the proposed research.

i) palaeoclimatology

Depending upon site-ecology and local climate conditions (**Fig. 3**), variations in TRW and MXD (e.g., Frank and Esper 2005b) and isotopic composition (Treydte et al. 2006, 2007) can skillfully represent temperature, precipitation, or drought variations making them the most important annually resolved proxy archive spanning the past millennium (IPCC 2007). Chronology development, removal of biological age-trend (Jacoby and D'Arrigo 1989, Esper et al. 2003), quantification of signal (Frank et al. 2007a), calibration/verification procedures (Cook et al. 1994), and error-estimation (Esper et al. 2007b) are all important aspects of utilizing tree-ring data to properly reconstruct past climatic variations.

We have experience in the development and analyses of long tree-ring chronologies, and using these chronologies to reconstruct regional (D'Arrigo et al. 2005) and hemispheric-scale temperature (Frank et al. 2007b) and drought (Esper et al. 2007b) variations. Preservation and analysis of the full range of climatic variation – from inter-annual to multi-centennial time-scales – has received particular focus for studying both long-term climate change and extremes (Frank et al. 2005, Frank et al. 2007a, Esper et al. 2007b). Such concepts are broadly applicable in discriminating between long and short-term climatic impacts to tree-growth.

Within the Greater Alpine Region (GAR), we have developed networks of living trees with investigations of growth responses to climate and other environmental factors (Frank and Esper 2005a) and have reconstructed temperature variations for the past centuries (Frank and Esper 2005b) to over the millennium (Büntgen et al. 2006b). Our results suggest that the strong rise in European temperatures known from instrumental measurements (**Fig. 1a**, Frank et al. 2007a) appears to represent unusual warmth for the past millennium (**Fig. 1b**). Based on tree-ring and other multi-proxy data, we have reconstructed the North Atlantic Oscillation and linked this pressure system with conditions associated with the Medieval Climate Optimum (Trouet et al. 2008, Esper and Frank 2008). These efforts suggest that the absolute climatic conditions at a given location are certainly unprecedented within the lifespan of the forests growing there.

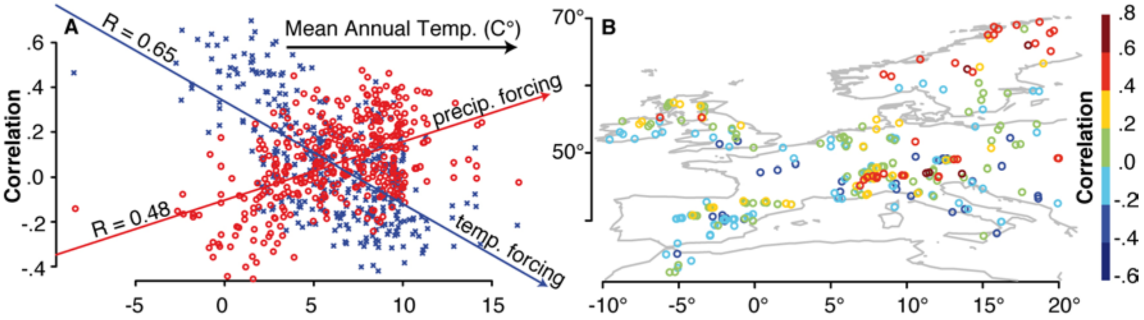

Figure 3. *Growth climate relationships of European tree sites (376 sampling locations) illustrated by **A)** the correlation with JJA temperature (blue crosses) and precipitation (red circles) as a function of the mean annual temperature at each site and **B)** the geographical position of data in **A** with their correlation to summer temperatures from the nearest 0.5°x0.5°gridpoint (Mitchell and Jones 2005). In accordance with well-known dendrochronological principles, highest correlations with precipitation are obtained for sites with high mean temperatures and vica-versa for temperature. These results indicate how the growth response depends on local climate and imply shifts in growth forcing which may occur under future warming. See Frank et al. (2008a) for details.*

ii) quantitative wood anatomy

Wood anatomical features that can be repeatedly measured may provide unique insights into processes and environmental conditions that are unidentifiable by TRW, MXD, or isotopic measurements. Features such as vessel area or size and their intra-annual position, tracheid dimensions, and numbers are all quantifiable characteristics of wood (Schweingruber 2007) that provide snapshots of growth via the repeated collection of microcores and quantification of change between time-slices (**Fig. 2**, Wodzicki 1971, Deslauriers et al

2003a, Rossi et al. 2006a, Rossi and Deslauriers 2007). Growth behavior may also be retrospectively quantified by analyses of decades or centuries of growth via larger core samples (Yasue et al. 2000, St. George et al. 2002, Wang et al. 2002, Panyushkina et al. 2003, Kirdyanov et al. 2003, Fonti and García González 2008).

