



Shifting Growth Drivers in the Alptal: The Influence of Climate, Slope Gradient, and Soil Moisture on Norway Spruce Growth over Time

ESS 511 Master's Thesis

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Abstract

Climate change is altering the hydrological cycle. Understanding how dominant species like Norway spruce (*Picea abies* (L.) Karst.) adapt to shifting local conditions is critical for understanding carbon sequestration potential, future hazard management (e.g., slope stability), and sustainable forestry strategies. This study examines how regional climatic shifts affect recent growth rates and whether these changes are influenced by the local heterogeneity in moisture conditions and slope. While the influence of slope on tree growth and forest stability and the relationship between tree growth and local hydrology are both well documented, research that explicitly investigates the interaction between slope gradient and soil moisture on tree growth is lacking in comparison. To determine the relative impact of these correlated variables, this study utilizes a two-way factorial design in the Studibach catchment (Alptal, Switzerland), analyzing increment cores from 64 Norway spruce trees stratified into four distinct groups based on slope and moisture, paired with GIS analysis to investigate potential additional drivers of growth. By determining the roles of these drivers, this research aims to better understand catchment-scale variation in tree growth. The results of this thesis show a considerable shift in the climatic drivers of Norway spruce growth, transitioning from a historically energy-limited system to a moisture-limited one following a 2.5°C increase in average temperature since 1980. Correlation analysis suggests that while historical growth was stimulated by summer heat, modern growth has a greater correlation with prior summer precipitation and warm May temperatures. Despite a long-term positive growth trend for Norway spruce in the catchment, a considerable recent decline in BAI growth (2013-2025) highlights the compounding effects of repeated extreme heat and droughts. The impact of local topography has also shifted over time. Steep dry slopes had the greatest estimated growth before 1980, perhaps by avoiding waterlogged conditions, but with modern warming, these sites have become the most vulnerable (with basal area increment (BAI) decreasing by an estimated 801 mm²/year). Conversely, flat wet sites have emerged as the only classification to show a growth increase post-1980, acting as a hydrological buffer against increasingly prevalent summer droughts. These findings suggest that the increasing vulnerability of spruce on steep slopes may compromise slope stability in the Studibach catchment. Future forest management and hazard mitigation strategies should consider prioritizing topography-based approaches, favoring deeper-rooting species on steep gradients to promote resilience in a changing climate.

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List of acronyms

BAI	Basal area increment
CI	Confidence interval
CV	Coefficient of variation
DBH	Diameter at breast height
EMMs	Estimated marginal means
GEE	Google Earth Engine
GIS	Geographic Information Systems
GLK	Gleichläufigkeit
LAI	Leaf area index
LMM	Linear mixed-effects model
LOESS	Locally estimated scatterplot smoothing
NDVI	Normalized difference vegetation index
NSCs	Non-structural carbohydrates
RWI	Ring-width index
TWI	Topographic wetness index
VPD	Vapor pressure deficit
WSL	Swiss Federal Institute for Forest, Snow and Landscape Research (Eidg. Forschungsanstalt für Wald, Schnee und Landschaft)

1. Introduction

Climate change is leading not only to an increase in average global temperatures but also major shifts in the global hydrological cycle, with significant implications for terrestrial ecosystems (Trenberth, 2011). Forests play an important role in mitigating the effects of climate change by sequestering carbon from the atmosphere via biological tissue growth (Sedjo & Sohngen, 2012). As global temperature and moisture patterns change, however, the carbon uptake potential of terrestrial ecosystems is becoming more uncertain (MeteoSwiss & ETH Zurich, 2025). In particular, changes in water availability, whether through increased drought frequency or intensity, changing precipitation patterns, or local soil moisture variability, are expected to have a strong influence on tree growth and survival rates (Kreuzwieser & Gessler, 2010).

In Switzerland, these climatic shifts are particularly pronounced, as the region has experienced a temperature increase of approximately 2.9°C since pre-industrial times, double the global average temperature rise of 1.3-1.4°C (MeteoSwiss & ETH Zurich, 2025). This rapid warming has led to several challenges for Swiss forests and forestry management. While higher temperatures and a reduced snow-cover duration have lengthened the growing season (Gharun et al., 2020), they have also intensified vapor pressure deficit (VPD), or atmospheric moisture demand (Babst et al., 2019), and increased the risk of early-spring frost damage (Vitasse et al., 2018). Recent droughts have also had a considerable impact on forest health. For example, a study by Sturm et al. (2022) found that approximately half of Swiss forests negatively affected by the 2018 drought had prolonged negative effects. These include needle discoloration, vulnerability to insect attacks, and an increase in mortality (Schuldt et al., 2020). Thus, shifting precipitation patterns and rising temperatures are increasingly challenging the stability of Swiss forests (Etzold et al., 2019).

Because climatic shifts can vary across the local landscape, understanding how forest growth responds to local hydrological and topographic variability is vital. A large body of literature demonstrates that water availability is one of the primary limiting factors of tree growth (Larcher, 2003; Schweingruber, 1993). However, the relationship between hydrology and forest productivity is complex. While sufficient soil moisture is necessary for transpiration and photosynthesis, an overabundance of water can also be harmful. Waterlogged soils create anoxic conditions that inhibit root respiration and nutrient uptake, hindering growth (Parent et al., 2008).

Local soil moisture is largely governed by topography (Beven & Kirkby, 1979). Soil moisture generally has an inverse relationship with slope gradient; steeper slopes lose water quickly via surface runoff and lateral flow, while gentler slopes act as water accumulation zones (Parker, 1982; Qiu et al., 2001; Q. Zhu et al., 2014). Because of this, topography affects how trees fare in relation to the overall climate. During drought

periods, trees on steep, well-drained soils may experience greater water stress, while those on flatter terrain may benefit from less excess water (Wang et al., 2024). In contrast, waterlogging in flatter areas may subject trees to hypoxia during periods of extreme precipitation, while steep slopes provide more drainage.

Understanding the interaction between slope and moisture is vital for both climate change mitigation and land management. Determining which topographic sub-types sequester more carbon under variable moisture conditions can inform nature-based climate solutions. Additionally, identifying where a decline in tree growth or risk of increased mortality is more likely has direct implications for forestry and natural hazard management, especially in mountainous landscapes where vegetation contributes significantly to slope stability (Cohen & Schwarz, 2017; Greenwood et al., 2004).

Despite the noted importance of topography and hydrology, a gap in the research remains. While the relationship between slope and moisture is well documented in many catchments, there is a lack of high-resolution dendrochronological data investigating how these factors interact with forest growth in high-precipitation pre-Alpine catchments. As traditional energy-limited wet areas transition toward moisture-limited or disturbance-prone ecosystems, it remains unclear how local topographic variation will affect the long-term resilience and growth response of forests (Babst et al., 2019; Mastrotheodoros et al., 2019).

To address these gaps, this thesis investigates how the climatic drivers of Norway spruce have changed over time and how slope gradient and soil moisture interact to shape tree growth in the Studibach catchment in canton Schwyz, Switzerland. The main objectives of this thesis are 1) to investigate the climatic factors that affect growth and if growth trends have changed in response to climate change, and 2) to determine how slope gradient and local soil moisture influence Norway spruce growth in the Studibach catchment. This study focuses on Norway spruce (*Picea abies* (L.) Karst.), one of the most ecologically and economically significant conifers in Switzerland (Caudullo et al., 2016).

RQ₁: How have Norway spruce growth rates in the Alptal changed over the past century, and what climatic and environmental factors led to these trends?

- H_{1-0} – There is no significant change in Norway spruce growth in the past century.
- H_{1-1} – Growth rates of Norway spruce trees have increased significantly in the past century due to warmer conditions.

RQ₂: How do soil moisture and slope affect the growth of Norway spruce trees in the Alptal?

- H_{2-0} – There is no significant difference in Norway spruce growth between trees growing on steep versus flat slopes, or between trees in wet versus dry soil locations.
- H_{2-1} – Norway spruce trees on steep slopes grow significantly less quickly than trees on flatter slopes.
- H_{2-2} – Norway spruce trees in drier soil conditions grow significantly more quickly than trees in wetter soil locations.

2. Background

2.1 Environmental controls on tree growth in pre-Alpine forests

2.1.1 Temperature and seasonality

In temperate climates, tree growth generally occurs between spring and autumn (Fritts, 1976), although growth periods vary slightly between species and climates. Trees enter a state of dormancy at the end of the growing season to protect themselves against the cold and reduce their nutrient demand (Nilsson, 2022). This annual cycle of alternating growth and dormancy is the fundamental biological mechanism that creates distinct tree rings and allows for dendrochronological analysis and climate reconstruction (Fritts, 1976) (see Section 2.5). Because of this reliance on seasonality, longer winters and late-spring frosts generally lead to decreased tree growth in the corresponding year (Ogana et al., 2022; Spiecker, 2000). In Swiss forests above 800 m a.s.l., low temperatures are often the main limiting factor of tree growth (Mastrotheodoros et al., 2019).

2.1.2 Light availability

Tree growth and light availability are directly related, particularly in dense forest stands where competition is high (Schweingruber, 1993). When growing under dense, closed canopies, younger and shorter trees often allocate their limited resources toward vertical growth to reach the sunlight, resulting in decreased radial growth and smaller rings (Waring, 1987). After management, storms, or fires have thinned the canopy, the trees that were left behind often produce considerably wider rings due to decreased competition for light (Schweingruber, 1993).

2.1.3 Slope and topography

Opposite slopes of a valley, particularly in east-west-oriented valleys with northern and southern aspects, often have a distinctly different microclimate (Geiger et al., 2003). These variations are driven by differences in solar insolation (duration and intensity) (Holland & Steyn, 1975), which directly influence local temperatures, snowmelt timing, and soil evaporation. In the Northern Hemisphere, south-facing slopes receive more direct sunlight, therefore experiencing warmer and drier microclimates (Holland & Steyn,

1975). The relationship between slope aspect and tree growth has been well-researched across biomes (Måren et al., 2015; Martínez-García et al., 2018; Ogana et al., 2022). In pre-Alpine environments, southern slopes often have denser forests and trees with a larger basal area due to the longer, warmer growing season. This is particularly true for Norway spruce (Krumm et al., 2011).

It can be difficult for trees to establish on steep slopes or unstable ground, potentially leading to long-term reductions in growth (Greenwood et al., 2004). Furthermore, acute mechanical stress, such as soil creep, landslides, or severe snow pressure, can push a tree out of its physical balance, triggering the formation of reaction wood to help the stem return to an upright position (Stoffel & Bollschweiler, 2008). Conifers like Norway spruce grow compression wood on the underside of leaning stems to “push” the tree upright, while hardwood trees grow tension wood on the upper side of the leaning stem to “pull” the stem back into the correct position (Du & Yamamoto, 2007; Schweingruber, 1993).

2.1.4 Moisture

Water availability is widely considered one of the most important factors controlling tree growth (Larcher, 2003). This is the case for many ecosystems; however, an overabundance of water can also reduce tree growth. Waterlogged soils can create anoxic conditions, depriving the soil of oxygen and inhibiting root respiration and nutrient uptake (Parent et al., 2008). Hydrological modelling suggests that this is the case in central Switzerland (Mastrotheodoros et al., 2019).

Atmospheric demand for moisture, quantified by vapor pressure deficit (VPD), can also limit tree growth (Grossiord et al., 2020). VPD is the mathematical difference between the amount of moisture the air can hold at full saturation and the amount it actually holds (Anderson, 1936), often considered the “drying power” of the air. High VPD forces trees to close their stomata to prevent excessive water loss via transpiration (McDowell et al., 2008). However, this process also limits photosynthesis and the transport of carbohydrates within the tree (Grossiord et al., 2020). Rising temperatures have heightened the atmospheric moisture demand (Grossiord et al., 2020). Even cold-humid climates are not immune to increased atmospheric water demand, and this increased drying power may offset the benefits of a longer growing season (Babst et al., 2019).

A recent modeling study by Mastrotheodoros et al. (2020), however, suggested that evapotranspiration in some Alpine regions was above average during drought conditions (the “drought paradox”). It is thought that the abundant sunlight and high temperatures stimulate tree metabolism, while trees at higher elevations often still have access to sufficient soil moisture from winter snowmelt to meet the heightened evaporative demand. Consequently, these trees are not immediately water-stressed during droughts and instead maintain high transpiration rates while inadvertently depleting the

catchment's runoff. This study suggests that meteorological drought conditions do not always translate to a drought signal in the tree.

2.2 Relationship between moisture and slope

Soil moisture is inversely related to slope gradient, meaning moisture generally increases as soil gradient decreases (i.e., on a gentler slope) and vice versa (Parker, 1982; Qiu et al., 2001; Q. Zhu et al., 2014). The relationship between topography and soil moisture is primarily driven by the balance between vertical infiltration and lateral flow. Drainage depends on the total potential, which is equal to the sum of the matric and gravitational potential (Hendriks, 2010). In steep areas, the gravitational potential drives the differences in total potential, and water drains quickly. Thus, on steep slopes, a higher proportion of precipitation is lost to surface runoff and subsurface lateral flow. Conversely, gentler slopes act as water accumulation zones (Q. Zhu et al., 2014). In areas where water is a limiting factor, flatter areas downslope can lead to increased tree growth (Adams et al., 2014). However, in areas with excess soil moisture, poor drainage, exacerbated by a decrease in slope gradient, can hinder growth (Kozłowski, 1997). In pre-Alpine catchments with low-permeability soils, this phenomenon can be further intensified, leading to the anoxic conditions mentioned in Section 2.1.4.

The spatial distribution of soil moisture is often quantified using the Topographic Wetness Index (TWI), which represents the effects of expected water accumulation based on the upstream contributing area and the effects of drainage on the local slope (Equation 1) (Beven & Kirkby, 1979). High TWI values indicate flat areas where water pools, and low values indicate steep areas with rapid drainage.

Equation 1: Topographic Wetness Index equation, as described by Beven and Kirkby (1979), where a represents the upslope contributing area per unit of contour length and β represents the slope angle.

$$TWI = \ln\left(\frac{a}{\tan(\beta)}\right)$$

2.3 Forest stability and resistance in changing climates

2.3.1 Biomechanics and slope stability

Many studies have identified trees as a critical aspect of slope stability on steep gradients (Hales & Miniati, 2017; Rees & Ali, 2012; Ziemer, 1981). Tree roots are known to reinforce the soil by forming a network that binds and anchors soil in place. This mechanical reinforcement is especially important for preventing shallow landslides and is directly proportional to root strength and density (Cohen & Schwarz, 2017; Schwarz et al., 2010). Consequently, if roots experience damage or a decrease in growth (due to, e.g., aluminum toxicity, waterlogging and anoxia, compaction, drought, or pathogens), the stability of the slope is threatened (Puhe, 2003).

2.3.2 Future projections of climate in pre-Alpine ecosystems

Climate change is rapidly altering the availability of limiting resources in the pre-Alps (Schröter et al., 2005), where the minimum average temperature has increased by 2°C over the last century, outpacing the global average (Krumm et al., 2011). While low temperatures have historically been the main limiting factor for trees in temperate and boreal forests, colder regions are becoming increasingly limited by water availability due to rising temperatures (Babst et al., 2019; Mastrotheodoros et al., 2019). A major aspect of this shift is the role of VPD. Zweifel et al. (2021) demonstrated that radial stem growth is limited by high VPD, with the majority of growth occurring during the night when VPD is very low. Rising VPD driven by a warmer climate is expected to increasingly limit tree growth, even in cold-humid climates (Babst et al., 2019). While the growth season may be lengthening, the 24-hour temporal window for growth may shrink, regardless of soil water abundance (Zweifel et al., 2021).

This atmospheric demand can also trigger a positive feedback loop. During heatwaves, evapotranspiration in some alpine forests was found to increase regardless of precipitation because of greater atmospheric vapor pressure deficit and increased solar radiation (see Section 2.1.4) (Mastrotheodoros et al., 2020). This increased evapotranspiration further depletes soil moisture reserves and leads to an increased threat of drought for areas further downstream (Mastrotheodoros et al., 2020; Teuling et al., 2010). For Norway spruce and many alpine species, these stressors are compounded by biological threats. Warmer conditions are optimal for the spread of insect pests like the bark beetle (*Ips typographus*) (Caudullo et al., 2016). Stressed trees are less able to defend against such outbreaks, threatening the health of spruce in the pre-Alpine region and the ecosystem at large (Caudullo et al., 2016; Seidl et al., 2017).

2.4 Norway spruce (*Picea abies* (L.) Karst.)

2.4.1 Ecology and range

Norway spruce (*Picea abies* (L.) Karst.) is a dominant coniferous species across Central and Northern Europe (Figure 1) (Caudullo et al., 2016). While it is a native species in this region, it has been introduced and cultivated across and outside of Europe due to its favorable characteristics for timber production (Caudullo et al., 2016; Skrøppa, 2003). In Switzerland, spruce makes up over 30% of forests (Spiecker, 2000).

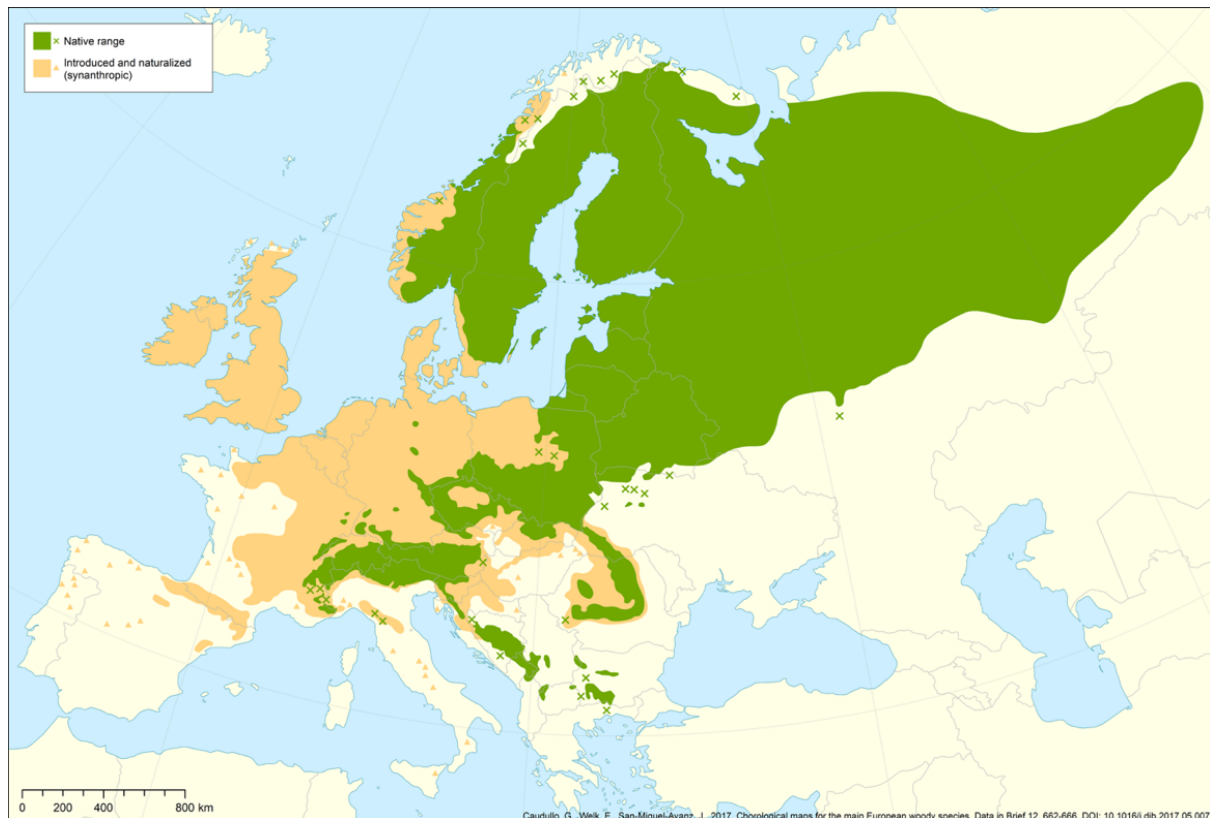


Figure 1: Map of the natural and introduced range of Norway spruce across Europe (Caudullo et al., 2025).

In the Alps, spruce are typically found between 800 and 2100 m, although their elevation range extends from sea level to approximately 2400 m (Caudullo et al., 2016). They generally inhabit regions in the Alps that range from -4°C to 17°C on average (Schweingruber, 1993). Trees may reach heights of over 60 m, though they often reach a maximum height of 30 m in mountain regions (Schweingruber, 1993). They can live for 200 years or longer (Caudullo et al., 2016), but due to their value to the timber industry, it is often difficult to find trees with more rings in lower elevations (Schweingruber, 1993).

This species is known to be shade-tolerant and often grows in dense canopies (Caudullo et al., 2016). It can grow in a variety of soil conditions, though both waterlogged and insufficiently moist soils are unfavorable for growth (Caudullo et al., 2016). Its root system is known to be shallow (Figure 2), and a lack of oxygen access exacerbates this trait (Caudullo et al., 2016; Puhe, 2003).



Figure 2: The underside of a fallen Norway spruce tree in the Studibach catchment showing the shallow root network.

2.4.2 Climate sensitivity and threats

Spruce, like many tree species, are susceptible to severe weather events and pathogens. The main pathogen of this species is *Ips typographus*, or the bark beetle, but various insects and fungi are known to damage spruce across Europe (Caudullo et al., 2016). They have a poor fire tolerance and are easily felled by strong winds due to their shallow roots. Their rooting system also makes them particularly susceptible to drought due to a lack of access to deep groundwater (Caudullo et al., 2016).