We have competence in monitoring both on-going cambial activity and xylomorphogenesis (Fonti et al. 2007, Moser 2008) and the use of quantitative wood cell anatomy to retrospectively identify the environmental controls on wood cell formation (Fonti and García-González 2004, Fonti et al. 2008c, Fonti and García-González 2008). Wood anatomical measurements require specific techniques and procedures for surface preparation, imaging, and efficient and accurate survey of cell anatomical features. Advances introduced in recent publications (Fonti et al. 2008a) and a microtome developed at the WSL (http://www.wsl.ch/staff/holger.gaertner/Microtome.pdf) contribute towards better and more efficient quantification of intra-seasonal growth features and allow, for the first time, multi-centennial records to be developed (Fonti et al. 2008b). We have developed approaches ensuring correct and representative cell selection (García-González and Fonti 2006, 2008a,b). General experience and resources for wood anatomical analysis at the WSL (e.g., http://www.woodanatomy.ch/) provide an outstanding foundation for further and detailed investigations.

iii) cambial growth models

Mechanistic modeling of tree-ring formation can be used to objectively evaluate climatic influences on tree-ring chronologies (Vaganov et al. 2006, Fritts et al. 1999). Cambial growth models, by simulating environmental forcing on cellular growth, allow assessments of both inter-annual to longer term growth changes (point *i* above) and intra-seasonal cellular characteristics (point *ii* above). Such models are particularly useful for understanding potential temporal instabilities (Jacoby et al. 2000, Büntgen et al. 2006c) and/or mixed influences of climate on tree-growth (Friedrichs et al. 2008). Such instability might be particularly important for environments where both temperature and precipitation can be important controls on tree growth (Nemani et al. 2003) and for high-latitude and montane temperature-sensitive trees under anthropogenic climate forcing (**Fig. 3**).

Our experience in the calibration, verification, and interpretation of cambial model outputs for both intra-annual cellular development (Vaganov et al. 2008), and inter-annual to centennial-scale growth variations (Evans et al. 2006) will serve to understand the role of climatic variations in forcing intra-seasonal growth variations. We have validated cambial growth models for hundreds of sites in the southwestern US and northern Russia (Evans et al. 2006) and have used such models for understanding shifting and mixed climatic influences (Anchukaitis et al. 2006). While this project will represent the first application of cambial modeling for central European trees, compilations of tree-ring data (**Fig. 3,** Frank and Esper 2005a, Frank et al. 2008a) and long instrumental records (Frank et al. 2007a) will allow results derived from the Lötschental transect to be placed in an Alpine to continental spatial scale and centennia-long context.

iv) time-series analyses/detection methods

Even though the temperature difference along the elevational gradient provides a general research framework (Körner 2007), it is clear that forest growth, comprising the cumulative effects of numerous biotic and abiotic forcing agents, is a complicated eco-physiological process. Temporally varying factors, including changes in settlement, harvesting, land use/cover or insect activity, if not properly accounted for, may confound analyses.

Experience gained in the detection of the larch-budmoth signal (Esper et al. 2007a, Büntgen et al. 2008b), competition between trees (Weber et al. 2008), adaptation after land-use changes (Fonti et al. 2006), and reconstructions of forest disturbance (Anchukaitis and Horn 2005) will be broadly applicable to assess possible disturbance factors. Signal calibration / verification methodologies (Frank and Esper 2005b, Esper et al. 2005a, Anchukaitis et al. 2008) in concert with moving window analyses (Büntgen et al. 2006c, Rutishauser et al. 2008) will be useful to determine the stability of climatic forcing upon stem productivity. We have considerable experience in analyses of high (Frank et al. 2005) to low-frequency signals (Büntgen et al. 2006b) over time-scales ranging from the most recent centuries (Frank et al. 2007a) to pre-Holocene forest growth variations that currently represent the earliest calendrically dated tree-ring data (Schaub et al. 2008). Biases in climatic signal strength related to changes in sample replication, quality (Frank et al. 2007b), and age-structure (Esper et al. 2008), familiarity with bootstrapping techniques (Fonti et al. 2008a, García González and Fonti 2008b), and experience in error estimation (Frank and Esper 2005b, Esper et al. 2005b, 2007b) should prove useful in robustly attributing changes in growth as a function of temperature.

v) pre-investigations related to the proposed research

The proposed project is a continuation of self-funded exploratory research started in 2007. For details on the general setting of the transect see the “Detailed Research Plan” below. Initial results indicate approximately a 4°C temperature change over the transect and clearly demonstrate the strong influence of this temperature gradient in determining differences of growing season length and growth rates. In comparison to the ~6 day advance in spring events over more than 30 years (Menzel and Fabian 1999, **Fig. 1a**), during the 2007 growing season we observed a lag of 25-30 days between the lower (1300 m asl) and upper (2200 m asl) sites (**Fig. 4**). This delay is also evident in the timing of cellular development and total growth throughout the 2007 warm-season (**Fig. 5**).

In addition to specific pre-investigations of intra-seasonal growth changes, we have also developed an extensive network of local and international people and institutions interested for our activities on the Lötschental transect. These include: Hans Henzen (local forester); Ignaz Bellwald, Hans Kalbermatten, Werner Bellwald (local historians); Thomas Antonietti (Lötschental museum); Martin Schmidhalter (dendroarcheology); Geographical Institute, University of Bonn, Germany (high-mountain research); WSL Research Units (e.g., soil science); Geographical Institute, University of Bern, Switzerland (climatology & multi-proxy reconstructions); Geobotany Department, University of Trier (plant physiology).