Anthropogenic influence and climate change have been major drivers of spruce decline in the past 50 years (Caudullo et al., 2016). Summer droughts and increasing temperatures are thought to cause spruce to retreat towards higher elevations and less exposed slopes, and mortality is closely linked to climatic stresses (Caudullo et al., 2016; Spiecker, 2000). However, Spiecker (2000) showed that Norway spruce growth accelerated across Europe in the 20th century. While the true reason is unknown, this trend could perhaps be due to forest management or an increased growing season, among other things (Spiecker, 2000).

A study in the subalpine coniferous forest of Davos Seehornwald, Switzerland, consisting primarily of Norway spruce, found that warming conditions have lengthened the growing season by over 30 days (Gharun et al., 2020). It surmises that higher elevation sites typically have temperatures lower than ideal for maximum plant growth, as well as excess precipitation. Therefore, slightly warmer and drier conditions may be more optimal in some cases. However, Norway spruce is especially vulnerable to excessive drought and

heat and is expected to be negatively affected as the climate continues to change (Caudullo et al., 2016).

2.5 Dendrochronology

The study of dendrochronology is based on the fundamental principle of limiting factors, which states that tree growth can proceed only as fast as allowed by the most scarce resource (Fritts, 1976). This growth is physically recorded in tree rings, which are the result of a tree's secondary (radial) growth (Ragni & Greb, 2018). In temperate regions, a definitive dormancy period (see Section 2.1.1) forces this secondary growth to pause, resulting in annual layers of wood that appear as rings in a cross-section of the tree stem (Nilsson, 2022).

Each ring is a record of the year in which it grew, allowing scientists to study environmental conditions and events recorded in the characteristics of the wood (E. R. Cook & Kairiukstis, 1990). Additionally, the principle of crossdating allows for the identification of the exact year a ring was formed. Crossdating is the process of matching tree-ring patterns across different trees to ensure each ring is assigned to its exact year of formation (E. R. Cook & Kairiukstis, 1990). By matching ring-width patterns across multiple trees, researchers can account for potential anomalies such as false or missing rings, ensuring temporal precision and agreement (Fritts, 1976).

Conifers, including Norway spruce, are known to have distinct rings, making them especially valuable for dendrochronology compared to species with less distinguishable ring boundaries (Schweingruber, 1993). This distinctiveness is driven by the contrast at the annual boundary itself. Specifically, a visible line is formed where the thick-walled, flattened latewood cells at the end of one growing season abruptly meet the larger, thin-walled cells at the beginning of the subsequent growing season (Schweingruber, 1993). This clear cellular boundary allows for easier differentiation between annual rings.

Previous dendrochronological studies on Norway spruce in Switzerland have generally focused on the relationship between radial growth and climate variables (Cunningham et al., 2006; King et al., 2013; Lévesque et al., 2013; Zweifel et al., 2006). For example, King et al. (2013) found that modern warming has led to increased Norway spruce growth at higher elevations and decreased growth in lower, drier valleys, and all elevations have a significant positive correlation with prior and current summer precipitation. Additionally, Lévesque et al. (2013) found that spruce in drier sites are particularly vulnerable to drought.

3. Study area

3.1 Location and research history

The study area coincides with the Studibach catchment (47.04° N, 8.72° E), which is part of the greater Alptal catchment in canton Schwyz, Switzerland. It is located about 40 km southeast of Zürich, approximately 20 km south of the closest point of Zürichsee, and 10 km south of Einsiedeln. The Alptal village is also nearby, not to be confused with the Alptal valley (Bundesamt für Landestopografie (swisstopo), 2026).

The Alptal is an intensively monitored mountain catchment. Systematic hydrological monitoring began in 1960 when the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL) established multiple research stations (Stähli et al., 2021). Since 1968, water discharge has been consistently measured at three catchments in the study area, and the Studibach was instrumented in 2010 (Eidg. Forschungsanstalt für Wald, Schnee und Landschaft WSL, 2025; Stähli et al., 2021).

Ecological studies in the forest began in the 1980s, and dendrochronological studies began shortly after and continue to this day (Krause et al., 2012; Schleppi et al., 1999). These studies have focused largely on the impacts of nitrogen addition on Norway spruce growth. Krause et al. (2012) found that low-dose nitrogen addition can be slightly beneficial for a tree's ability to sequester atmospheric carbon, though Schleppi et al. (1999) emphasizes the threat that the leaching of excess nitrogen can have on water quality.

Since 1981, the Erlenhöhe meteorological station has provided a continuous record of the local climate, allowing researchers to correlate long-term tree-ring data with local temperature and precipitation measurements (Stähli et al., 2021). The intersection of long-term dendrochronological records and high-frequency sensor data makes the Alptal an optimal location to continue performing scientific studies.

3.2 Climate

The Alptal is characterized by a cool, wet climate, with a mean annual temperature of 4.8°C and approximately 2,200 mm of annual precipitation (MeteoSchweiz, 2025). The climate of the Alptal is classified as humid continental (Dfb). Precipitation is abundant year-round, with summer being the wettest season. Due to its position on the northern edge of the Alps, the valley acts as a barrier for humid air masses, resulting in significant orographic lift (Schwarb, 2000). This phenomenon makes it one of the wettest places in Switzerland (Burch, 1994; Stähli et al., 2021).

Snow is often present from late autumn to early spring, with continuous snow cover at elevations over 1300 m a.s.l. The snowmelt keeps the soil saturated well into the growing season, but the timing of this melt has become increasingly earlier (Stähli et al., 2021).

The mean annual temperature is approximately 5.7°C at the Erlenhöhe station (Stähli et al., 2021). July temperatures historically average 13.8°C, while January temperatures historically average as low as -3.8°C (Figure 3). However, as noted in Section 2.3.2, minimum temperatures in the region have risen by 2°C over the last century, significantly lengthening the potential growing season while simultaneously increasing the risk of spring frost events (Vitasse et al., 2018).

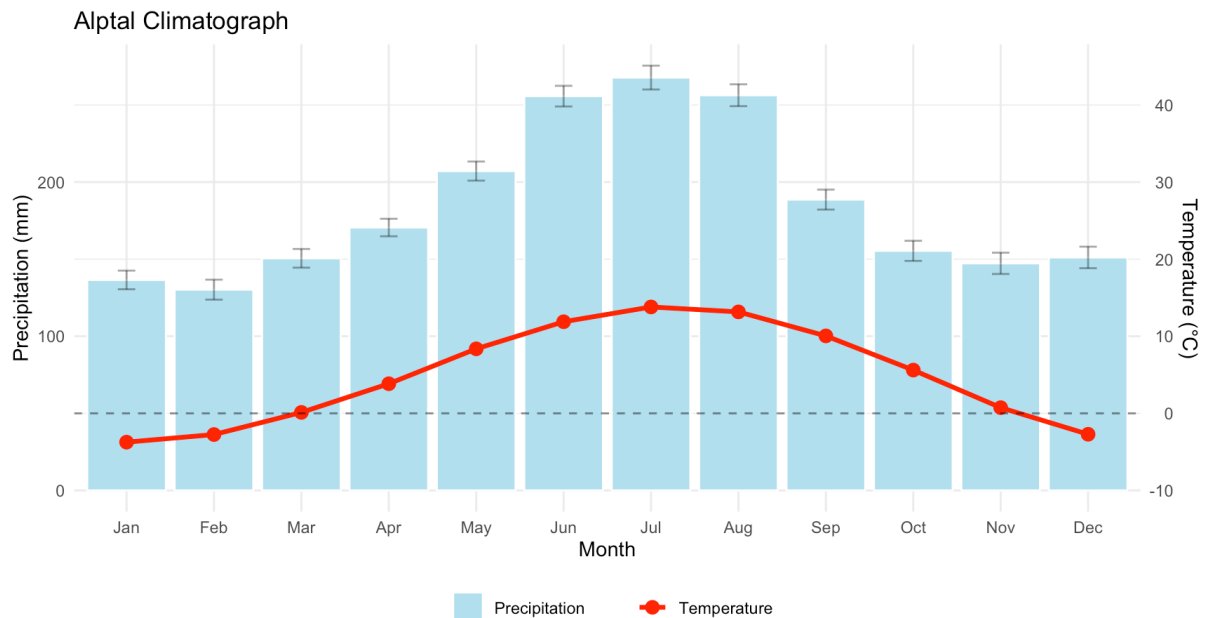


Figure 3: Climatograph of the Alptal constructed with the homogenized climate data described in Section 4.4.1. Error bars and band represent the standard error; however, the error band is narrower than the mean trendline and is therefore not visible.

3.3 Hydrology

The hydrology of the Alptal is dominated by the interaction between high annual precipitation and low-permeability gleysols. Due to the high clay content of the gleysols and flysch bedrock, vertical infiltration is limited, leading to a high groundwater table that frequently reaches the soil surface during snowmelt and heavy rainfall events (Rinderer et al., 2014). This creates a flashy hydrological regime where runoff occurs quickly (Stähli et al., 2021), primarily as overland flow or through preferential lateral pathways in the topsoil (Hendriks, 2010). The extent and duration of saturated conditions vary considerably across space and time. While flat areas maintain a shallow groundwater table almost year-round, steeper slopes have more variability, typically experiencing saturation during storms and draining shortly after (Rinderer et al., 2016). Consequently, trees in this catchment are subjected to frequent periods of soil saturation, potentially inducing root anoxia despite the steep gradients.

3.4 Geomorphology and soil

The bedrock in the valley is composed of flysch, a type of sedimentary mélange (Reynard, 2021; Roth, 1998). Weathered flysch is notorious for shallow landslides, and large landslides are also a potential hazard (Berti et al., 2017). The soils in the study area are predominantly gleysols, and they are characteristic of saturated conditions and have a low permeability due to the high clay content (Schleppi et al., 1998). They are often found throughout the Swiss pre-Alps.

The Southern Alptal is a U-shaped glacial valley containing the Alp River. Due to the general northward flow of the Alp River, the sides of the Alptal have distinct east- and west-facing slopes. The Studibach catchment is predominantly west-facing, a configuration that subjects the forest to higher solar radiation and higher soil temperatures in the afternoon compared to east-facing slopes (Geiger, 1942). The catchment is characterized by steep slopes, with the average slope for the study area being 29° (Bundesamt für Landestopografie (swisstopo), 2026). These steep inclines, paired with unstable bedrock, facilitate rapid lateral flow and contribute to soil creep and geomorphic instability characteristic of the flysch zone.

3.5 Forest composition and changes over time

The forest is composed mostly of Norway spruce (*Picea abies* (L.) Karst.) and silver fir (*Abies alba* Mill.). The species can be distinguished by their needles, as shown in Figure 4: spruce have four-sided needles that grow spirally along the length of a twig (Marín et al., 2016), while firs have flatter and thinner needles (Hess et al., 1984; Marín et al., 2016). Other vegetation includes shrubs from the *Vaccinium* genus and various mosses (Schleppi et al., 1998).



Figure 4: Needles of (A) Norway spruce and (B) silver fir.

During the pre-industrial period, considerable portions of the valley were thinned or cleared to provide space for livestock grazing and agricultural cultivation. Much of this land was allowed to revert to forest cover, resulting in a stand structure that more closely resembles its natural state (Stähli et al., 2021). Despite this transition toward a more heterogeneous and natural composition, the forest remains actively managed under a selection silvicultural system, which maintains a continuous cover by harvesting individual trees rather than entire stands (Eidg. Forschungsanstalt für Wald, Schnee und Landschaft WSL, 2026).

The most significant changes in recent decades have been caused by natural disturbances. Winter storms Vivian and Lothar (1990 and 1999, respectively) caused severe windthrow across the northern pre-Alps, damaging over 8% of the Alptal forest (Scherstjanoi et al., 2010). These events not only physically altered the canopy but also triggered a secondary disturbance in the form of bark beetle outbreaks, further increasing mortality in Norway spruce stands. These disturbances are critical to consider in dendrochronological studies, as the sudden removal of neighboring trees often results in an increase in growth in surrounding trees due to reduced competition for light and nutrients (Schweingruber, 1993), which must be distinguished from climatic signals.

4. Methods

4.1 Study design and site selection

4.1.1 Study design

The study aimed to obtain tree cores from four site types to differentiate the effects of moisture and slope in a two-way factorial design, as this gives the project the best chance of determining which of these correlated factors has the dominant influence on tree growth. This method is widely used by ecological studies in which it is impossible to control for every potential factor affecting natural variation (Cheng, 2014).

The sample groups consist of “flat wet,” “flat dry,” “steep wet,” and “steep dry.” As the catchment is wet and steep overall, the “flat” and “dry” areas are not necessarily flat or dry, rather simply flatter and drier than their “steep” and “wet” counterparts. For each of the four groups, two replicate sites were chosen, and 8 trees were selected in each site, for a total of 64 trees cored.

4.1.2 Site selection

Seventeen sites were evaluated during a field scouting campaign in which slope gradient, soil moisture, tree size, and tree straightness were qualitatively assessed. The eight sites with conditions that best represented the aforementioned moisture and slope classes and with straight, relatively similar-sized trees were selected for sampling (Figure 5). Each site is approximately 1500 m².

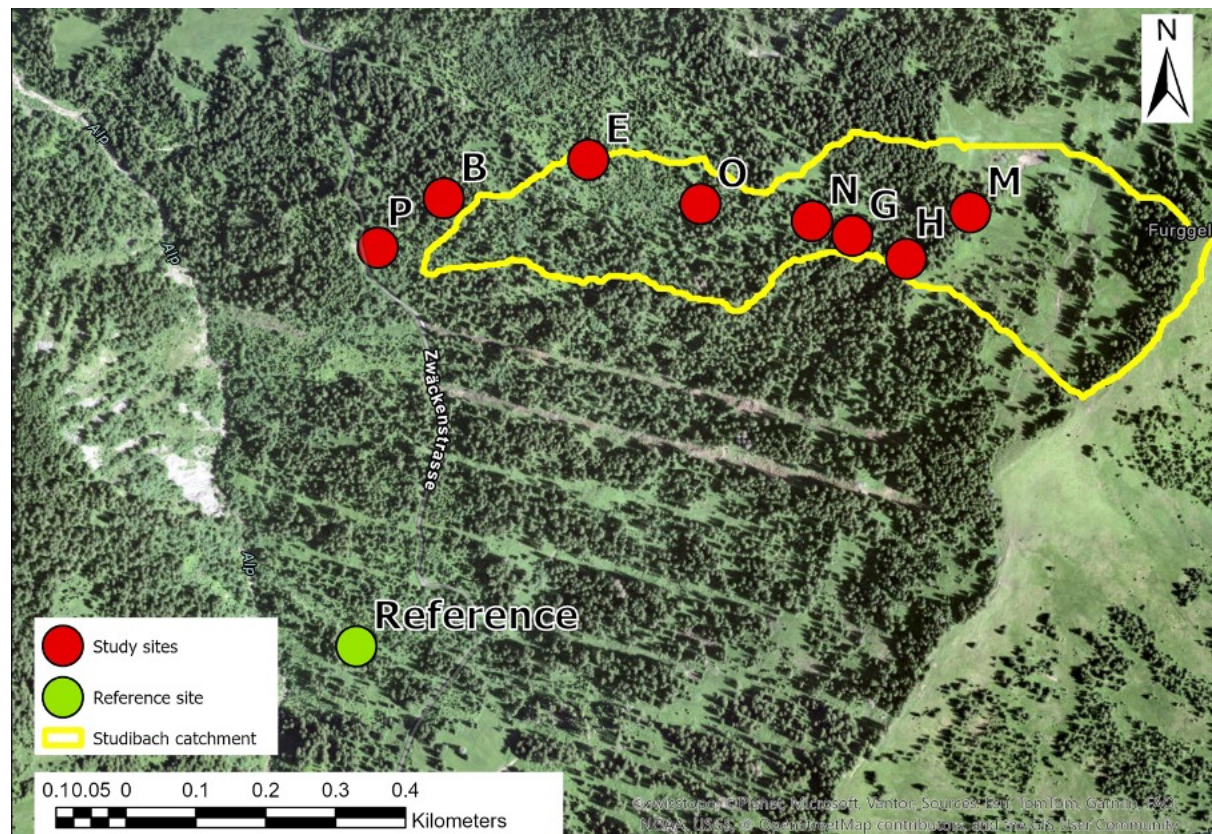


Figure 5: Locations of study sites in the Studibach and the reference site (see Section 4.2.3). For study site classifications, see Figure 6.

Slope and soil moisture were later quantified with measurements from an inclinometer and soil moisture sensor (ML3 ThetaProbe from Delta-T Devices). Soil moisture (0-6 cm depth) was measured after a dry period of >5 days at 16 randomly selected points per site. Inclinometer measurements were taken at 5 transects per site. To validate the site classifications before the main analyses, linear mixed-effects models (LMMs) were fitted using the `lme4` and `lmerTest` packages in R (Bates et al., 2015; Kuznetsova et al., 2017). Site was included as a random intercept to account for repeated measurements within sites. Their elevations range from approximately 1260-1510 m a.s.l. (Bundesamt für Landestopografie (swisstopo), 2026). Sites B and O were ultimately selected as steep wet, E and H as steep dry, M and N as flat wet, and G and P as flat dry (Figure 6).

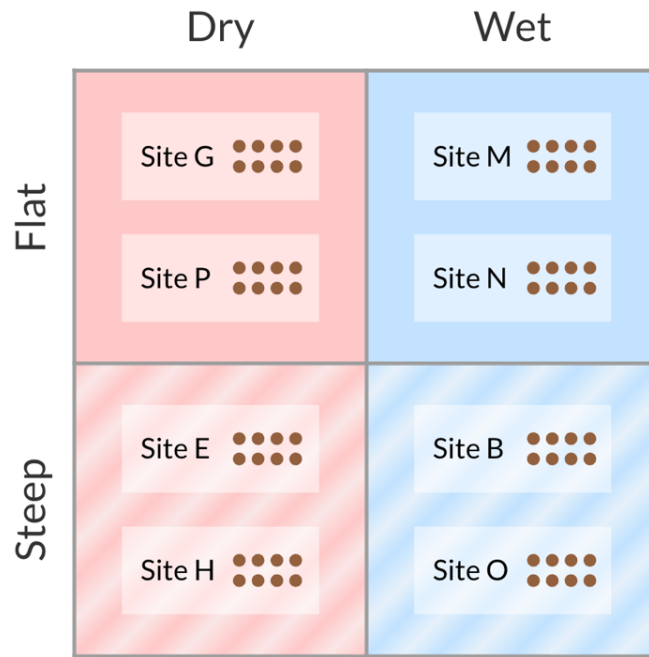


Figure 6: Schematic of the two-way factorial study design and classification of each study site. Brown circles represent individual trees. See Figure 5 for the locations of the study sites.

4.2 Dendrochronological sampling and processing

4.2.1 Fieldwork

At each site, eight representative trees were selected for coring (Table 1). Increment cores were extracted with a cordless drill and a torque booster attachment following the workflow described in Gärtner et al. (2023). A 5 mm increment corer was placed in the drill adapter and then used to drill perpendicular to the tree stem (Figure 7a). Once a depth greater than the stem radius was reached, the drill was detached, and the core was separated from the tree by manually turning the corer two complete rotations in the opposite direction (Figure 7b). Then, the core was retrieved using a standard extractor (Figure 7c). This setup allowed for a constant speed and pressure to be maintained, leading to better quality samples and a more time-efficient process compared to manual coring (Gärtner et al., 2023).

Table 1: Description of the sites, including the elevation and diameter at breast height (DBH) for the 8 trees that were cored at each site.

Site	Site category	Number of cores	Elevation (m a.s.l.)	DBH (cm)		
				Min.	Median	Max.
P	Flat dry	16	1260	25.5	37.1	67.8
B	Steep wet	32	1280	36.0	45.4	53.2
E	Steep dry	32	1350	17.5	22.4	51.6
O	Steep wet	32	1393	24.2	46.5	64.6
N	Flat wet	16	1433	22.3	30.2	50.9
G	Flat dry	16	1448	27.7	40.6	53.5
H	Steep dry	32	1476	29.6	49.0	58.9
M	Flat wet	16	1504	38.5	51.4	66.2



Figure 7: Images from the coring process. (A) shows the initial drilling perpendicular to the tree stem. (B) shows manual turning of the corer. (C) shows the retrieval of the increment core.

Increment cores were immediately stored in 3D-printed core holders with the wood fibers oriented upright. This storage method prevents fungal growth, eliminates the need for later gluing and mounting, and reduces the risk of human error (Gärtner et al., 2024). The cores were labeled and stored in paper bags to prevent damage during transport and storage.

Each tree in a flat site was cored twice (once on each side perpendicular to the slope of the ground), as is consistent with typical dendrochronological practices (Gärtner et al., 2023). Each tree in a steep site was cored four times to detect potential reaction wood from slope movements, allowing the effect of reaction wood on the measurements to be reduced, thus creating a more representative average tree-ring width. However, only the two cores perpendicular to the slope were ultimately necessary for use in the study due to the lack of excessive reaction wood in the cores. This resulted in 192 total cores, of which 128 were analyzed in this thesis.

The use of increment cores is far less destructive than cutting discs and is considered to be minimally invasive (E. R. Cook & Kairiukstis, 1990; Gärtner et al., 2024). The bore holes from this field work were left uncovered, as wounds often heal over in a few years (E. R. Cook & Kairiukstis, 1990; Schweingruber, 1993). Ultimately, coring has not been found to have an influence on the mortality of Norway spruce (Wunder et al., 2011).