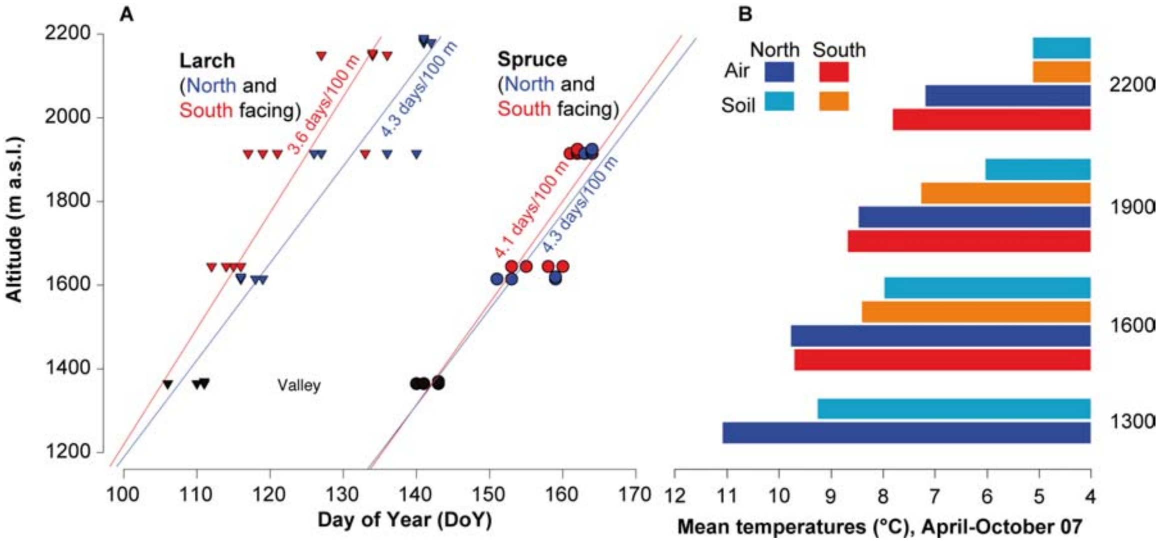

Figure 4. Observations along the transect during the 2007 growing season for A) date of bud break for larch and spruce and B) April-October stem and soil average temperature for each site. The delay in phenology during 2007 was approximately 4 days / 100 meters in elevation, with the deciduous larch forming new needles approximately 1 month before the evergreen spruce. The soil and stem temperature measurements demonstrate the approximately 4 °C / km gradient along the transect, the slightly warmer conditions of the southern exposed sites, and the differences between stem and soil temperatures. The temperature difference between the top and bottom of the transect is greater than the range of April-September temperatures as measured at the nearby Ried meteorological station from 1974 – 1999 with the extremes of 8.2° C in 1978 and 10.7° C in 1992. Data from Moser 2008.

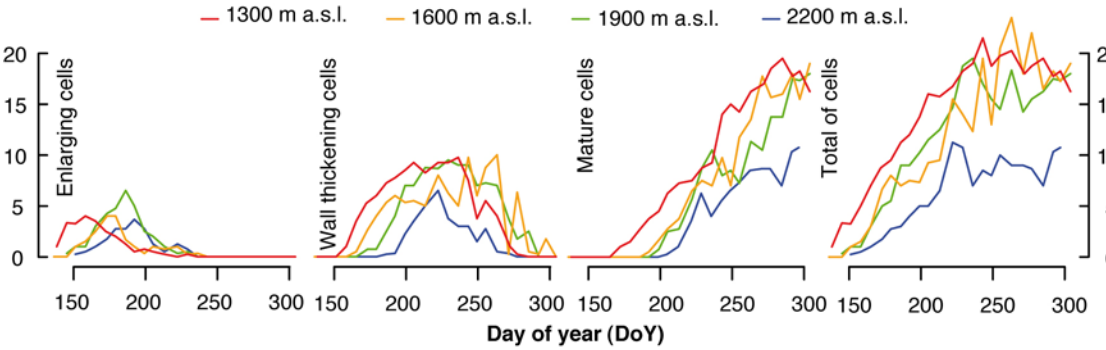

Figure 5. Observation of cellular development of larch observed during the growing season 2007 along the north facing slope of the transect. Lines indicate the number of cells counted in samples collected weekly during the growing season. In addition to total counts, xylem cells were differentiated by development phases (enlarging, cell wall thickening, and maturing). Data from Moser 2008.

2.3 Detailed research plan

To analyze and model intra-seasonal to century long variability as related to warming environments we have selected a study area in the Lötschental valley in the Swiss Alps (**Fig. 6**). While high-mountain systems, such as the Alps are likely to be particularly vulnerable to climate change (Beniston et al. 1997), they simultaneously present unique opportunities for its study, both in terms of the quality and quantity of ecological and instrumental data and due to the temperature gradient (Körner 2007). The Lötschental valley offers continuously forested slopes covering an elevational gradient of ~1000 meters. The forests are a mixture of larch and spruce, with individuals commonly reaching ages of up to 400 years.

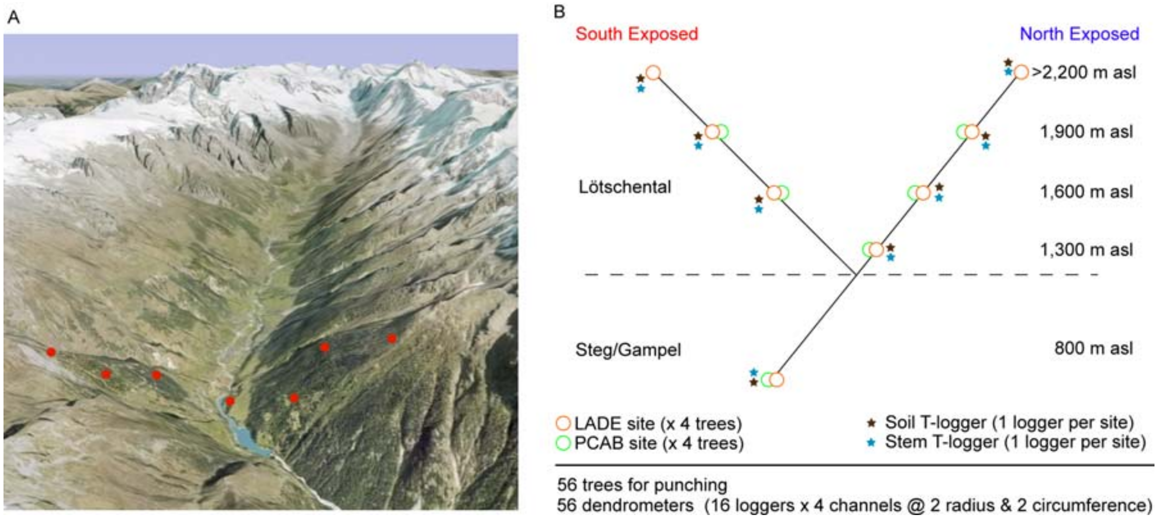

Figure 6. *Illustration of the Lötschental transect.* ***A)*** *Map (GoogleEarth) with the locations of the seven sites in the Lötschental marked by red circles.* ***B)*** *Schematic diagram for the 8 study sites with the existing equipment (temperature loggers and dendrometer bands).*

According to our objectives and pre-investigations, we have selected four different altitudinal belts (1300m, 1600m, 1900m, and 2200m asl) within the Lötschental, and an additional location at 800m asl in the main Rhone Valley (**Fig. 6**). Plots within each belt (except at the highest, where only larch is present) all consist of two physiologically different species: larch and spruce. For each elevational belt, intra- and inter-seasonal measurements of tree growth and climate will be conducted over two vegetation periods, adding to data collected during 2007 and scheduled for collection in 2008.

Proposed research activities have been compartmentalized into four work-packages to provide knowledge of climatic influence upon intra-seasonal growth rates, growing season length, and long-term variations:

(i) Measurement & analysis of high-resolution climatic variations (hourly soil, air & stem temperature, precipitation, soil moisture content, photosynthetically active radiation)

(ii) Intra-seasonal growth analysis (punching, cambial analyses, dendrometer measurements, phenology)

(iii) Reconstruction of longer-term climate-growth variations (TRW, MXD, cell-size & number)

(iv) Application and verification of a cambial model (considering i-iii)

(i) Measurement & analyses of high-resolution climatic variations

At each site, soil and stem temperatures will be recorded via temperature loggers. We will also measure relative humidity, which will be important for understanding dendrometer band variations (Deslauriers et al. 2003b) and also for possible future isotopic measurements. Under guidance of the Soil Science Division at the WSL, soil moisture content will be measured continuously at two depths (~10 and 70 cm) at all sites as a measure of water available for growth. A single meteorological station is scheduled for installation at no additional costs to the proposed project. This station will act as an "anchor" for the in-situ measurements and will also provide data (e.g., photosynthetically active radiation, precipitation) to more generally quantify changes in environmental conditions. Daily data from nearby meteorological stations (Institute of Geography, University of Bonn; MeteoSwiss) will compliment and extend in-situ measurements after application of appropriate transfer functions.

Expected output: A full suite of environmental variables that will be used for interpretation and quantification of the intra-seasonal measurements and provide transfer functions for more seamless integration of surrounding daily resolved and long-term instrumental data.

(ii) Intra-seasonal growth analysis

This work-package will quantify the patterns and timing of tracheid production and cambial activity, including tracheid emergence, enlargement, wall thickening, lignification, and maturity by applying established and novel measuring techniques (Rossi et al. 2003, 2006b, Vaganov et al. 2006, García-González and Fonti 2006, Deslauriers et al. 2006). Micro-samples will be collected frequently (~ every week) during two full vegetation seasons for 4-8 dominant trees of each species at each elevation band (**Fig. 6**). Each micro-core sample ideally contains the wood of the previous two or three years, the growing annual layer within the cambial zone, and the adjacent phloem (**Fig. 2**). We will employ existing and explore novel data standardization techniques, which are required for xylem development analysis (Rossi et al. 2003). Such standardization helps to account for substantial anatomical variations (cell number, diameter, and wall-thickness) at different positions along the stem (Schweingruber 1988), resulting from different cambial activities (Creber and Chaloner 1984).