4.2.2 Sample preparation

All increment cores were planed, or shaved down, using a core microtome (Figure 8). This is necessary to scan the cores in the future, as a flat surface is required for optimal camera focus. It is preferred over sanding as it avoids problems of cell damage and obfuscation due to dust (Gärtner & Nievergelt, 2010). This process began by fixing each core, still inside its holder, in the core holder on the microtome. Each core was individually brushed with water to allow for more flexibility, a smoother cutting process,

and a greater chance of preserving the sample (Gärtner & Nievergelt, 2010). Each core was then shaved down with an NT-Cutter blade (A-type) in $\pm 3 \mu\text{m}$ increments until the plane surface was approximately 3 mm wide (Gärtner & Nievergelt, 2010).

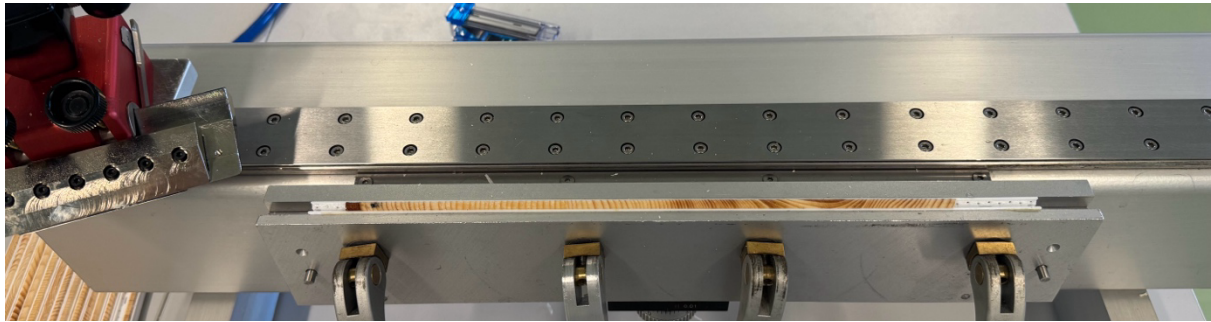


Figure 8: Photo of an increment core in a core microtome.

The planed core surfaces (Figure 9) were digitized using the WSL Skippy imaging system, as described in Gärtner et al. (2024) and shown in Figure 10. The system uses a high-resolution digital camera (Sony Alpha 7R IV) with a macro lens (Sony FE 90 mm f/2.8) mounted on a motorized stage. Samples remained fixed in core holders, which were brought to Skippy after drying from the microtoming process. The system automatically captured a series of overlapping, high-resolution images along each core. The overlapping images were then used to create a composite image of the full core using PTGui, a distortion-free stitching software. Millimeter paper was placed at the end of each core for calibration.



Figure 9: Composite images of planed cores.

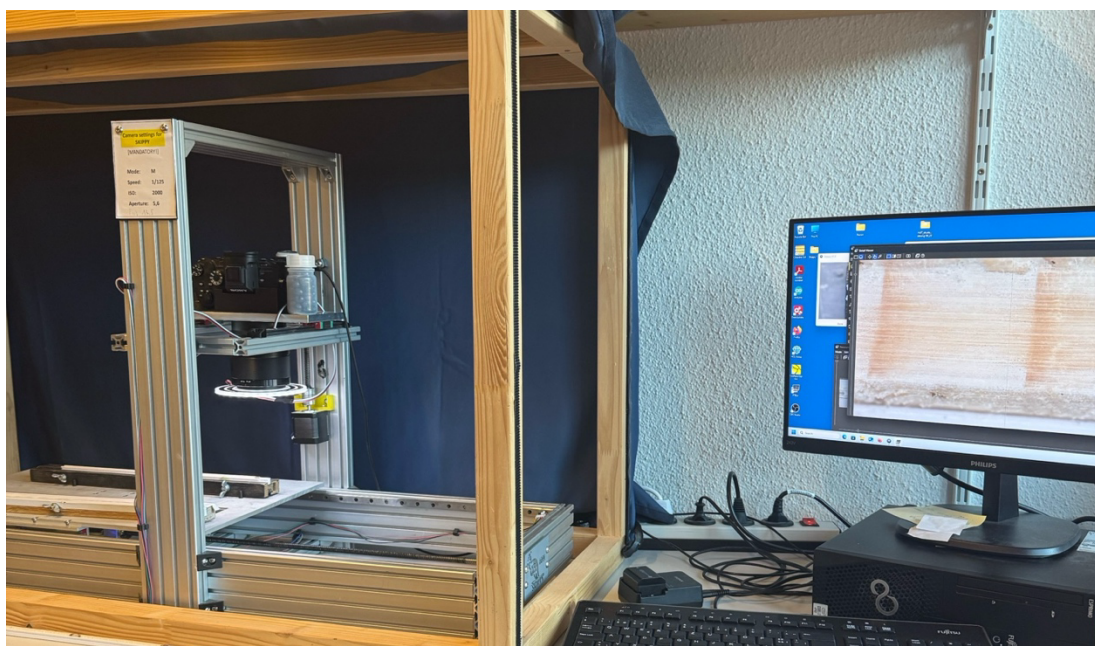


Figure 10: Photo of the WSL Skippy imaging system.

4.2.3 Sample analysis

High-resolution core images were imported into Coorecorder (Larsson, 2020a) to manually place coordinates on the tree-ring boundaries (Figure 11), allowing for the conversion of visual data into raw ring-width series (.pos files). The pos files for each core were imported into CDendro to be converted to vector graphic (.fh) files (Larsson, 2020b), which were then imported into TSAP-Win for crossdating. In crossdating, core samples are matched with one another to create dated chronologies for each tree, each site, and the forest as a whole (Rinntech, 2018).



Figure 11: Image of an increment core in Coorecorder with coordinates at ring boundaries.

Comparison of the study sites against a reference chronology for the same region from a previous study (Krause et al., 2012) was performed using both parametric (Pearson's r) and non-parametric (Gleichläufigkeit) tests. The location of this reference site compared to the study sites can be found in Figure 5.

Gleichläufigkeit (GLK) is a non-parametric test that is widely used in dendrochronology to show the percentage of parallel variation in different chronologies. It was calculated using the `dplR` package in R (Equation 2) (Buras & Wilmking, 2015; Eckstein & Bauch, 1969; R. M. Visser, 2020). Both chronologies were prewhitened using the same method (see Section 4.3.1).

Equation 2: Corrected gleichläufigkeit (GLK) equation, as described by Buras & Wilmking (2015), where n is the total number of years in the overlapping period, and G_{ix} and G_{iy} are the directional growth changes of the two chronologies (x and y).

$$glk_{(x,y)} = 1 - \frac{1}{n-1} \sum_{i=1}^{n-1} |G_{ix} - G_{iy}|$$

4.3 Tree-ring standardization and metrics

4.3.1 Detrending and chronology development

Raw ring-width measurements were standardized as follows to isolate the climatic signal from non-climatic noise associated with age-related growth patterns and local stand dynamics (E. R. Cook & Kairiukstis, 1990). This was performed in R using the `dplR` package (Bunn, 2008).

A smoothing cubic spline function with a 50% frequency cutoff of 32 years was used on each individual series (E. Cook & Peters, 1981) to remove slow, rolling trends and leave behind year-to-year changes, as is recommended when non-climatic variability is present due to forest management (Bošela et al., 2011; Rukh et al., 2020). The main objective of this standardization process is to remove the age trend, which refers to the fact that trees produce narrower rings over time because the same amount of new wood growth is spread over a larger circumference (E. R. Cook & Kairiukstis, 1990; Fritts, 1976). The spline approach is adaptive, calculating a unique stiffness for each tree based on its age. This was especially important for the data used in this thesis, which included a wide spread of tree ages. This standardization process produces a ring-width index (RWI) for each tree, which is calculated by dividing each ring width by its spline (E. R. Cook & Kairiukstis, 1990). By using a spline that adapts to each tree, the resulting dimensionless RWIs are more easily compared regardless of age and site conditions.

Temporal autocorrelation was then removed via prewhitening, an autoregressive modeling process used to account for biological persistence, or the lag effect in which a previous year's growth reserves influence the current year's ring formation (Babst et al., 2013; Fritts, 1976). The resulting residual chronologies were calculated by subtracting the model's predicted growth from the observed RWI. This process ensures that the final RWIs primarily reflect the influence of climate drivers in the corresponding year.

Finally, the prewhitened time series were averaged for each of the eight sites across the study area, as well as averaged all together to produce a single master chronology using Tukey's biweight robust mean. Tukey's biweight robust mean calculates a weighted average by minimizing the effect of outliers. It does so by assigning them lower weights (and in the case of extreme outliers, zero weight), and is thus more suitable than a simple arithmetic mean (Bunn et al., 2025).

4.3.2 Basal area increment (BAI) conversion

To approximate long-term changes in ring width to absolute tree growth, raw ring-width measurements were converted into basal area increment (BAI). Unlike raw ring widths, which naturally decrease as a tree's circumference grows, BAI quantifies the two-dimensional area of wood grown annually, providing a more accurate proxy for total biomass accumulation over time (H. Visser, 1995). By preserving the absolute magnitude

of growth rather than converting the data into dimensionless, standardized indices via detrending, BAI still allows for direct site comparisons. This calculation was performed in R using the `dplR` package (Bunn, 2008).

BAI data was used for overall growth trend analysis, as well as for the analyses described in Section 4.5.2. To prevent pseudoreplication, cores from individual trees were averaged to create a single tree-level raw ring-width series. True tree radii (distance to pith) were calculated using diameter at breast height (DBH), which was measured in the field. The `bai.in` function was then used to calculate BAI from the bark inward (Bunn et al., 2025). Note that since bark thickness was not recorded in the field, the total radius derived from DBH was used in this calculation, which may result in a slight overestimation of absolute basal area. A linear regression was applied to the mean annual BAI to determine the statistical significance and slope of the growth trend.

4.4 Environmental data

4.4.1 Climate data and homogenization

Climate data was collected from multiple sources to reconstruct a long-term climatological time series for use in this thesis. Data is available from the Erlenhöhe climate station, located approximately 1 km from the closest study site and 1.7 km from the furthest study site, since 1983 (provided by the WSL). Data is also available from the Einsiedeln Monastery, located approximately 8.5 km from the study sites, since 1864 (MeteoSchweiz, 2025). This not-yet-published dataset was provided courtesy of MeteoSwiss and is part of a continuation of the nationwide climate homogenization project as detailed in Begert et al. (2003) and Begert et al. (2005).

The Erlenhöhe dataset underwent rigorous quality control to ensure internal consistency based on the two measurements for temperature (standard air temperature sensor and ventilated air temperature sensor) and precipitation (tipping bucket and pluviometer).

For temperature, the ventilated air temperature sensor was selected as the primary data source to minimize radiative errors (Begert et al., 2003). Comparison with the standard air temperature sensor showed a near-perfect agreement ($r^2 = 0.99$). For precipitation, the pluviometer was selected as the primary data source to reduce evaporative errors and mechanical errors associated with bucket sensors (Begert et al., 2003). Comparison with the Erlenhöhe precipitation measurements revealed distinct measurement discrepancies, including missed events by the tipping bucket in June and July 2021, a pluviometer error during February and March 2022, a precipitation event missed by the pluviometer on 31 July 2024, and a precipitation event missed by the tipping bucket on 26 June 2025. After correcting these discrepancies and excluding them from the correlation test, the two methods were found to be strongly correlated ($r^2 = 0.95$). This allowed the tipping bucket data to be used to fill gaps in the pluviometer data.

The data from the Erlenhöhe and Einsiedeln stations were compared for a period of 42 years (January 1983-December 2025) to establish their climatological relationship and to use the Einsiedeln data to reconstruct the climate for the Erlenhöhe station. Strong correlations were observed for both monthly average temperature ($R^2 = 0.98$) and total precipitation ($R^2 = 0.84$), justifying the use of the monastery as a reference station to extend the time series.

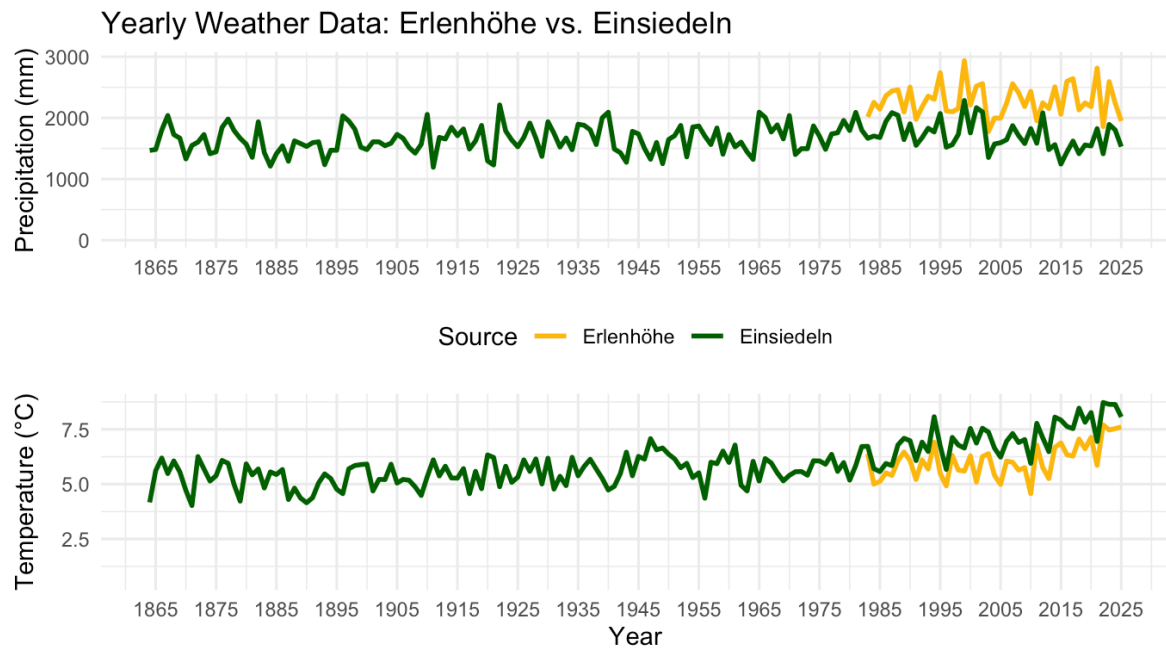


Figure 12: Time series of the annual precipitation and annual average temperature for the Erlenhöhe and Einsiedeln climate stations, pre-homogenization.

Systematic biases between the two stations were corrected following standard World Meteorological Organization guidelines for relative homogenization to prevent artificial jumps (Figure 12) (Aguilar et al., 2003). For temperature, an additive correction was applied. The temperature at the Erlenhöhe station (1089 m a.s.l.) was consistently lower than the Einsiedeln station (919 m a.s.l.), likely due to the elevation difference (Bundesamt für Landestopografie (swisstopo), 2026). A consistent offset of -1.09°C (calculated from the mean difference during the overlap period) was applied to the historical Einsiedeln temperature data to obtain an estimate of the annual and monthly average temperature at the Erlenhöhe climate station. For precipitation, a multiplicative correction was applied to account for orographic effects. A scaling factor of 1.33 (ratio of cumulative precipitation sums) was applied to the historical Einsiedeln precipitation data to obtain an estimate of the monthly and annual precipitation at the Erlenhöhe climate station.

The final time series was constructed by merging the two datasets. The measured era (1983-2025) is based on direct observations from the Erlenhöhe climate station, while

the reconstructed era (1864-1982) extends the time series by using the bias-corrected Einsiedeln data (Figure 13).

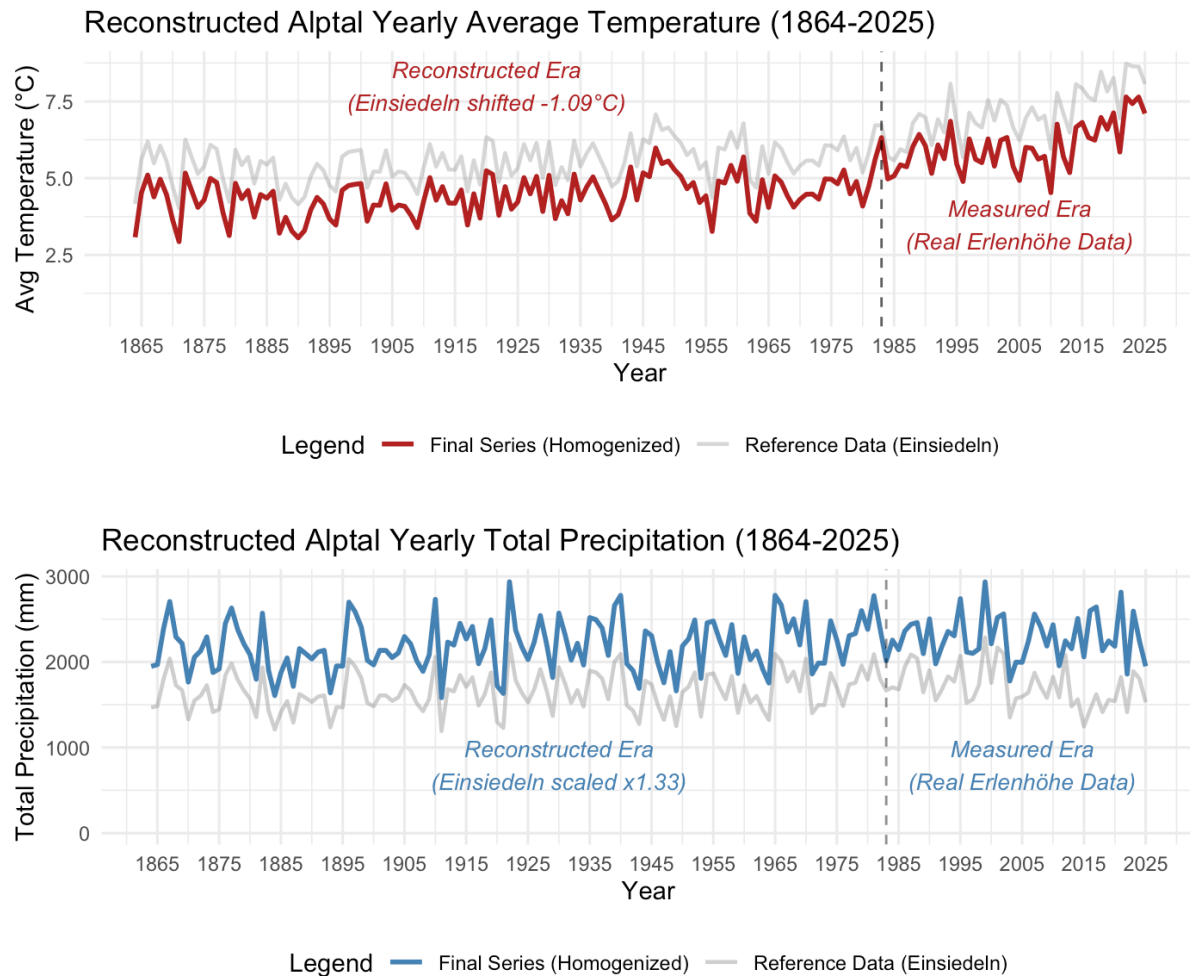


Figure 13: Reconstruction of the annual average temperature (top) and annual total precipitation (bottom) data based on the data from the Erlenhöhe and Einsiedeln climate stations to create a long time series of the study area.

4.4.2 GIS and winter albedo analysis

Spatiotemporal changes in forest cover and land use in the Alptal were calculated in ArcGIS pro using the Swiss Land Use Statistics (Arealstatistik) hectare-resolution geodata for the survey periods of 1979-85, 1992-97, 2004-09, and 2013-18 (Bundesamt für Statistik, 2025). A trajectory analysis was performed by concatenating the land-use codes across all four periods, creating a unique “history string” for every point. This allowed for the identification of specific change signatures, such as succession (meadow to forest) and natural disturbances (forest to damaged stands). To visualize these changes, the vector-based points were rasterized into grid cells, overlaid on the SwissALTI3D high-resolution digital elevation model, and integrated into a time-enabled ArcGIS environment (Bundesamt für Landestopografie (swisstopo), 2025). The standard 72-category land cover and use nomenclature (NOAS04) was further classified into six functionally relevant groups (forest, groups of trees, meadows and pastures, wetlands

and watercourses, anthropogenic forest damage, and natural forest damage) to facilitate easier interpretation of forest changes over time. The exact land-use categories that comprise these groups are listed in Table A1 of the appendix.

To further reconstruct the historical timeline of forest change, analysis was also performed using 30 m resolution multispectral Landsat data in Google Earth Engine (GEE). The bands of interest have a spatial resolution of 30 m, and satellite images have been taken at least every 16 days (now every 8 days), both notably finer resolution than the previous dataset (U.S. Geological Survey (USGS), 2026). While standard vegetation indices (e.g., NDVI, LAI) are effective for detecting canopy loss in many biomes, they are not as reliable in productive ecosystems, in which deforested or damaged areas are quickly recolonized by grasses (Hislop et al., 2018). This results in a fast recovery of spectral greenness and moisture signals during the growing season. To combat this, winter albedo (January 1 – March 31) was derived from Landsat imagery (Landsat 5 TM, 8 OLI, and 9 OLI-2) from 1984 through 2025. This approach takes advantage of the high spectral separability between the high-albedo open snowpack and the lower-albedo forest canopy. Snow-covered coniferous forests typically have an albedo of around or less than 0.2, while fresh snow often has a high albedo ($\alpha > 0.7$) (Betts & Ball, 1997). The median albedo values of open fields can be as low as 0.45; however, due to the influence of old and interfered-with snow (Robinson & Kukla, 1985; Pomeroy & Brun, 2001).