Micro-samples will be complimented by automatic dendrometer measurements, which will record stem circumference or radius (depending upon installation) at hourly resolution. Dendrometer band measurements allow continuous monitoring of stem variation throughout the year and help understanding trees' reactions to short-term environmental changes including changes in temperature, soil-water content, frost, and rainfall. Fluctuations related to water flow / storage which may be superposed upon the seasonal growth will be detected via comparison with the micro-samples and verified by climatic measurements.

Results (xylogenesis stages, total cellular growth, lignification timing, and cambial cells) will be analyzed via ANOVA to reveal dominant controls in terms of temperature (~elevation), species, and aspect. These and additional time-series methods will be applied to detect the climatic influences on growth and understand/mitigate confounding factors including tree age, competitive status, and site productivity. Inter-annual climatic/growth relationships will be identified via simple correlation and/or response analyses using high-resolution temperature, precipitation, solar radiation, and soil-moisture measurements. These empirical approaches will be supplemented with results derived from cambial models (see below).

Expected output: Quantification of the onset and termination of the growing season in relation to temperature/altitude. Additionally, specific knowledge about the seasonal activity (number of cells in the cambial zone and the specific growth rate) and tracheid formation (number of enlargement and matured cells) and the relationships to climatic variation will be derived. Empirical data needed for parameterization and validation of cambial models will also be a critical output. Differences in climate sensitivity and reactions related to general species differences (needle retention / rooting depth) will be uniquely understood for two species along an elevational gradient at intra-seasonal resolution.

(iii) Reconstruction of longer-term climate-growth variations

The longer-term growth history will be derived from increment samples collected from larch and spruce populations within each elevational band. For each species, at each point along the transect, 2 cores will be taken from 20-30 trees. This sampling should be sufficient to provide a robust estimate of the mean chronology signal (Frank et al. 2007b) and allow assessment of the inter-annual to centennial-scale variations. For all samples, TRW will be measured as the most basic assessment of growth variation and forest productivity. A subset of samples will be processed for MXD measurements by WSL staff. While MXD data tend to be much less sensitive to site ecology and local climate than TRW (Frank and Esper 2005a), these measurements will allow the boundary conditions related to latewood formation to be defined and potential non-linearities in response to be understood. Retrospective quantification of wood anatomical features (e.g., cell size, number, and wall thickness) will complement the MXD measurements, but more importantly will provide a past analog for the intra-seasonal measurements (point *ii* above) and will also be utilized for comparison with the cambial growth model output (point *iv* below).

Climate/growth relationships will be defined from both long monthly records (e.g., Auer et al. 2007) and more highly resolved instrumental station data (Della Marta and Wanner 2007). Temporal stability of defined relationships (via e.g., moving window correlation analyses) will be conducted to identify possible shifts or long-term drifts in seasons and parameters (e.g., May-August and temperature) most important for forest growth.

Expected output: Long time-series of historical changes in growth. Definition of growth/climate relationships and assessment of their temporal stability (based on available meteorological data) as a function of species and growing season temperatures (position along transect).

(iv) Application and Verification of a cambial model

To integrate the (i) high resolution instrumental data, (ii) intra-seasonal growth data , and (iii) retrospective TRW and anatomical characteristics, we will utilize a variant of the Vaganov-Shashkin (VS) cambial growth model (Vaganov et al., 1999, 2006, Anchukaitis et al. 2006, Evans et al. 2006). This model is based on the fundamental hypothesis that climatic influences are associated directly, but potentially nonlinearly, with tree-ring characteristics through controls on the rates and duration of cellular processes (division, growth, and maturation) in developing wood. The modeled cambial growth rate is determined by comparing the daily temperature and soil moisture budget to quasi-parabolic growth functions, and using the most limiting factor to scale the various component processes of tree-ring formation. Advantages of the VS model in comparison to full ecophysiological models (Fritts et al. 1999) include its relative simplicity and the need for relatively few input variable time-series.