Annual winter composites were produced by computing the median albedo for each pixel utilizing Equation 3 (Liang, 2001) after filtering out cloud cover and cloud shadows while preserving the stable snow signal (Z. Zhu & Woodcock, 2012).

Equation 3: Formula for calculating shortwave albedo using Landsat 5, 8, and 9 data as described by Liang (2001), where α_1 , α_3 , α_4 , α_5 , and α_7 refer to spectral bands 1, 3, 4, 5, and 7.

$$\alpha_{short} = 0.356\alpha_1 + 0.130\alpha_3 + 0.373\alpha_4 + 0.085\alpha_5 + 0.072\alpha_7 - 0.0018$$

Satellite-derived albedo estimates were compared with ground-based snow depth data to distinguish true canopy loss from weather-driven snowpack variations (data provided by the WSL). Snow depth records were obtained from the Erlenhöhe weather station in the Alptal, and the median value between January 1 and March 31 was calculated to match the satellite composite period. This comparison allows for the identification of instances where the albedo was low due to a lack of snow cover rather than a change in forest cover.

4.5 Statistical analyses

4.5.1 Monthly climate correlation analysis

The specific meteorological drivers of tree growth were evaluated using bootstrapped correlation functions using the `treeclim` R package (Zang & Biondi, 2015). The

prewhitened master chronology was correlated against the homogenized mean monthly temperature and total monthly precipitation.

Because radial growth is heavily influenced by the previous year's conditions (Fritts, 1976), the climatic window was set to 19 months, spanning from April of the previous year to October of the current growing year. To test for non-stationarity and shifts in climate sensitivity, the climate and prewhitened RWI time series were divided into two eras: historical (1864-1979) and modern (1980-2025). The function `dcc` was used to calculate the correlation coefficient (Pearson's r) for each month in each era. Because traditional p-values often underestimate error and produce false positives with this type of analysis (Biondi & Waikul, 2004), statistical significance (at the $\alpha = 0.05$ level) was determined with the same function using 1,000 stationary bootstrap resamples to 95% confidence intervals around the correlation estimates (Zang & Biondi, 2015). Correlations were considered significant if the absolute value of the median exceeded half the difference between the 97.5th and 2.5th bootstrap quantiles, a threshold that ensures the 95% confidence interval excludes zero (Biondi & Waikul, 2004). This method is commonly used in dendrochronological analyses (E. R. Cook, 1990; Rao et al., 2019).

4.5.2 Linear mixed-effects modeling and estimated marginal means analysis

To determine the effects of slope gradient and soil moisture on long-term forest growth, a linear mixed-effects model (LMM) was used. LMMs allow for the simultaneous modeling of fixed effects (effects that are present across the entire population of an experiment) and random effects (effects present in certain groups that may differ from the general trend) (Brown, 2021). This method was selected over an analysis of variance (ANOVA) due to its capability of handling unbalanced datasets and its ability to account for nested, non-independent experimental designs in a more straightforward way (Zuur et al., 2009).

Absolute growth, measured as BAI, was modeled as the continuous response variable of the unaggregated dataset. Slope (flat vs. steep) and soil moisture (wet vs. dry) were designated as categorical fixed effects.

To separate the influence of slope gradient and soil moisture from tree geometry, cambial age was included as a continuous fixed effect to control for age trends in tree growth. Cambial age is defined as the ring number from the pith, or the biological age of the tree at the sampling height (Spicer & Gartner, 2001).

To prevent pseudoreplication associated with repeated annual measurements, individual trees were nested within their respective sampling sites, and these sites were treated as a random intercept (`1|SiteCode/TreeID`). Additionally, to control for temporal autocorrelation and isolate long-term ecological shifts from year-to-year

climate variability, the calendar year was included as a crossed random intercept (Harrison et al., 2018).

The analysis was conducted in two phases. First, a baseline model was used to assess the dominant topographical factors across the entire 1864-2025 timeline. Then, the time series was split to test how drivers may have changed over time. For this later analysis, climatic era (pre-1980 vs. post-1980) was designated as an additional categorical fixed effect.

Models were fitted using the `lme4` package in R (Bates et al., 2015). Because the dataset is unbalanced across the full time series, significance testing was conducted using a Type III Wald chi-square analysis of deviance via the `car` package to isolate the unique contribution of each fixed effect. Due to the large sample size of the unaggregated dataset (>3,000 observations), degrees of freedom and confidence intervals were calculated asymptotically via the `lmerTest` package (Kuznetsova et al., 2017). Finally, estimated marginal means (EMMs; also called least-squares means) were calculated using the `emmeans` package to extract baseline productivity estimates and visualize interactions (Lenth, 2016; Lenth et al., 2026).

A simple summary schematic of the overall workflow described in this thesis, specifically the analysis each data type was used for, can be found in Figure 14.

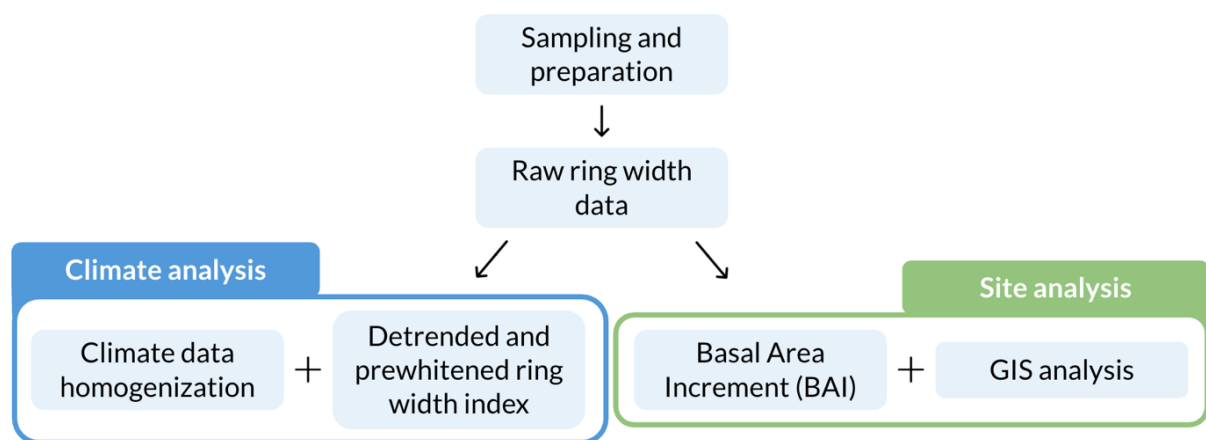


Figure 14: Schematic of the workflow described in this thesis.

5. Results

5.1 Site classification validation

The average slope in each site ranges from 13° at the flattest to 47° at the steepest, and the soil moisture averages range from 22% to 51% at the wettest (Figure 15). Soil moisture was significantly higher in sites categorized as wet (mean = 39%) compared to dry sites (mean = 22%) ($p = 0.008$). Similarly, slope gradients were significantly higher in steep sites (mean = 40°) compared to flat sites (mean = 17°) ($p = 0.002$).

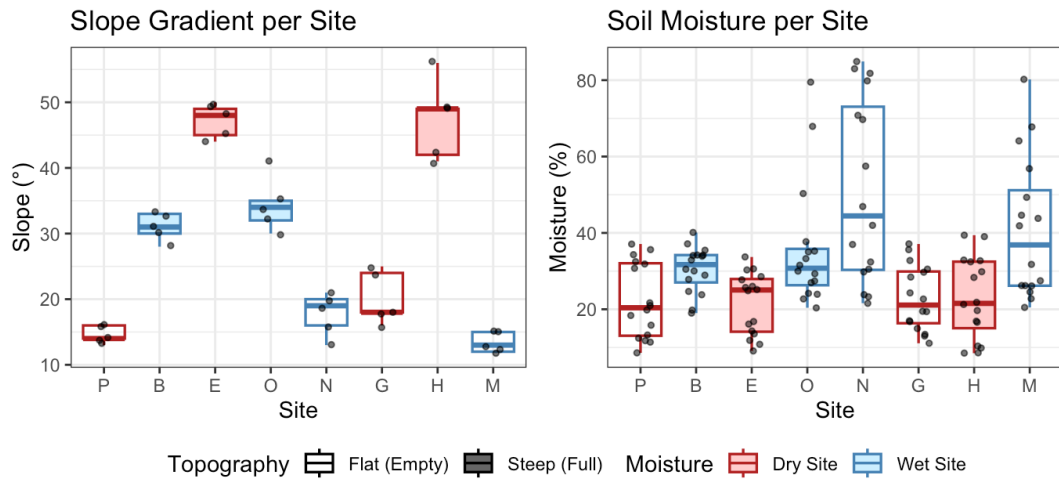


Figure 15: Box plots of the slope and soil moisture conditions of the eight study sites. The box represents the 25th to 75th percentile, the horizontal line the median, and the whiskers extend to the minimum and maximum data points. The dots represent individual measurements. The sites are ordered by elevation.

5.2 Climate trends

5.2.1 Temperature

The study region has experienced significant warming since instrumental records began in 1864 (Figure 16). From 1864 to 1979, the annual average temperature was stable, maintaining an average of approximately 4.4°C with a negligible warming trend (+0.06°C per decade). However, beginning around 1980, a period of sustained warming began. In the modern era (1980-2025), the rate of warming accelerated to +0.37°C per decade. This warming is particularly pronounced in the most recent decade (2015-2025), which recorded a yearly average temperature of 7.0°C, an increase of over 2.5°C compared to the historical average. The severity of this modern warming is highlighted by the distribution of temperature extremes. The five warmest years on record all occurred in the 2020s, while the five coldest occurred in the 19th century.

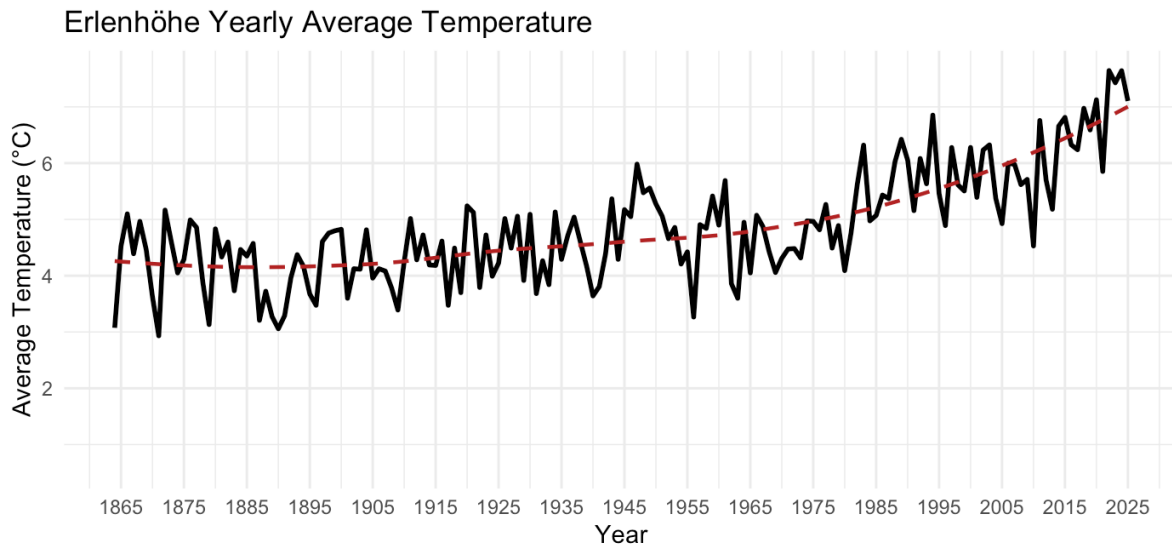


Figure 16: Erlenhöhe annual average reconstructed (1864-1982) and observed (1983-2025) temperature with LOESS trendline overlaid. For more information, the decadal climate data table can be found in Table A2 of the appendix.

The monthly average temperature has increased across all months, though the most pronounced absolute warming has occurred during the winter (Figure 17). Average January temperatures increased by 2.9°C (from -4.6°C historically to -1.7°C in the modern era), and December temperatures rose by 3.1°C (from -3.6°C to -0.5°C). Summer temperatures also increased, with July warming from 13.6°C to 14.3°C.

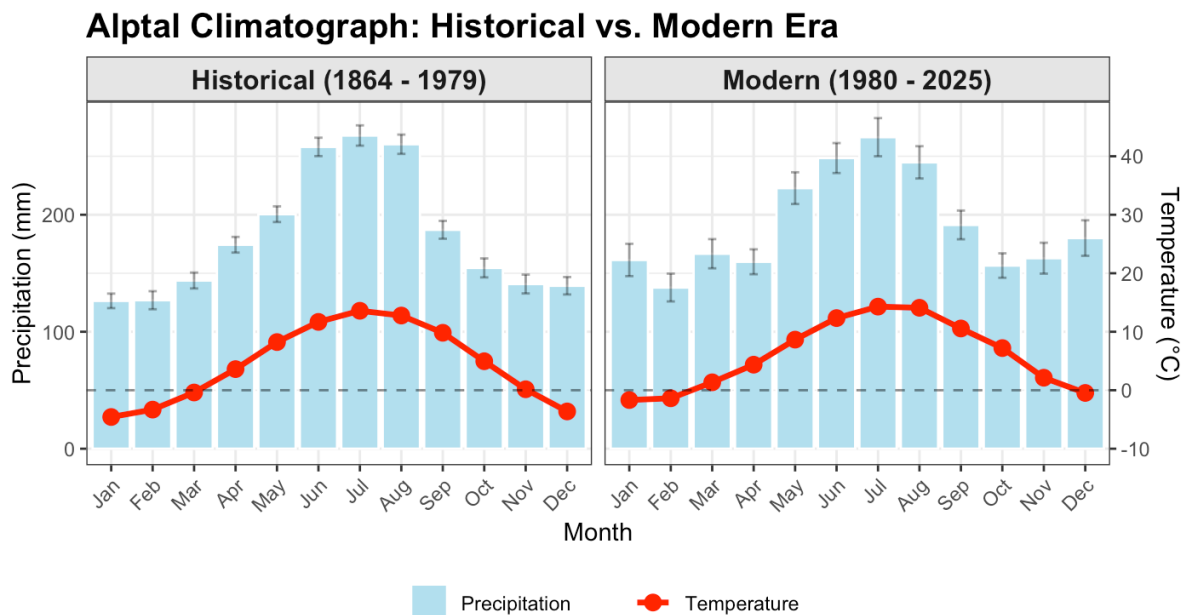


Figure 17: Dual climatograph of the Alptal created using the homogenized climate dataset divided into historical (1864-1979) and modern (1980-2025) eras. Error bars and band represent the standard error; however, the error band is narrower than the mean trendline and is therefore not visible.

5.2.2 Precipitation

In contrast to the upward trend observed with temperature, precipitation in the study area is characterized by multi-decadal variability (Figure 18). For example, the 1880s and

1940s were relatively drier (averaging 1989 and 2059 mm/year, respectively), while the 1930s, 1980s, and 1990s were characterized by higher annual rainfall, regularly exceeding 2300 mm/year.

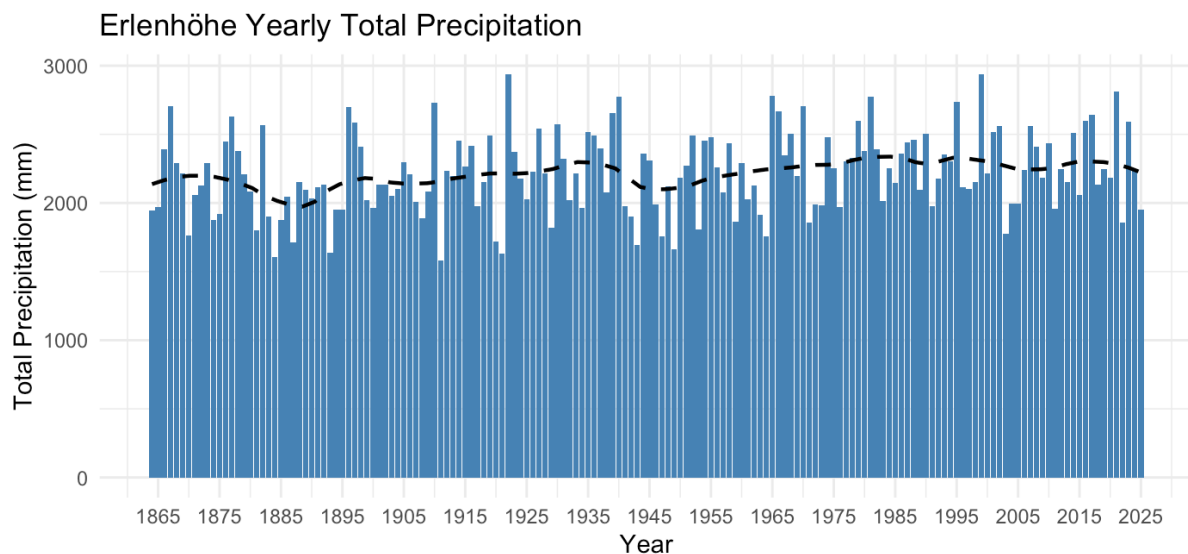


Figure 18: Erlenhöhe annual total reconstructed (1864-1982) and observed (1983-2025) precipitation with LOESS trendline overlaid.

However, the dual climatograph (Figure 17) reveals distinct seasonal changes in precipitation distribution. While average summer rainfall has remained relatively stable or slightly decreased (e.g., June dropping from 258 mm to 249 mm), winter precipitation has increased, with January averages increasing from 126 mm to 161 mm. July had the largest increase in precipitation variability in the modern era, with the coefficient of variation (CV) rising from 34.9% in the historical era to 41.6% post-1980, though this increase is not significant ($p = 0.15$). The largest decrease occurred in October, whose CV fell from 56.5% to 45.3% in the modern era, though this is also not statistically significant ($p = 0.11$).

5.3 Changes in forest cover

5.3.1 GIS analysis

Spatiotemporal forest cover analysis revealed a trend of natural forest damage between 1985 and 2018, with most of the change occurring in the western, downslope portion of the study area (Figure 19). Trajectory analysis indicated that once a hectare transitioned from normal to damaged forest, the majority of land remained in this damaged state through the 2009 and 2018 survey periods. All study sites, apart from Site H, appear to have experienced natural or anthropogenic forest damage. The reference site maintained normal forest conditions until the survey period of 2013-2018.

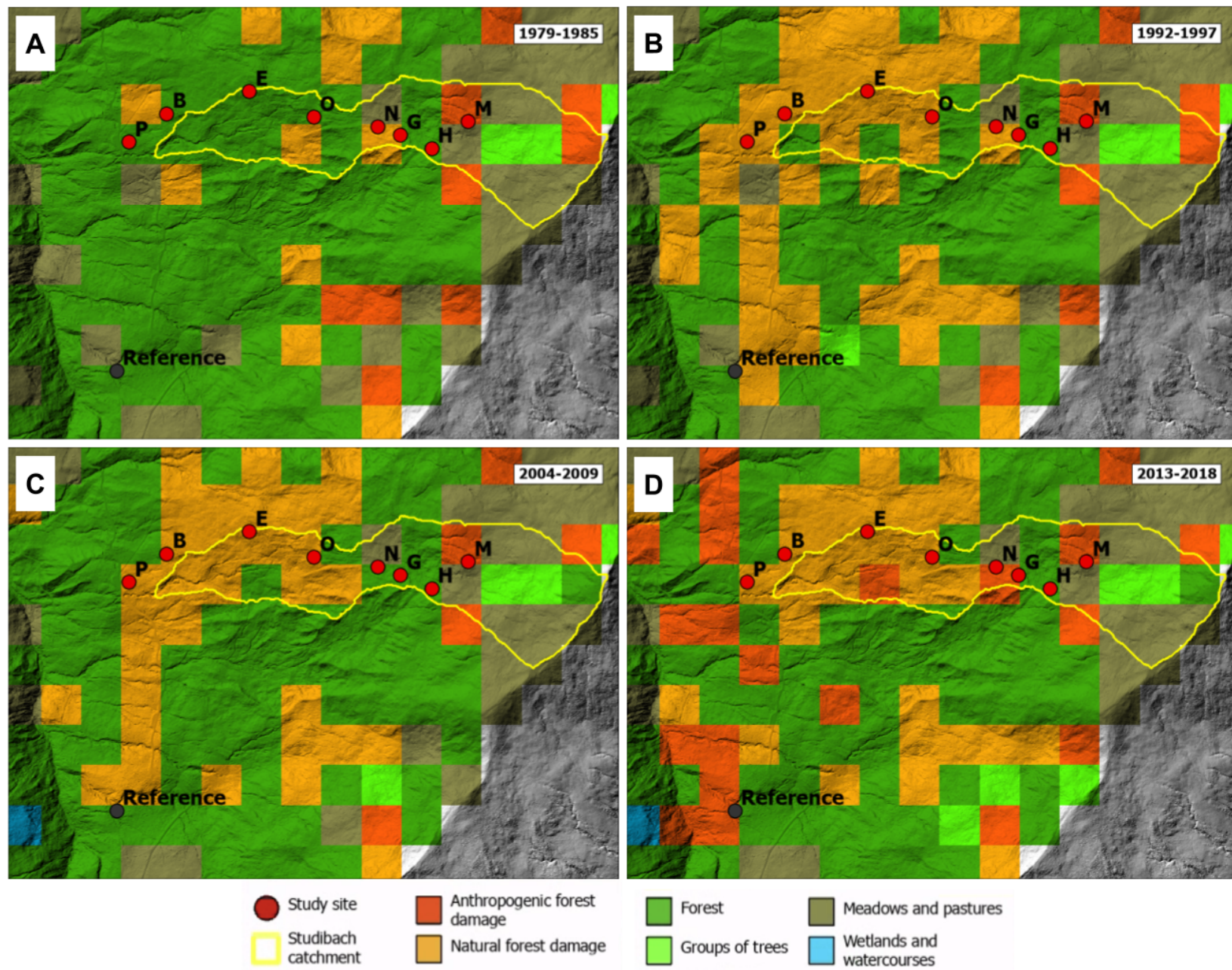


Figure 19: Land cover in the study area over the periods of (A) 1979-1985, (B) 1992-1997, (C) 2004-2009, and (D) 2013-2018

5.3.2 Winter albedo analysis using Google Earth Engine

Analysis with higher spatiotemporal resolution Landsat data over the period 1984-2025 showed that all monitored sites had a low median winter albedo (often $\alpha < 0.2$) between 1984 and 1993 (Figure 20). Most sites (B, G, H, M, N, and O) maintained this low reflectance baseline throughout the entire observation period, with mean albedos between 0.08 and 0.17 (see Table A3 in the appendix). However, a distinct albedo increase was detected at all sites in 1994, a year with an average snowpack. The majority of sites returned to their baseline in the following year; however, Sites E and P maintained higher albedos (average $\alpha > 0.4$ and $\alpha > 0.3$, respectively) until 2018. Importantly, these sites maintained their high reflectivity even during years with low snow depth.