Because the model operates at a daily and cellular spatiotemporal scale, regular intra-annual xylem sampling and continuous dendrometer measurements will be used to validate the model over short time periods and for growth at different mean temperatures (i.e., elevational band). These intra-seasonal growth and climate data will allow model parameters to be derived for larch and spruce and the model run using long instrumental records from the Alpine region (e.g., Frank et al. 2008b) to simulate past radial and cellular growth. Model hindcasts will be compared with both the tree-ring width and wood anatomical measurements and the empirical assessments of growth/climate relationships. Running the cambial model driven by future scenarios, either from global or regional climate simulations, will be useful to understand growth under warming conditions and will provide a further analogue for growth/temperature changes along the transect (from 2200 m asl to 1300 m asl to 800 m asl).

Expected output: Growth simulations spanning at least 1900AD – 2100AD for larch and spruce representing the different elevational belts in the Lötschental. Improved parameterization of growth models based on results and data from work packages i, ii, and iii. Estimates for future conifer tree productivity, growth constraints, and potential non-linearities, as a function of projected temperature increase.

2.4 Schedule

The proposed project would start February 01, 2009 and last for three years. The starting period will allow two PhD students to familiarize themselves with existing data and methods with enough time for implementing this knowledge during the spring fieldwork. Research activities of the PhD students are broadly in accordance with the four (*i-iv*) work packages detailed above: one student will concentrate on the quantification and analysis of intra-seasonal growth and the other on cambial modeling and longer-term investigations. Scheduled research steps and temporal goals are outlined in **Fig. 7.**