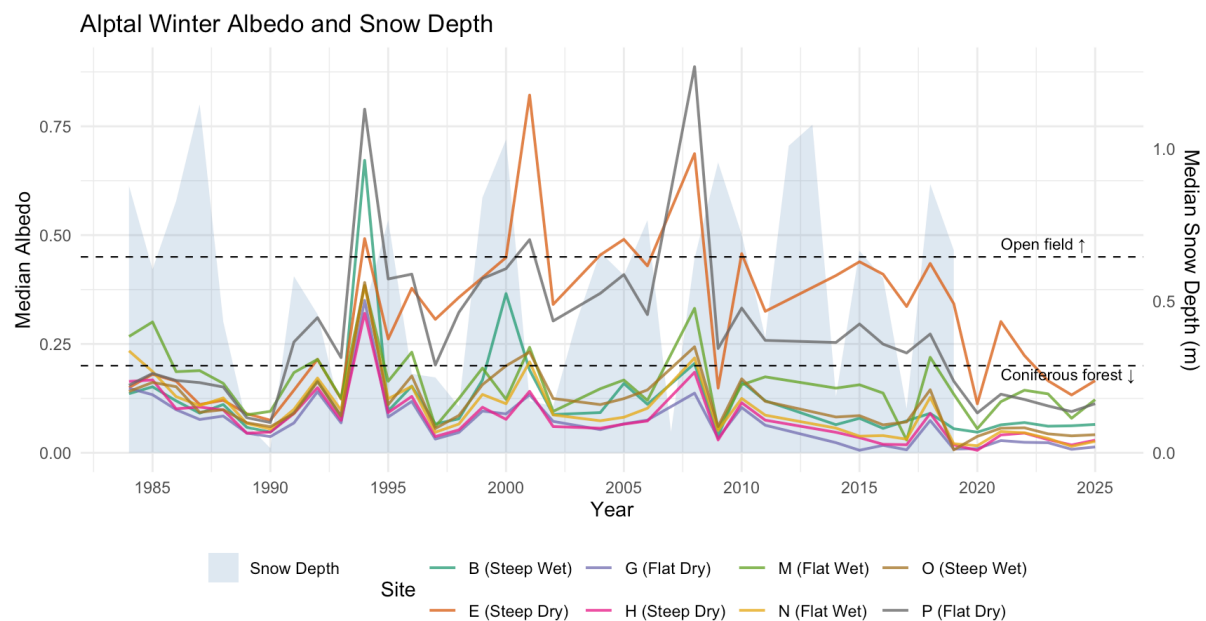


Figure 20: Time series of the median winter (January-March) albedo derived from Landsat data for the eight study sites and median snow depth at the Erlenhöhe climate station (January – March). The horizontal dashed lines indicate the albedo thresholds that are associated with coniferous forests and open fields (Betts & Ball, 1997; Pomeroy & Brun, 2001; Robinson & Kukla, 1985).

5.4 Tree-ring data

5.4.1 Raw and prewhitened chronologies

Radial growth chronologies were successfully constructed for all eight study sites (Figure 21). Visual inspection of the chronologies revealed differences between sites. Specifically, records are shorter for Sites E and P, and rings are wider compared to the other sites.

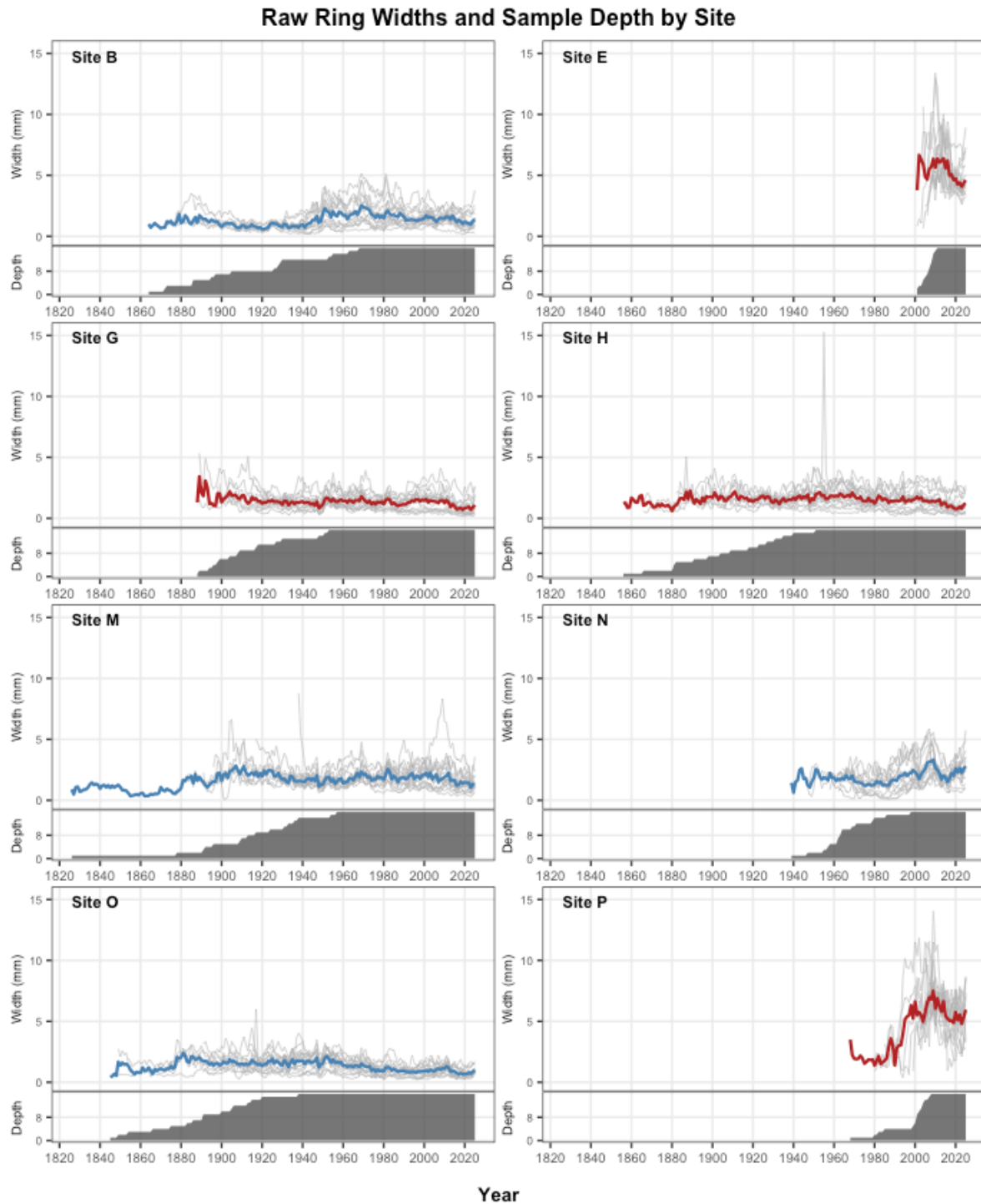


Figure 21: Plot of each site with mean raw chronology in color and records for all individual cores in gray. Blue denotes wet sites and red denotes dry. The number of cores (also known as sample depth) of the corresponding year is denoted below each subplot in dark gray.

The master residual chronology of the study area (Figure 22) spans from 1826 to 2025. Visual inspection reveals clear interannual variability and several notable extreme years. For example, sharp growth surges can be seen in 1947, 1953, 1969, and 1983, while years with severe negative growth include 1872, 1877, 1948, and 1980. See Figures A1, A2, and A3 in the appendix for site-level raw, detrended, and prewhitened average time series.

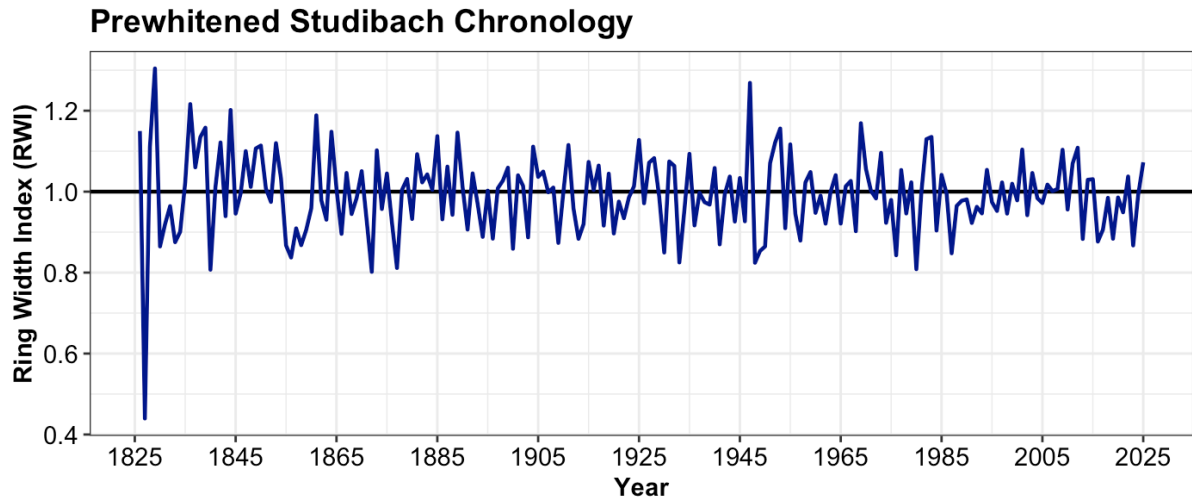


Figure 22: Time series of the master prewhitened chronology of the study area (all sites) going back to 1826.

5.4.2 Comparison to reference chronology

To validate the climate signal of the Studibach forest, the master residual chronology was compared with the residuals of an independent regional reference chronology (see Figure 23). The series are significantly positively correlated ($r = 0.50$, $p < 0.001$) and the Gleichläufigkeit is strong ($GLK = 74.3\%$, $p < 0.001$). Together, these metrics suggest a strong synchronization between the areas, confirming that the trees in the study and reference areas share a dominant regional climate signal and are suitable for historical analysis.

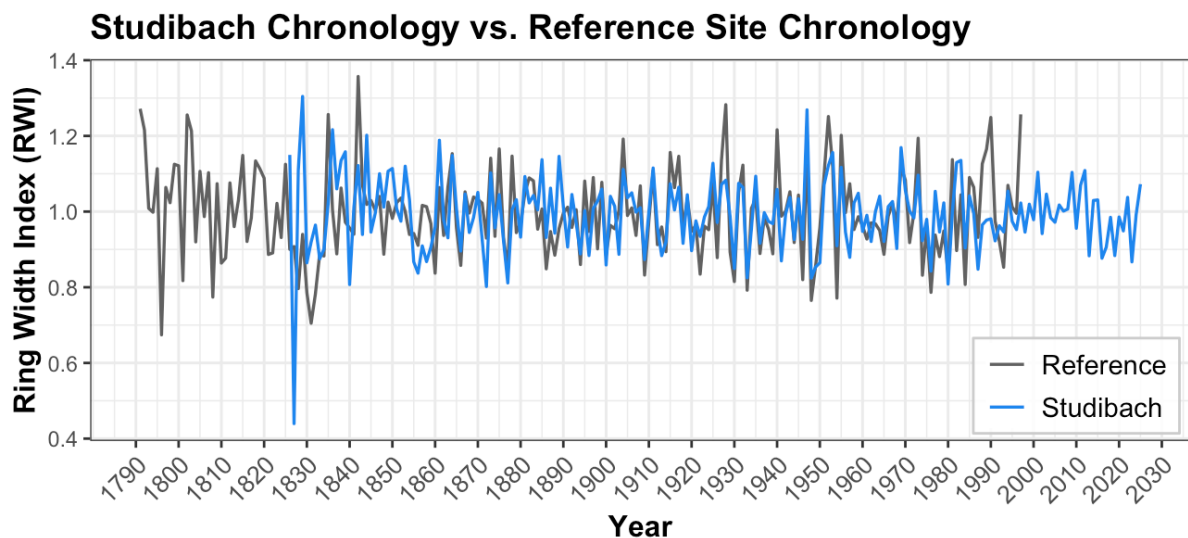


Figure 23: Time series of the mean prewhitened chronologies of the entire study area (Studibach, as in Figure 22) and the reference area.

The most notable periods of discrepancy between the Studibach and reference chronologies occur in 1827-1829, 1988-1990, and 1997. To assess the influence of site conditions on these discrepancies, the prewhitened time series of each site was plotted atop the prewhitened reference chronology to assess the influence of site conditions on

these discrepancies (Figure 24). Only records from Site M are available for comparison with the reference for the 1827-1829 period. The chronology for Site M appears to be highly variable and has an overall higher growth than the reference site during this time frame. For both the 1988-1990 and the 1997 discrepancies, the reference has greater growth than the sample sites, and there is no discernible difference in growth between site conditions. A notable exception is Site P, with sharp growth changes in either direction present during the period of 1988-1990.

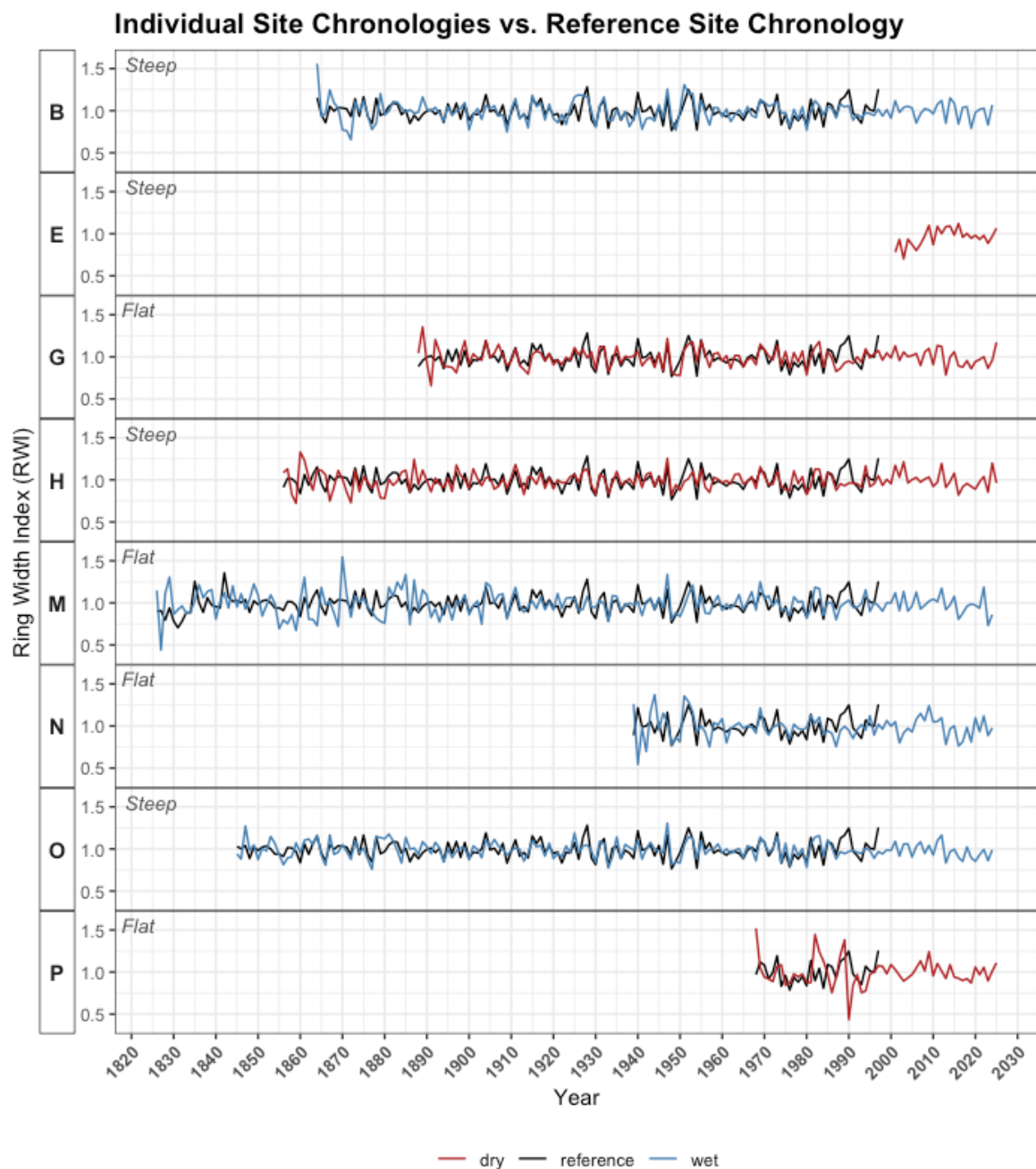


Figure 24: Time series of the prewhitened site chronologies compared to the reference chronology. Colored lines represent the sites, and black lines represent the reference.

5.5 Change in the influence of climate drivers on radial tree growth

5.5.1 Monthly precipitation

Bootstrapped correlation analysis revealed a pronounced shift in the forest's sensitivity to precipitation between the historical and modern eras (Figure 25). During the historical period, the prewhitened master chronology was slightly correlated with precipitation in the prior-year growing season. The correlation was statistically significant for August ($r = 0.20$, 95% CI [0.02, 0.36]) and September ($r = 0.20$, 95% CI [0.01, 0.38]). There was a generally negative relationship with current growing season precipitation, with a significant correlation for July ($r = -0.26$, 95% CI [-0.41, -0.11]).

For the modern (i.e., warmer) era, the correlations were different. Precipitation during the previous July was the single strongest moisture-related driver of current year growth, shifting from a non-significant factor in the historical era to being highly significant post-1980 ($r = 0.58$, 95% CI [0.42, 0.72]). There was a similar, though weaker, significant positive correlation with previous October precipitation ($r = 0.30$, 95% CI [0.08, 0.50]). In contrast to the historical period, no current year precipitation variables were significantly correlated to radial growth in the modern era, although there was still a general negative relationship.

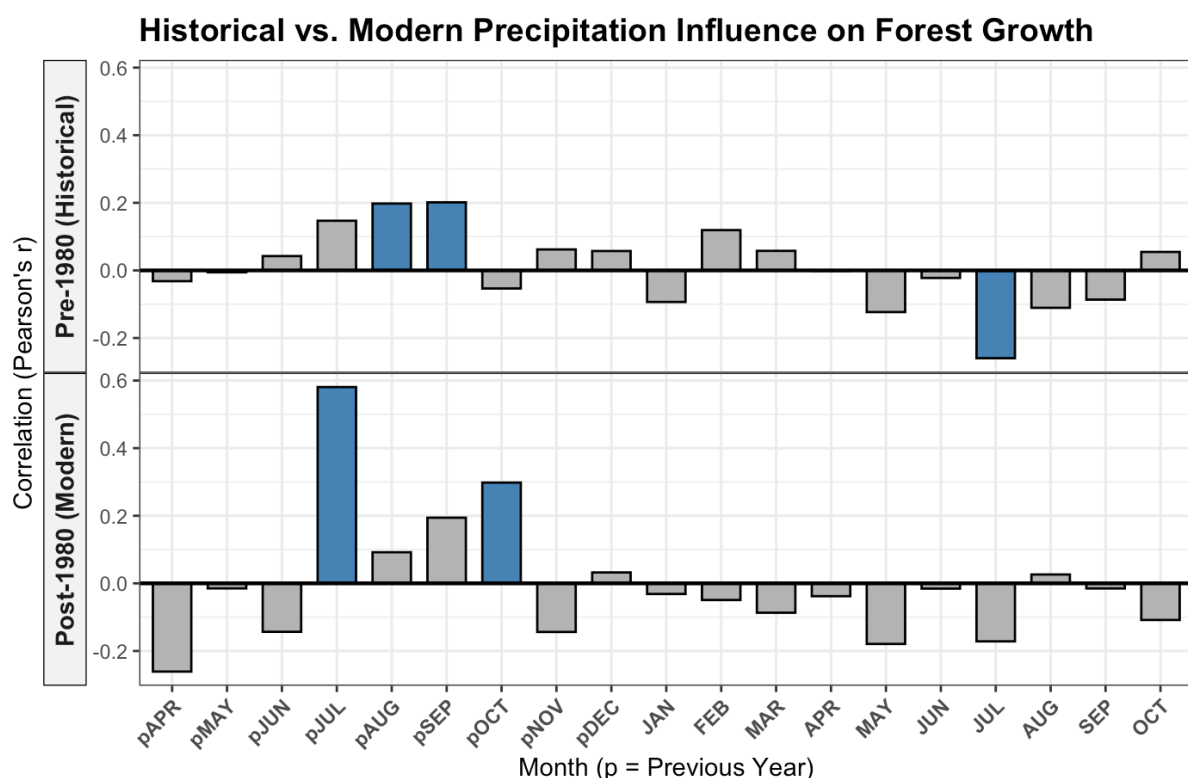


Figure 25: Correlation between the prewhitened RWI for the entire Studibach catchment and monthly precipitation for the historical (1864-1979, above) and modern (1980-2025, below) periods. Blue bars represent statistically significant correlations (95% confidence). For the full output of the correlation model, see Tables A4 and A5 in the appendix.