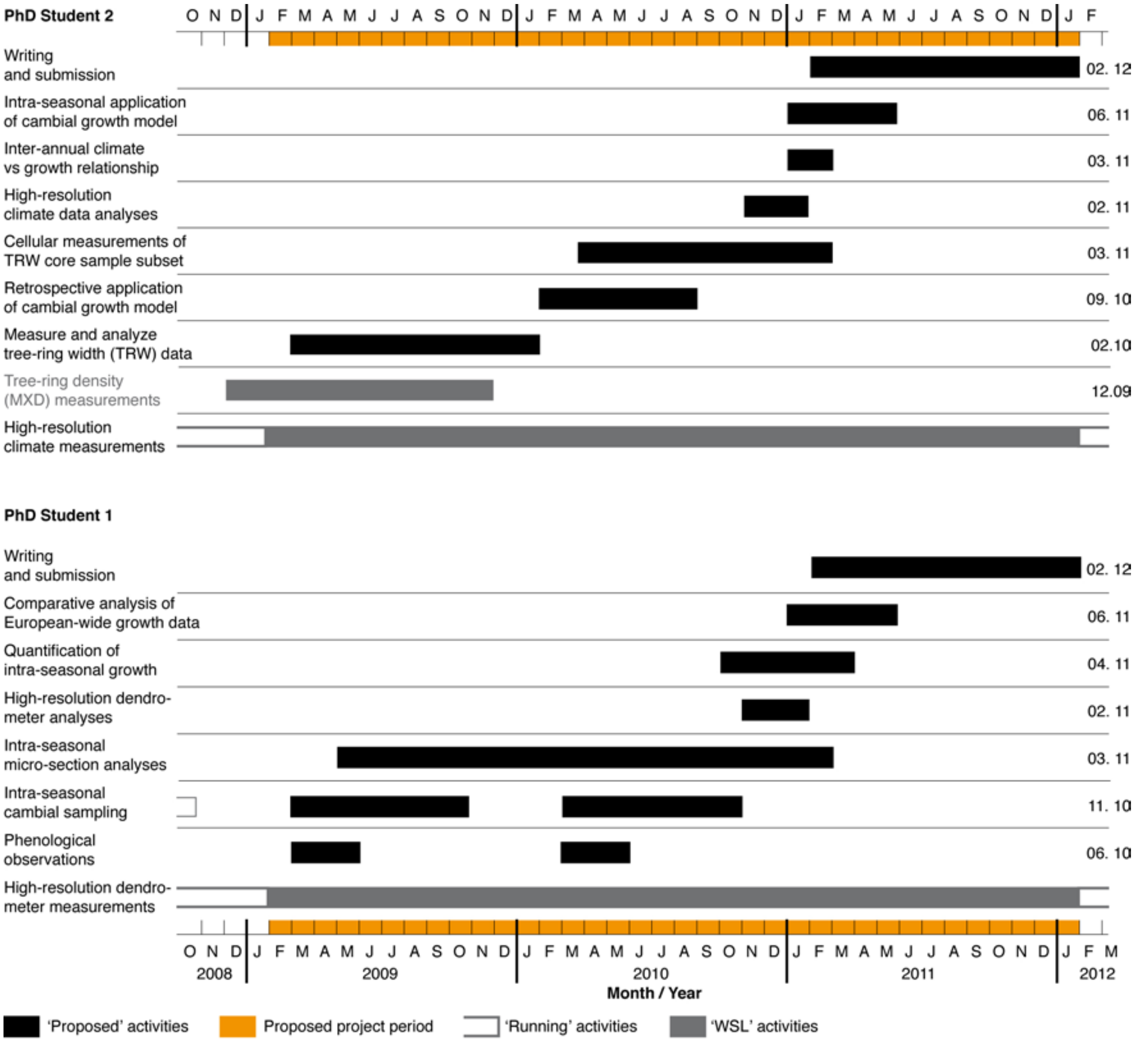

Figure 7. *Schematic showing the proposed research steps and temporal and topical division of activities.*

Measurements of intra-annual cellular development, inter-annual TRW and MXD, as well as all statistical analyses will be performed at the WSL/Birmensdorf and supervised by D. Frank, P. Fonti as well as by K. Anchukaitis and J. Esper. The WSL, at no additional cost to this proposal, will fund 10 months salary for an experienced technician to conduct the x-ray densitometry measurements and an additional 2 months of salary to support field activities and the operation/repair of equipment. Funds requested are to support two Ph.D. students. Costs associated with fieldwork and equipment, as well as collaboration meetings, conferences, and publications will be supplemented by WSL funding. A workshop to bring together international experts on cambial modeling is scheduled for the autumn of 2010. It is expected that a minimum of six papers will be published in international peer reviewed journals, of which at least four are ISI-listed.

2.5 Significance of proposed research

By analyzing intra-annual and longer-term growth variations along an elevational gradient of approximately 1000 m and an absolute difference in mean temperature of 4 °C, the proposed project will increase understanding of how projected 21st century warming may influence future tree growth. Specifically, this research will provide new data and insights as to how growing season length, cellular division rates, and cellular characteristics vary as a function of temperature for two widespread coniferous species. The fusion of high-resolution meteorological data, intra-seasonal growth measurements, and retrospective quantification of cellular and radial growth will allow improvements to cambial growth model parameterization and possibly even model architecture. Application of such growth modeling techniques with climate ensembles will provide estimates for tree responses to future warming scenarios.

In addition to increased knowledge of intra-seasonal and future growth patterns, the proposed research will yield insights into how larch and spruce have responded to past climatic variations. Knowledge gained about the timing of cell formation and growth will allow for better interpretation and characterization of tree-ring based temperature, precipitation, and drought reconstructions. Of special interest in this regard, due to its strong temperature signal at the upper treeline and utility as a proxy, yet poorly understood intra-seasonal controls, is the characterization of the cell wall thickening as related to MXD.

The basic infrastructure maintained and environmental data collected as part of this project will be available for other research groups to further conduct associated research activities. We anticipate that both expected and surprising synergies will arise. For example, the Soil Science Group at the WSL, the Geobotany Group at the University of Trier, Germany, and colleagues from the Geographical Institute of the University of Bonn, Germany have scheduled preliminary measurements to understand and quantify the hydrological cycle of the valley, including isotopic variations of soil water, needles, phloem water, and stem wood. The instrumental and basic growth data generated and analyzed during the proposed project will be available and possibly even crucial for associated research activities.

Results will be relevant to local and regional organizations and authorities, and to scientific programs and databases dealing with climate variability, impacts, and global change issues. Examples include:

(i) Forum for Climate and Global Change (ProClim), Bern, Switzerland.

(ii) The National Center of Competence in Research on Climate (NCCR), Bern, Switzerland.

(iii) The International Geosphere-Biosphere Program (IGBP), Stockholm, Sweden.

(iv) National Geophysical Data Center (NOAA), Boulder, Colorado.

(vi) The Intergovernmental Panel on Climate Change (IPCC), WMO and UNEP, Geneva, Switzerland.

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