5.5.2 Monthly temperature

The correlation between radial growth and monthly average temperature similarly changed across the two periods (Figure 26). For the historic period, warmer current-year summers were correlated with higher growth. The correlations were statistically significant for current May ($r = 0.21$, 95% CI [0.04, 0.35]), July ($r = 0.23$, 95% CI [0.06, 0.39]), and August ($r = 0.22$, 95% CI [0.05, 0.38]).

Post-1980, the benefit of mid-summer heat is no longer significant. Instead, growth became more sensitive to early spring temperatures. The positive correlation with current May temperature increased from $r = 0.21$ in the historical period to $r = 0.49$ (95% CI [0.18, 0.69]) in the modern period. While historical growth was negatively correlated with prior August and September temperatures, modern growth negatively correlates with previous July temperature ($r = -0.33$, 95% CI [-0.59, -0.03]), mirroring the newly established positive correlation with previous July precipitation.

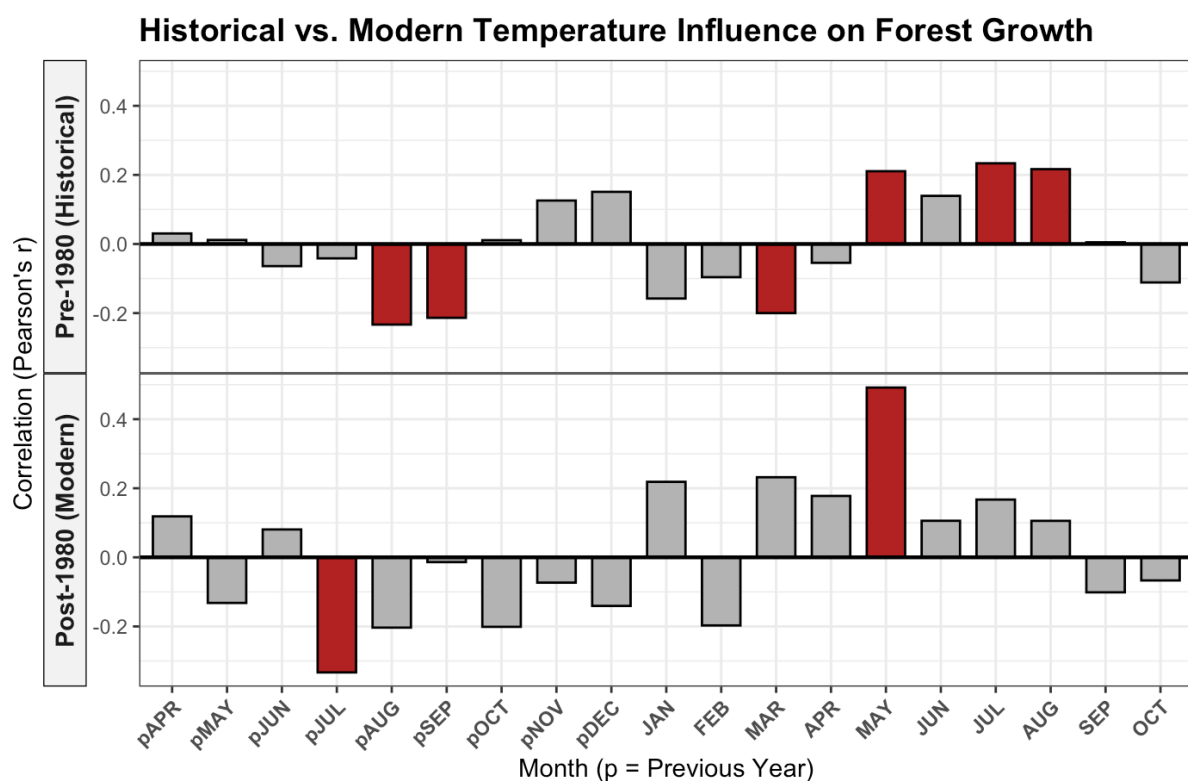


Figure 26: Correlation between the prewhitened RWI for the entire Studibach catchment and monthly average temperature for the historical (1864-1979, above) and modern (1980-2025, below) periods. Red bars represent statistically significant correlations (95% confidence). For the full output of the correlation model, see Tables A6 and A7 in the appendix.

5.6 Change in forest growth

While prewhitened ring-width indices allow for the investigation of climate triggers that influence spruce growth, assessing absolute forest productivity trends over time requires basal area increment (BAI), which retains the biological momentum of the stand. A plot of the mean annual BAI from 1864 to 2025 revealed a significant positive growth trend

across the study area ($p < 0.001$) (Figure 27), with an average increase of 16 mm^2 per year ($r^2 = 0.65$) when all sites were included in the analysis. When excluding Sites E and P, linear regression still showed a highly significant positive trend ($p < 0.001$), but the magnitude of growth acceleration was notably reduced. The rate of increase in mean annual BAI was 8 mm^2 ($r^2 = 0.42$). Despite this reduction in slope, the persistent significant positive trajectory shows a long-term increase in tree growth.

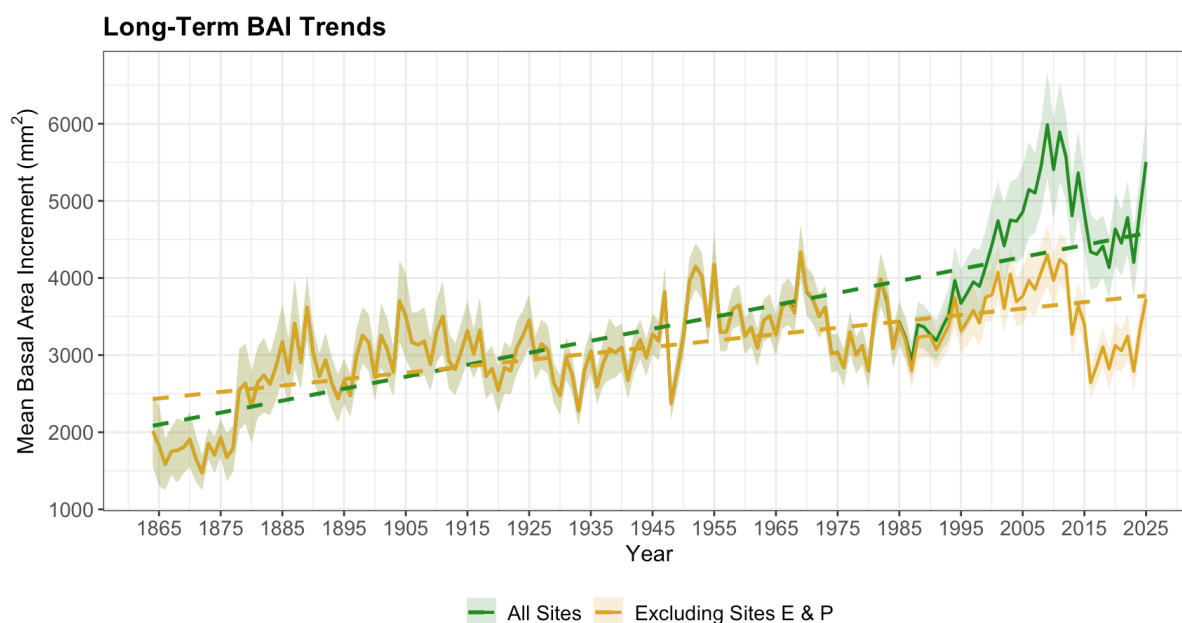


Figure 27: Time series of the annual average basal area increment when averaged across all sites (green) and when excluding sites E and P (yellow). The solid lines indicate the catchment-wide average BAI for each year, the dashed lines indicate the linear trend line, and the shaded areas indicate standard error.

Although there is an overall positive growth trend, there has been a considerable decrease in BAI growth between 2013 and 2024. During the two decades before this dip, the catchment experienced a steady increase in growth, coinciding with favorable meteorological conditions across the significant climate drivers identified in Section 5.5. Specifically, the 3-year rolling average of temperature in July was normal (generally between 13.4°C and 14.6°C , compared to an average of 13.6°C for the entire study period), and May temperatures were slightly warm, with a 3-year rolling average mostly above 8.5°C (compared to an average of 8.2 for the entire study period).

Beginning in 2013, BAI growth slowed. This period was characterized by a distinct increase in July heat and high interannual precipitation variability (Figure 28). The most pronounced shift occurred in July, with the 3-year rolling temperature average crossing 15°C in 2015 and remaining almost entirely above this threshold through 2025. Simultaneously, July precipitation varied considerably between low precipitation years (e.g., 105 mm in 2015, 77 mm in 2018, and 114 mm in 2022) and extreme surplus years (e.g., 530 mm in 2014 and 548 mm in 2021). Compounding these summer stressors, May temperatures had lower lows and higher variability.

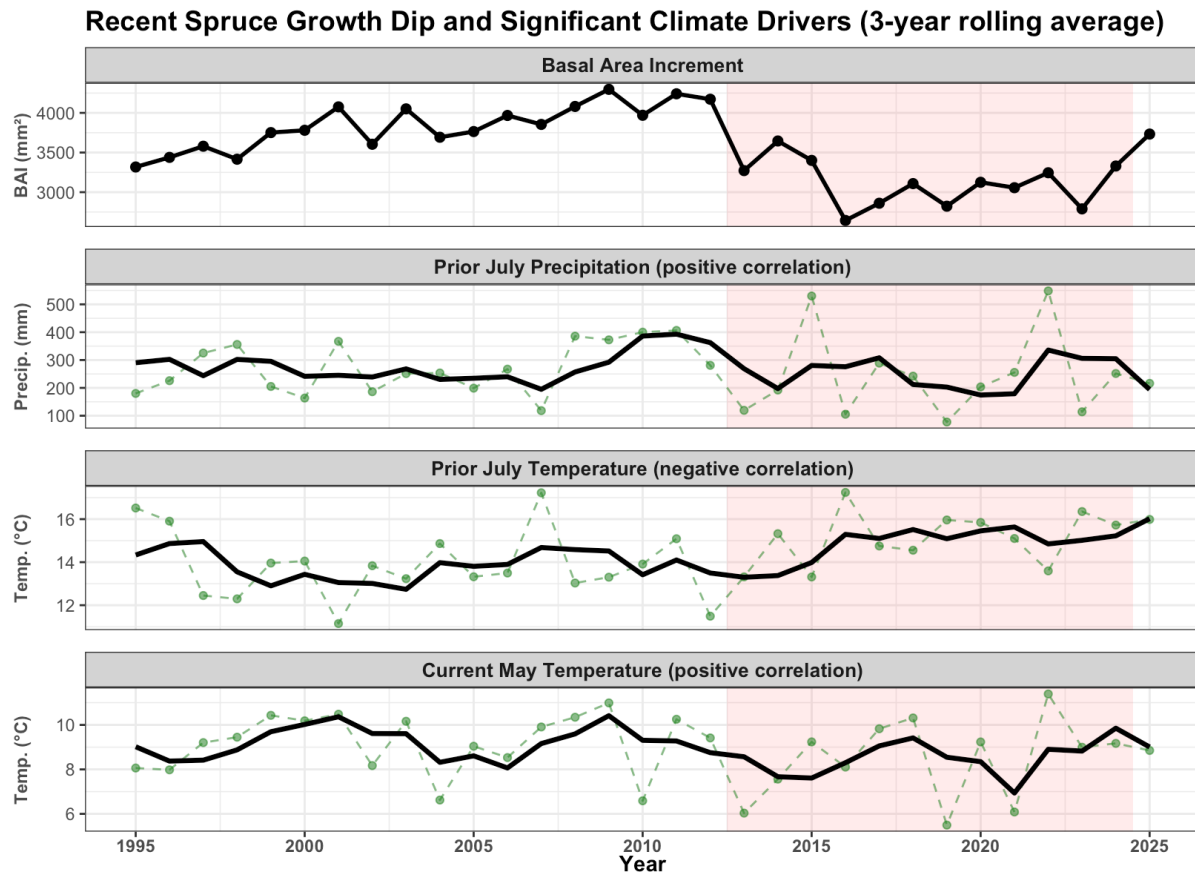


Figure 28: Time series of average BAI across all sites (top) and the annual (green) and 3-year rolling average (black) of climate drivers that were found to be significantly correlated with growth (see Section 5.5). The red shaded area represents the period with lower growth. Note that previous July precipitation and current May temperature were found to have a positive correlation to tree growth, while previous July temperature has a negative correlation.

5.7 Influence of local site conditions on BAI

5.7.1 Baseline effects of slope and moisture

To evaluate the influence of local factors on absolute growth, sites with historical canopy damage (Sites E and P) were excluded from the analysis to prevent differences in sunlight competition from skewing the results. A linear mixed-effects model (LMM) was applied to the remaining sites across the entire 1864-2025 chronology. The model controlled for cambial age, which proved to have a highly significant influence on BAI ($p < 0.001$). Over the entire timeline, the baseline effects of slope and moisture were not significant ($p = 0.78$ and $p = 0.66$, respectively). The output of the LMM can be found in Table A8 of the appendix.

Estimated marginal means (EMMs) of the time series indicated that, overall, trees growing on flat terrain grew on average 219 mm^2 of BAI more per year than trees on steep slopes. Comparatively, trees in wet sites grew on average 377 mm^2 more annually than trees in dry sites. Flat wet sites had the highest predicted absolute annual growth (3582

mm²/year $\pm$ 633 SE) and steep dry sites had the lowest (2986 mm²/year $\pm$ 799 SE). (Figure 29). The output of the EMM model can be found in Table A9 of the appendix.

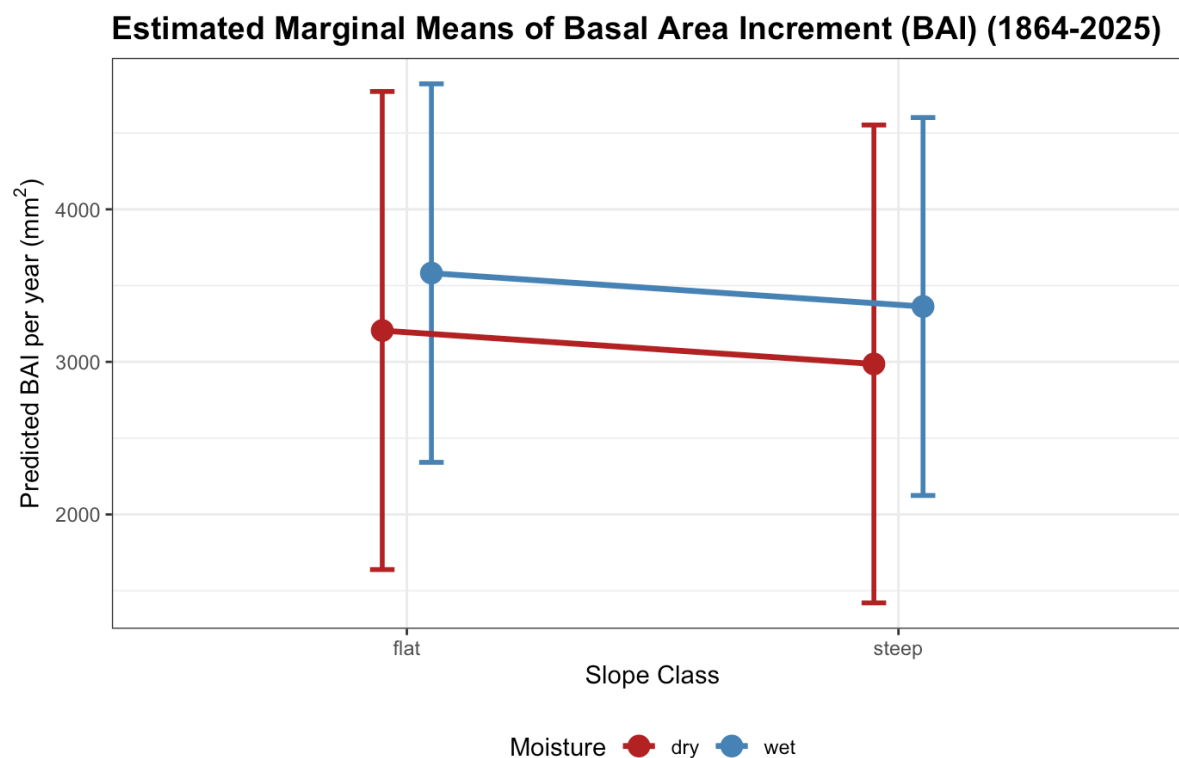


Figure 29: Estimated marginal means of basal area increment for all sites except E and P over the entire time series (1864-2025). Error bars represent 95% asymptotic confidence intervals derived from the linear mixed-effects model.

5.7.2 Shifts in forest response to local conditions over time

To determine if the influence of site conditions on tree growth has shifted in response to modern climate change, an LMM was fitted for the historical (1864-1979) and modern (1980-2025) periods. The analysis revealed a highly significant three-way interaction between soil moisture class, slope class, and climatic era ($p < 0.001$). Additional highly significant two-way interactions were observed for slope and era ($p < 0.001$) and moisture and era ($p < 0.001$). The presence of this three-way interaction indicates that the combined effect of topography and soil moisture on absolute biomass accumulation differed between the pre-1980 and post-1980 periods. The output of the LMM can be found in Table A10 of the appendix.

EMMs illustrated varying growth patterns across the catchment (Figure 30). In the historical period, the estimated absolute annual growth was highest in steep dry sites (3922 mm²/year $\pm$ 898 SE) and flat wet sites (3643 mm²/year $\pm$ 642 SE), while steep wet sites (3298 mm²/year $\pm$ 636 SE) and flat dry sites (2686 mm²/year $\pm$ 899 SE) exhibited lower productivity.

However, during the post-1980 warming era, spatial growth patterns diverged. Flat wet sites were the only classification to increase in absolute productivity, rising by 608 mm² to an estimated annual BAI growth of 4251 mm² ($\pm$ 637 SE).

In contrast, growth declined across all other site types. Predicted annual growth for steep wet sites fell by 801 mm² to 2497 mm²/year ($\pm$ 640 SE), steep dry sites decreased by 627 mm² to 3295 mm²/year ($\pm$ 901 SE), and flat dry sites decreased by 382 mm² to 2304 mm²/year ($\pm$ 900 SE). The full output of the EMM model can be found in Table A11 of the appendix.

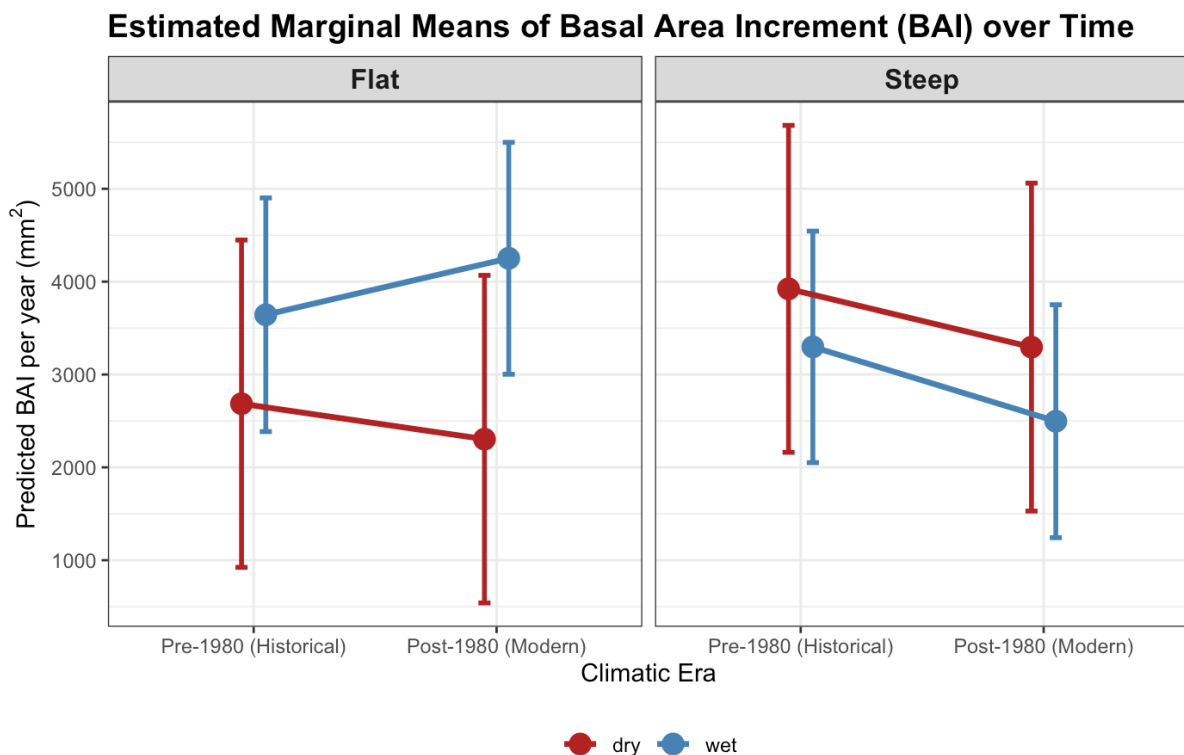


Figure 30: Estimated marginal means of basal area increment for all sites except E and P for the historical (1864-1979) and modern (1980-2025) eras. Error bars represent 95% asymptotic confidence intervals derived from the linear mixed-effects model.

The overarching three-way interaction confirms a highly significant catchment-wide shift in the relative influence of topographic factors. However, post-hoc pairwise comparisons did not detect a statistically significant effect for the isolated temporal shifts within individual site-type groupings.

5.7.3 Model comparisons

To confirm the validity of these spatial growth patterns, the results of the models excluding the influence of historical damage (i.e., excluding Sites E and P) were compared against a version of the model containing all sampled sites across the catchment. Although the sites with historical canopy damage inflated the absolute growth averages

of the dataset, the relative influence of local site conditions remained consistent across the models.

Most notably, flat wet sites consistently exhibited the highest predicted baseline annual growth, while steep dry sites consistently exhibited the lowest. Additionally, the baseline BAI differences between soil moisture types were unaffected by historical canopy damage. Wet sites produced an average of $\sim 377 \text{ mm}^2$ more annual BAI than dry sites in both models.

Finally, the divergent responses to modern climate change were also consistent. Under both models, flat wet sites were the only site classification to exhibit a growth increase during the post-1980 modern era. All other site classifications (steep wet, steep dry, and flat dry) experienced growth declines in both models, with steep wet sites suffering the most severe reductions in absolute productivity across all scenarios.

6. Discussion

6.1 Transition from energy-limited to moisture-limited growth

The monthly climate growth correlations (Section 5.5) suggest that the 2.5°C warming in the modern period has changed the limiting factors governing Norway spruce growth in the Alptal. In the historic period (1864-1979), the catchment functioned as a typical energy-limited sub-Alpine ecosystem where tree growth was primarily constrained by the short growing season and limited thermal energy (Mastrotheodoros et al., 2019). Because of this, higher current-year summer temperatures increased growth, while current-July precipitation was negatively correlated with growth, likely because heavy summer rainfall in this era was associated with greater cloud cover, reduced solar insolation, and potentially more waterlogged soil conditions.

For the post-1980 period, the benefit of mid-summer heat lost significance and was replaced by a greater sensitivity to prior-summer conditions. Higher precipitation in the previous July emerged as the single strongest driver of growth ($r = 0.58$), mirrored by a significant negative response to high prior-July temperatures ($r = -0.33$). This shift suggests a growing vulnerability to atmospheric moisture demand, exacerbated by the increasing variability of modern summer precipitation. As noted in Section 5.2.2, July precipitation has become increasingly unreliable (CV increasing from 34.9% to 41.6%). This could mean modern spruce are more likely to be subjected to summer moisture deficits, potentially driving the newfound significance of July precipitation. Higher summer temperatures and rising VPD may cause spruce to close their stomata to prevent water loss, reducing photosynthesis and carbon storage (Grossiord et al., 2020; McDowell et al., 2008). That this affects the next year's growth rather than the current year's highlights a shift in carbohydrate storage and the legacy effect of extreme years. Earlywood formation in the spring relies almost exclusively on non-structural

carbohydrates (NSCs) synthesized and stored during the previous summer (Tixier et al., 2019). If a tree experiences extreme drought and heat stress in July, it fails to store these important reserves, negatively influencing its ability to grow at the start of the following growing season (Stefaniak et al., 2024).

The reliance on stored reserves may also explain the amplification of the current-May temperature signal for the modern period ($r = 0.49$). Because the Alptal has experienced strong winter and early-spring warming (with January temperatures rising nearly 3°C), the snowpack melts earlier (Stähli et al., 2021). This is in concurrence with Churakova et al. (2014), who found that spring temperatures are increasingly important for tree growth in the modern climate. A warm May in the Alptal is now perhaps more important because it allows the tree to restart photosynthesis and replenish depleted carbohydrate reserves earlier, potentially compensating for the prior year's deficits and elongating the growing season (Gharun et al., 2020).

The emergence of prior-October precipitation as a significant positive driver ($r = 0.30$) of growth for the modern period is difficult to explain, especially when considered alongside the corresponding temperature signal. While prior-October temperature was not significantly related to growth, it had a negative effect ($r = -0.20$). This combination of beneficial wet and cool autumn conditions contradicts the hypothesis that trees benefit from an extended autumn photosynthesis period (Murphy et al., 2025), which would require warmer temperatures.

While statistical artifacts can certainly occur in bootstrapped correlations, an alternative hypothesis could explain this abnormality. In pre-Alpine conifers, survival during the frozen winter months depends heavily on internal water storage (Körner, 2012). Because a frozen stem and root system are temporarily disconnected from the hydrological system, trees cannot rely on liquid water from the ground to replace the moisture lost through transpiration on sunny winter days (Körner, 2012). Instead, they must rely on their stem moisture reserves to rehydrate their needles. Without this stored moisture, they risk damage via winter desiccation, or “frost drought” (Mayr et al., 2006). Within this context, the correlation between a wet prior October becomes more logical. Abundant October rainfall ensures that the tree's internal stem reserves are replenished before the soil and stem freeze for the winter.

Additionally, the negative temperature correlation showcases the impact of a warm autumn on NSC storage. As discussed by Piao et al. (2008), warmer autumns may lead to net carbon losses in terrestrial ecosystems due to increased respiration. Therefore, a cool and wet October may be favorable for tree growth because the precipitation recharges the soil as cooler temperatures slow respiration, preserving energy reserves for the spring. This reliance on autumn recharge is further supported by changes in precipitation variance. While modern July precipitation has become less reliable, October precipitation has increased in stability (CV decreasing from 56.5% to 45.3%).

Following increasing summer droughts, this stable October rainfall provides a reliable source of moisture prior to the winter freeze.

6.2 Stand dynamics and overall growth trends

6.2.1 Historical forest cover changes

While Swiss Land Use Statistics indicate the Studibach forest was generally damaged by natural events between 1979 and 2018, the coarse hectare spatial resolution was insufficient for diagnosing site-level changes and masked small-scale disturbances at the individual study sites, especially considering that the study sites are approximately 6.7 times smaller than the hectare resolution of the forest cover dataset. To overcome this limitation, higher-resolution Landsat winter albedo data was used as a proxy for canopy density, allowing for site-level reconstruction of historical forest cover.

Winter albedo analysis confirmed that Sites E and P existed as low-density canopy environments for decades and had highly reflective, snow-dominated average albedo values ($\alpha > 0.3$ for both) compared to the denser, darker canopies of the remaining sites ($\alpha < 0.2$). Because the trees in Sites E and P established in and/or were left behind in these open areas, their lack of competition for light allowed for rapid radial expansion, warranting their omission from the linear mixed models.

The canopy decline in these sites was likely initiated by damage from Winter Storm Vivian (1990) (Scherstjanoi et al., 2010). Rather than immediate clearing, Sites E and P possibly experienced a secondary disturbance, such as a bark beetle outbreak. Alternatively, delayed salvage logging could have progressively thinned the canopy, with severe density loss obvious after 1994. Subsequent increases in albedo at these sites (such as in 2001) likely reflect the sensitivity of the imagery to recent snowfall or additional damage from Winter Storm Lothar (1999) (Scherstjanoi et al., 2010).

While Landsat albedo serves as an effective proxy for historical canopy cover, it is inherently limited by the 16-day temporal resolution of the satellites and the necessity of clear images (U.S. Geological Survey (USGS), 2026). Thus, the annual winter median albedo is derived from a limited number of clear-sky snapshots rather than continuous observations. This temporal sampling bias explains why catchment-wide albedo spikes (e.g., 1994) do not perfectly align with years with a high median snow depth. If the few available clear-sky satellite images coincide with recent snowfall events, the resulting albedo will be higher.

6.2.2 Overall growth trend

Over the entire study period, the catchment exhibited a significant overall positive growth trend (with a growth rate increase of 16 mm² per year). However, a substantial portion of this trend was driven by non-climatic stand dynamics rather than meteorological changes. The growth of Sites E and P artificially inflated the catchment's overall growth

response to the climate signal. However, even after removing these two sites, the mature forest still exhibited a significant growth rate increase of 8 mm² per year.

It is important to consider the influence of the age effect on BAI data (as it has not been detrended), since carbon accumulation generally increases as trees get larger and older (Stephenson et al., 2014). It remains possible, though, that climate change drove a genuine long-term increase in overall tree growth regardless of the age effect. The lengthened growing season and warmer spring temperatures, or CO₂ fertilization (the hypothesis that increased atmospheric carbon from atmospheric emissions leads to increased tree growth), could be responsible (Huang et al., 2007). This hypothesis is supported by the findings of Pretzsch et al. (Pretzsch et al., 2014). This study found that Norway spruce growth rates in Central Europe have increased since the late 19th century, and the authors suggest this is because of the lengthened growing season.

6.2.3 Recent dip despite overall growth increase

Although the overall century-long growth trend is positive and consistent with the continental trend of increased spruce growth throughout the 20th century (Spiecker, 2000), the decrease in the rate of BAI growth between 2013 and 2025 reflects the shifting climate-growth relationships in the modern (warmer) era. As established in Section 6.1, the limiting factors in the Studibach catchment fundamentally differ for the periods before and after 1980. For the period after 1980, tree growth was positively correlated with prior-summer moisture and high May temperatures and negatively correlated with prior-summer heat.

Volumetric growth acts as a biological record reflecting the accumulation of physical stress. Thus, the recent decline in BAI may reflect the compounding biological consequences of these climate effects over time, particularly the high summer temperatures between 2013 and 2025. This perhaps resulted in sustained high respiration rates and depletion of stored non-structural carbohydrates (Piao et al., 2008), as discussed in Section 6.1.

Furthermore, the forest was repeatedly subjected to severe, single-year droughts (such as the summers of 2015, 2018, and 2022, which may have led to smaller tree rings in 2016, 2019, and 2023, respectively). These extreme dry shocks may have repeatedly drained the trees' carbohydrate reserves, leaving them unable to efficiently capitalize on the interspersed wet years. This aligns with the carbon starvation hypothesis presented by McDowell et al. (2008), which suggests that repeated stomatal closure during water scarcity conditions forces trees to rely on NSCs for survival, rather than storing them for later. Additionally, Buras et al. (2020) suggests that legacy effects from extreme droughts (e.g., 2018) can negatively impact forests for years after the event itself. Exacerbated by multi-year periods of cooler and highly variable May weather, this combination of heat, drought, and cooler springs may have prevented the forest from restocking its biological

reserves. Ultimately, these compounding climate stressors appear to have translated to a decade-long period of slower growth.

6.3 Varying topographic response to climate change

6.3.1 Reference comparison

While the Alptal master chronology corresponded well with the reference chronology (GLK = 74.3%), qualitative assessment revealed distinct periods of divergence. Understanding these periods of divergence is important, as they can highlight instances where localized factors temporarily overrode the greater regional climate signal.

The earliest notable divergence occurred around 1830; however, because the mean curve during this first decade is based on less than five cores, this discrepancy is almost certainly a statistical artifact of the unique growing patterns of a few individual trees rather than a true ecological phenomenon. More relevant are the more recent differences, particularly for the period from 1988 to 1990 and the anomaly in 1997. During both periods, the regional reference chronology recorded large growth surges, reaching an RWI of 1.25 in 1990 and 1.26 in 1997. In contrast, the Studibach chronology did not have a similar growth trend during these periods, instead remaining near or even slightly below the baseline average. The qualitative assessment of the individual chronologies suggests that these discrepancies were present across almost all sites. Only at Site P was there a notable difference, with a growth spike in 1989 and a large dip in 1990, although this is once again likely due to the low number of cores for the site (<5) during those years. There were no discernible differences between wet/dry or steep/flat sites. This suggests that the mechanism driving the divergence was not due to site topographical or moisture differences but was instead caused by a larger-scale driver.

Two hypotheses can explain these differences from the reference site. First, growth in the study area may have been hindered by localized adverse conditions or disturbance events that did not extend to the reference forest. This hypothesis is supported by the GIS analysis in Section 5.3.1, which identified patterns of canopy damage in the study forest that were not present in the reference site until more recently. A disturbance, such as isolated pest activity or localized forest damage, could have temporarily suppressed the forest in the Studibach catchment but not at the reference site. Alternatively, the discrepancy may not represent a true growth decline in the study area, but rather a growth spurt at the reference site. If the reference site experienced exceptionally beneficial microclimatic conditions during these specific years, such as escaping a spring frost event due to its comparatively low elevation or reduced competition for light due to windthrow removing nearby trees, its overall RWI would be greater. If this hypothesis proves accurate, the study area chronology may actually represent the more accurate baseline forest response, while the reference site reflects a more localized response.

Comparative analysis with additional surrounding chronologies would be required to definitively separate localized site damage from a reference-site anomaly.

6.3.2 Emerging climate resistance of flat wet topography

When evaluating the entire chronology as a single unit, BAI appeared to be largely independent of topography, with neither slope nor moisture having a significant effect on BAI. Rather than indicating that topography is irrelevant, this outcome may show the danger of assuming stability in long-term ecological studies.

Isolating the historic and modern periods revealed effects that shifted over time. Prior to 1980, the Studibach catchment functioned as a classic, energy-limited sub-Alpine ecosystem (Mastrotheodoros et al., 2019). In this historical climate characterized by cooler average temperatures and more reliable summer precipitation, water was rarely a limiting factor. Instead, the hydrological differences between steep (well-drained) and flat (water-retaining) sites appear to have driven differences in wood production. During this period, trees on steep dry slopes had the highest growth rate (estimated 3922 mm²/year), while growth was notably lower on flat dry sites (2686 mm²/year). In an energy-limited system, steep and well-drained slopes likely provided an advantage by preventing the waterlogged soil conditions more prevalent in flatter terrain (Q. Zhu et al., 2014). The highly significant three-way interaction between moisture, slope, and era ($p < 0.001$) suggests that climate change has shifted the climatic drivers of growth in this catchment. As the regional climate changed, certain aspects of the local topography of the Studibach began to provide a buffer for trees in the warmer climate.

The most alarming trend in the modern period is the decline in growth rates across steep sites. Predicted annual growth for steep wet sites is 801 mm² less in the modern period compared to the historic period, and growth in steep dry sites similarly decreased by 627 mm²/year. This decline aligns well with the recent increase in summer heat and precipitation variability (see Section 5.2). Steep slopes are characterized by faster runoff (Parker, 1982). While historically, this drainage may not have affected growth, it has become a liability under the current climate conditions (where prior-July temperatures consistently exceed 15°C) and multiple severe droughts. Paired with shallow root systems, Norway spruce on steep sites cannot access deeper groundwater and may exhaust their soil moisture reserves. The lower water table for steep sites (Rinderer et al., 2014) has left these trees vulnerable, resulting in a decrease in absolute productivity on steep slopes.

In contrast to steep sites, flat wet sites experienced more annual growth post-1980, increasing by over 608 mm²/year to a catchment high of 4251 mm²/year. This divergence suggests that growth conditions in flatter terrain have improved. The flat areas can act as a hydrological buffer as water tables remain high even during dry conditions (Rinderer et al., 2014), as flatter terrain promotes water pooling and higher soil water retention

(Parker, 1982; Q. Zhu et al., 2014). This aligns with the findings of Sturm et al. (2025), which states that local factors such as water availability are more important than VPD regarding drought resistance in forests. During the historical period, this pooling may not have been useful (and may have even bordered on harmful by creating hypoxic root conditions due to waterlogging). However, in the modern warmer period, these moisture conditions and a more stable groundwater level have become assets. Warmer spring temperatures and higher summer evaporation rates likely reduce waterlogging, while the retention of water acts as a bank during severe drought years (e.g., 2003, 2015, 2018) (Buras et al., 2020; MeteoSchweiz, 2025). Therefore, Norway spruce trees on flat wet sites appear to be in a position to capitalize on the extended growing season without suffering the severe drought penalties currently hindering the growth of their counterparts on steep slopes.

6.4 Implications for forestry management and hazard mitigation

The fact that climate change is uniquely influencing the growth of trees at different sites has great implications for the future of the forests in the Alptal and similar pre-Alpine catchments. As the climate continues to warm and summer precipitation becomes less predictable, traditional uniform forestry management strategies may no longer be sufficient. Instead, efforts should be more localized, leveraging topographical buffer zones while mitigating the risks emerging on steep gradients.

6.4.1 Forestry management adaptation

The increasing vulnerability of Norway spruce on steep slopes presents a challenge for Swiss forestry. Because spruce have a shallow root system, their inability to access deep groundwater stores makes them inherently unsuited to deal with the rapid drainage and high atmospheric moisture demand that characterizes the warming climate. If forestry management practices continue to favor spruce on these steep slopes, the region may risk higher mortality rates, increased susceptibility to pathogens, and potential economic damage to the timber industry.

To prioritize resistance in the changing climate, foresters could transition toward local-scale management based on topography and wetness conditions. On steep gradients, management could prioritize the gradual conversion of spruce-dominated stands into mixed-species forests. Promoting species that are already native to the catchment, such as silver fir, could be a potential alternative. Unlike spruce, firs develop deeper taproot systems, allowing them access to deeper soil moisture reserves during summer droughts (Schweingruber, 1993). Conversely, the flat, wet areas of the catchment, which currently have the highest absolute growth rates, can continue to safely and profitably remain forested with spruce. However, forests should also pay attention to spruce trees at wet sites to ensure the beneficial growth conditions in wetlands are being fully taken advantage of.

6.4.2 Geomorphic stability and hazard risk

Beyond timber production, the decline of Norway spruce on steep slopes poses a natural hazard threat. The Studibach catchment lies atop weathered flysch and has low-permeability gleysols, a combination notorious for its instability and susceptibility to shallow landslides (Berti et al., 2017). Historically, the dense and interconnected root networks of the forest have helped to anchor the soil and stabilize the steep slopes characteristic of the Alptal. The recent catchment-wide decline in absolute growth, especially on steep terrain, calls into question the long-term viability of these stabilizing root networks. When under generalized stress, spruce may attempt to compensate for water deficits by increasing their relative carbon partitioning to the root system (Puhe, 2003). Extreme drought stress, however, can lead to higher rates of root dormancy and a reduction in the growth of fine roots, and extreme conditions can lead to root desiccation and damage (Puhe, 2003).

The combination of weakened root anchoring plus more variable summer rainfall is therefore cause for concern. If an extreme drought in one year is followed by extreme precipitation in the next, it can create a dangerous combination for slope failure. Hazard mitigation planning in the Alptal should account for the potentially diminished stabilizing capacity of spruce on steep slopes. Steep stands should be prioritized for continuous monitoring and stabilization projects to prevent future mass movement events.

6.5 Limitations and future research directions

While this project utilizes high-resolution climate data and a robust chronology spanning many decades, certain limitations must be acknowledged. First, the division of the sites into qualitative topographic sub-categories (e.g., steep dry and wet flat) across different climatic eras inherently reduced the number of cores per site. Although the linear mixed-effects models controlled for unbalanced data and found significant interactions, future studies would naturally benefit from a larger sample size. Furthermore, the categorization of sites into “wet” and “dry” relies on present moisture conditions and inherently assumes long-term hydrological stability. In reality, local soil moisture conditions are dynamic. Historical shifts in precipitation patterns, small mass movement events, gradual soil profile development over the past century, or anthropogenic influence may have altered the soil moisture at each site over time, potentially introducing additional random error into the analysis.

Additionally, while the integration of Google Earth Engine winter albedo data successfully identified sites with historical canopy damage or openness, it is an imperfect proxy for stand density. The Landsat satellite record only extends back to 1984, leaving the preceding decades of stand dynamics entirely unaccounted for. Even for the modern era, the reliance on cloud-free imagery limits the temporal resolution of the satellite data.

Because of this, the exact timing and severity of localized stand management or damage events remain unknown and may introduce additional noise into the models.

The findings of this thesis can lead to several paths for future research. Most pertinent would be to study the decrease in the BAI growth rate since 2013. It remains unclear whether this recent decline in growth represents a temporary phenomenon from which the forest can recover or if it marks a critical tipping point leading to further decline. A follow-up dendrochronological study in the Studibach catchment in the coming decade would be beneficial for gaining insight into the resilience of Norway spruce in the changing climate.

In addition, future research could quantitatively assess the forestry adaptation strategies proposed in Section 6.4.1. A comparative dendrochronological analysis between Norway spruce and deeper-rooting trees like silver fir would provide critical information. Coring silver fir on the same steep gradients and subjecting them to identical analyses could show whether their deeper roots could effectively buffer them against the high-VPD conditions that spruce may suffer from. Some sites from this thesis have an adequate fir population, particularly Site P, but supplemental sites would likely need to be scouted for this extension project due to the lack of fir in higher elevation sites.

Finally, to further investigate the physiological mechanisms driving the observed shift to more moisture-limited growth, future studies could investigate transpiration in the catchment. Stable isotopes (specifically $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) in the existing Studibach cores could be analyzed, and the isotopic signatures of the rings formed during recent drought years (e.g., 2003, 2015, and 2018), as well as in situ methods such as sap flow sensors, could quantify the severity of stomatal closure and transpiration rates, potentially validating the high-VPD stress hypothesis proposed in this thesis.

7. Conclusions

The goal of this thesis was to disentangle the interacting effects of topography, hydrology, and a changing climate on the long-term radial growth of Norway spruce in the pre-Alpine Studibach catchment. By integrating high-resolution meteorological records, spatial canopy analyses, and tree-ring chronologies, this research successfully isolated a subset of localized conditions that influence forest resilience.

In addressing the first research question (RQ₁: How have Norway spruce growth rates in the Alptal changed over the past century, and what climatic and environmental factors led to these trends?), this study revealed a complex, non-linear trajectory over the past 160 years. Over the full time series, Norway spruce exhibited a significant long-term positive growth trend. In the historic era, factors that led to a longer growing season were positively correlated with growth, indicating a historically cold, energy-limited climate. However, the acceleration of modern warming (+2.5°C since 1980) appears to have

converted the forest into a moisture-limited system. Current radial growth is no longer stimulated by summer heat; instead, high summer temperature and a greater atmospheric moisture demand are correlated with a decline in growth in the subsequent year. Growth is also significantly correlated with prior-summer precipitation.

Regarding the second research question (RQ₂: How do soil moisture and slope affect the growth of Norway spruce trees in the Alptal?), this thesis demonstrates that local topography and moisture strongly influence tree growth, though their specific roles have changed over the last century. For the period prior to 1980, in a cooler, energy-limited climate, steep dry sites provided a slight growth advantage (likely by decreased chances of root hypoxia). However, current conditions (1980-present) have triggered a shift in growth. There was a decline in productivity on steeper slopes, possibly because rapid drainage leaves the shallow-rooted spruce highly vulnerable to drought events in a warmer climate. In contrast, flat wet sites were the only classification to experience a growth rate increase, suggesting that the ability of spruce to take advantage of accumulated water drives a modern growth increase.

Ultimately, the findings of this thesis highlight the danger of assuming long-term stability and spatial uniformity in forest ecosystems. While overarching climate trends govern the broad environmental stressors acting on pre-Alpine forests, local site conditions actively influence the overall growth response of trees. To ensure the continued viability of the timber industry and maintain slope stability in the Alptal, future forest management and hazard mitigation strategies should prioritize more tailored approaches that consider the effects of topography on the vulnerability of the changing forest.

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Appendix

Table A1: 72-category land cover and land use nomenclature (NOAS04) codes and labels with corresponding classifications for use in the thesis. Note: Absent codes were not present in the study area.

Code	Label	Classification
42	Natural meadows	Meadows and pastures
43	Home pastures	Meadows and pastures
44	Scrubby meadows and home pastures	Meadows and pastures
45	Alpine meadows	Meadows and pastures
46	Favourable Alpine and Jura pastures	Meadows and pastures
47	Scrubby Alpine and Jura pastures	Meadows and pastures
48	Petrified Alpine and Jura pastures	Meadows and pastures
50	Normal forest	Forest
51	Narrow forest	Forest
53	Logging	Anthropogenic forest damage
54	Forest damage	Natural forest damage
55	Dissolved forest (on agricultural land)	Anthropogenic forest damage
56	Dissolved forest (on unproductive land)	Natural forest damage
58	Field copses, hedges	Groups of trees
59	Groups of trees (on agricultural land)	Groups of trees
60	Groups of trees (on unproductive land)	Groups of trees
62	Watercourses	Wetlands and watercourses
63	Flood control structures	Wetlands and watercourses
64	Scrub, shrub vegetation	Meadows and pastures
65	Unproductive grass and herb vegetation	Meadows and pastures
67	Wetlands	Wetlands and watercourses

Table A2: Decadal climate summary of the Alptal summarized from the homogenized climate dataset.

Decade	Average annual Temperature (°C)	Total annual Precipitation (mm)
1860	4.4	2258
1870	4.2	2175
1880	4.1	1989
1890	4.0	2159
1900	4.1	2092
1910	4.3	2255
1920	4.6	2171

1930	4.5	2328
1940	4.9	2059
1950	4.7	2237
1960	4.6	2266
1970	4.7	2253
1980	5.4	2333
1990	5.8	2336
2000	5.8	2246
2010	6.1	2297
2020	7.1	2273

Table A3: Mean winter albedos for each study site from the period 1984-2025.

Site	Slope class	Wetness class	Mean albedo
B	Steep	Wet	0.13
E	Steep	Dry	0.33
G	Flat	Dry	0.08
H	Steep	Dry	0.09
M	Flat	Wet	0.17
N	Flat	Wet	0.11
O	Steep	Wet	0.13
P	Flat	Dry	0.30

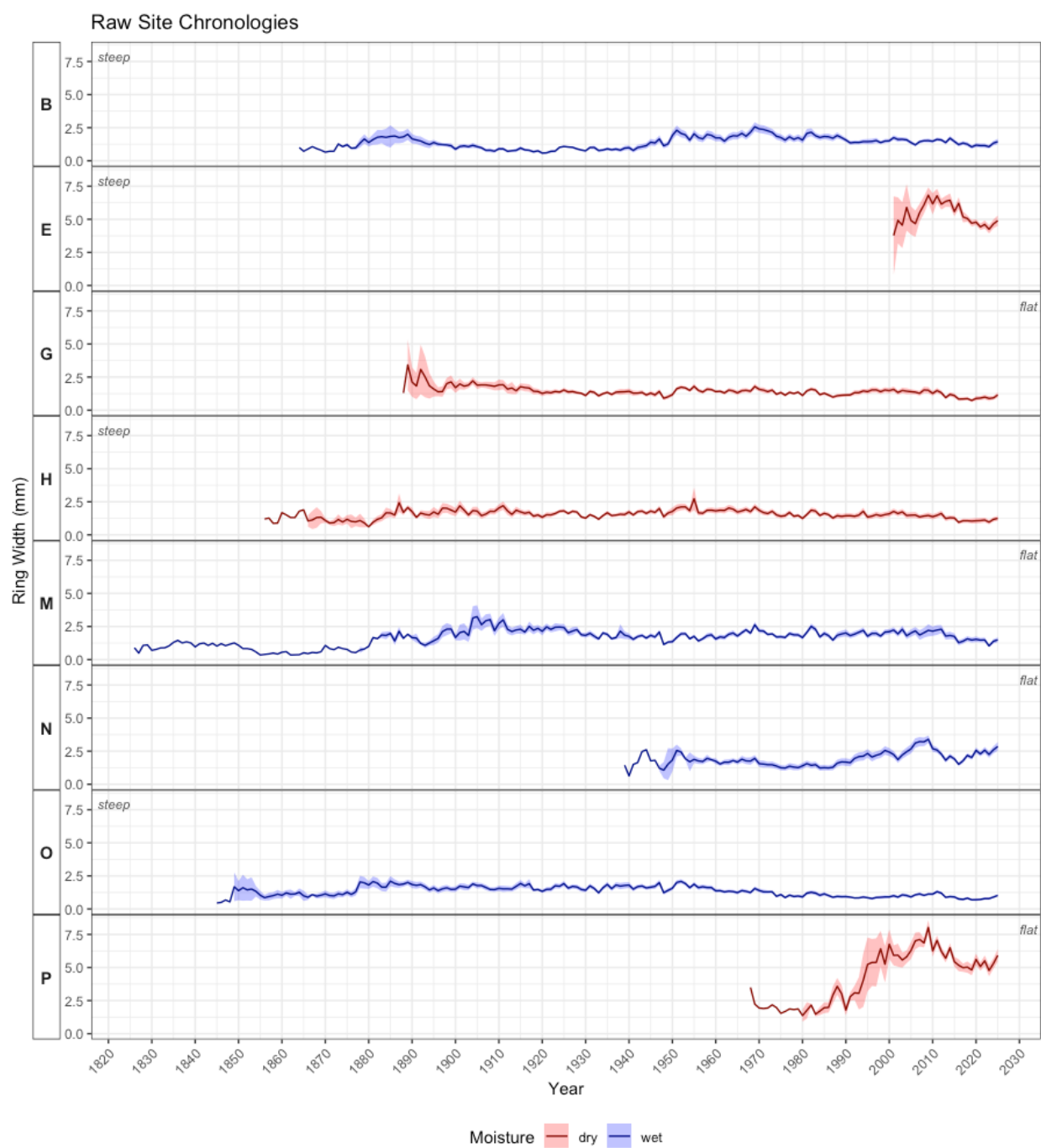


Figure A1: Time series of the average raw site chronologies. Shaded areas represent standard error.

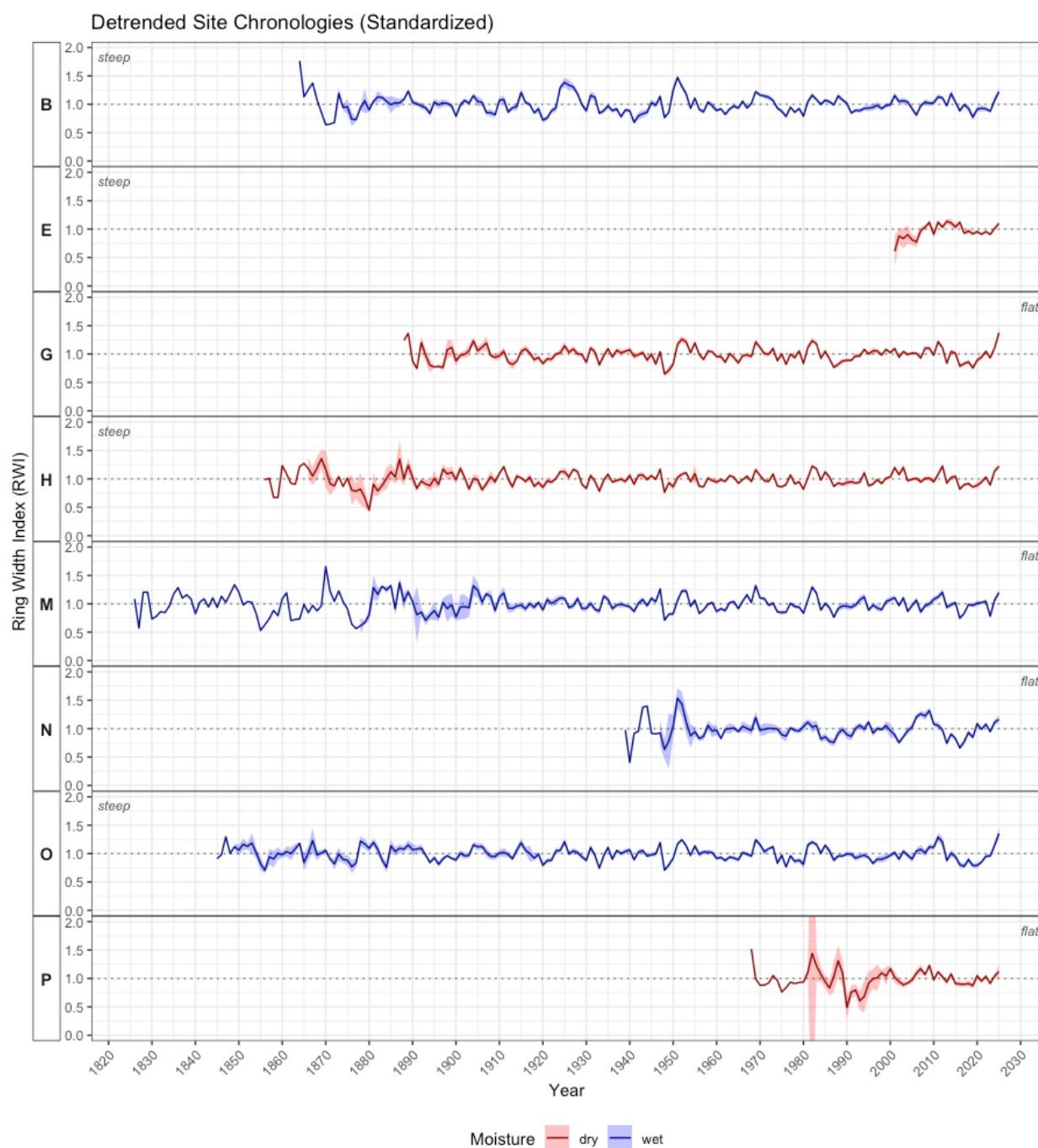


Figure A2: Time series of the detrended (standardized) average site chronologies. Shaded areas represent standard error.

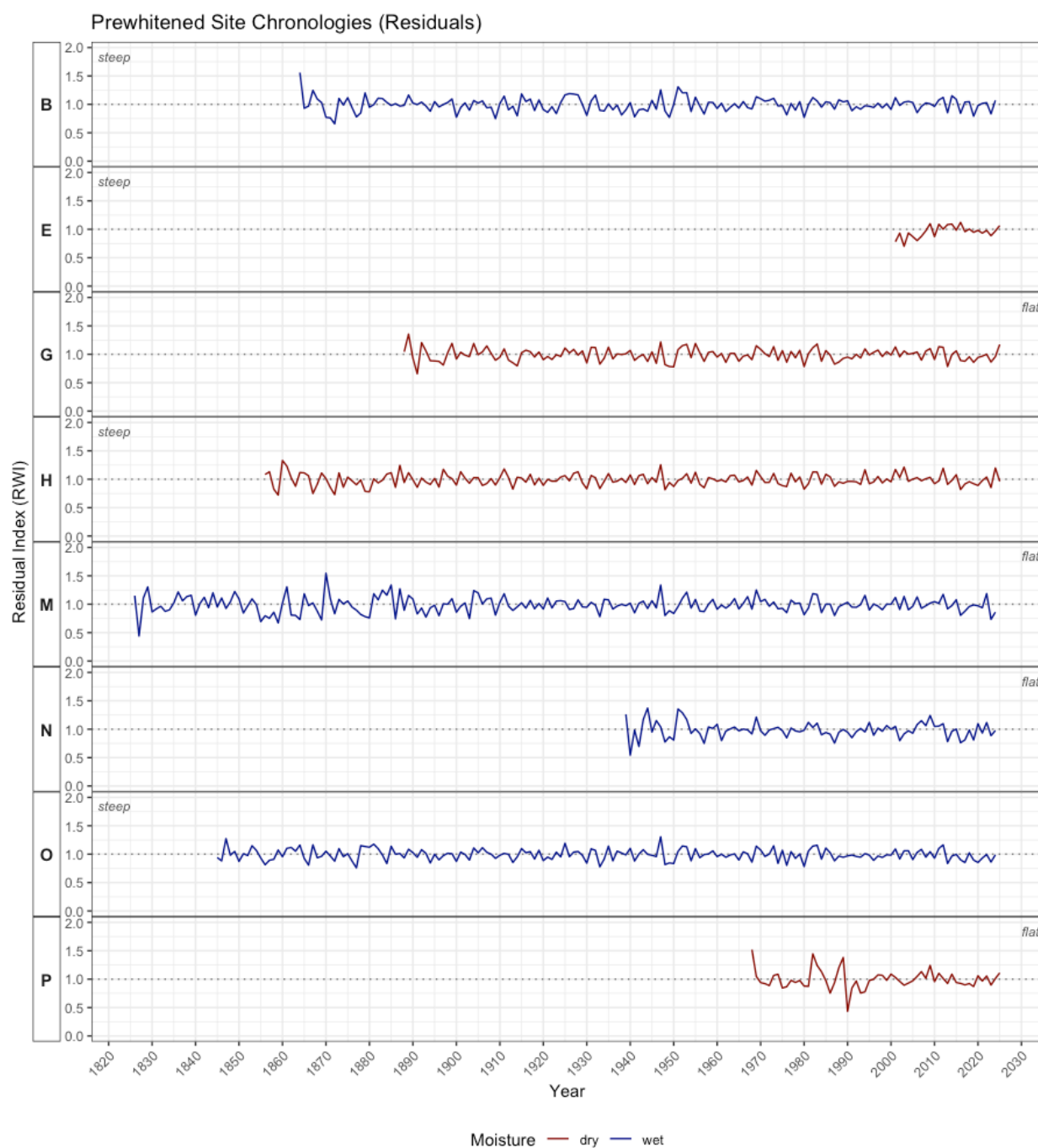


Figure A3: Time series of the prewhitened average site chronologies (residuals).

Table A4: Bootstrapped correlation output for precipitation in the historical period. (1864-1979). “p” represents the previous year.

Month	Correlation coefficient (r)	Significant	Lower CI	Upper CI
pAPR	-0.03	FALSE	-0.17	0.11
pMAY	-0.01	FALSE	-0.21	0.17
pJUN	0.04	FALSE	-0.19	0.28
pJUL	0.15	FALSE	0.00	0.29
pAUG	0.20	TRUE	0.02	0.36
pSEP	0.20	TRUE	0.01	0.38
pOCT	-0.05	FALSE	-0.24	0.14
pNOV	0.06	FALSE	-0.13	0.27
pDEC	0.06	FALSE	-0.10	0.23
JAN	-0.09	FALSE	-0.26	0.09
FEB	0.12	FALSE	-0.10	0.29
MAR	0.06	FALSE	-0.13	0.23
APR	0.00	FALSE	-0.20	0.20
MAY	-0.12	FALSE	-0.33	0.08
JUN	-0.02	FALSE	-0.22	0.18
JUL	-0.26	TRUE	-0.41	-0.11
AUG	-0.11	FALSE	-0.27	0.06
SEP	-0.09	FALSE	-0.29	0.13
OCT	0.05	FALSE	-0.11	0.24

Table A5: Bootstrapped correlation output for precipitation in the modern period. (1980-2025). “p” represents the previous year.

Month	Correlation coefficient (r)	Significant	Lower CI	Upper CI
pAPR	-0.26	FALSE	-0.51	0.04
pMAY	-0.01	FALSE	-0.30	0.27
pJUN	-0.14	FALSE	-0.41	0.18
pJUL	0.58	TRUE	0.42	0.72
pAUG	0.09	FALSE	-0.15	0.34
pSEP	0.19	FALSE	-0.11	0.43
pOCT	0.30	TRUE	0.08	0.50
pNOV	-0.14	FALSE	-0.43	0.14
pDEC	0.03	FALSE	-0.31	0.35

JAN	-0.03	FALSE	-0.29	0.23
FEB	-0.05	FALSE	-0.31	0.16
MAR	-0.09	FALSE	-0.33	0.18
APR	-0.04	FALSE	-0.33	0.25
MAY	-0.18	FALSE	-0.47	0.11
JUN	-0.02	FALSE	-0.40	0.38
JUL	-0.17	FALSE	-0.40	0.08
AUG	0.03	FALSE	-0.21	0.26
SEP	-0.02	FALSE	-0.33	0.30
OCT	-0.11	FALSE	-0.38	0.18

Table A6: Bootstrapped correlation output for temperature in the historical period. (1864-1979). “p” represents the previous year.

Month	Correlation coefficient (r)	Significant	Lower CI	Upper CI
pAPR	0.03	FALSE	-0.18	0.22
pMAY	0.01	FALSE	-0.13	0.17
pJUN	-0.06	FALSE	-0.26	0.15
pJUL	-0.04	FALSE	-0.18	0.09
pAUG	-0.23	TRUE	-0.41	-0.05
pSEP	-0.21	TRUE	-0.38	-0.03
pOCT	0.01	FALSE	-0.14	0.16
pNOV	0.13	FALSE	-0.02	0.29
pDEC	0.15	FALSE	-0.07	0.36
JAN	-0.16	FALSE	-0.30	0.01
FEB	-0.10	FALSE	-0.22	0.03
MAR	-0.20	TRUE	-0.36	-0.06
APR	-0.05	FALSE	-0.25	0.14
MAY	0.21	TRUE	0.04	0.35
JUN	0.14	FALSE	-0.05	0.34
JUL	0.23	TRUE	0.06	0.39
AUG	0.22	TRUE	0.05	0.38
SEP	0.00	FALSE	-0.19	0.18
OCT	-0.11	FALSE	-0.25	0.01

Table A7: Bootstrapped correlation output for temperature in the modern period. (1980-2025). “p” represents the previous year.

Month	Correlation coefficient (r)	Significant	Lower CI	Upper CI
pAPR	0.12	FALSE	-0.23	0.44
pMAY	-0.13	FALSE	-0.39	0.11
pJUN	0.08	FALSE	-0.11	0.29
pJUL	-0.33	TRUE	-0.59	-0.03
pAUG	-0.20	FALSE	-0.48	0.10
pSEP	-0.01	FALSE	-0.27	0.22
pOCT	-0.20	FALSE	-0.44	0.04
pNOV	-0.07	FALSE	-0.35	0.20
pDEC	-0.14	FALSE	-0.38	0.13
JAN	0.22	FALSE	-0.07	0.50
FEB	-0.20	FALSE	-0.42	0.04
MAR	0.23	FALSE	-0.09	0.50
APR	0.18	FALSE	-0.11	0.44
MAY	0.49	TRUE	0.18	0.69
JUN	0.11	FALSE	-0.22	0.38
JUL	0.17	FALSE	-0.18	0.45
AUG	0.11	FALSE	-0.11	0.33
SEP	-0.10	FALSE	-0.41	0.26
OCT	-0.07	FALSE	-0.38	0.23

Table A8: Analysis of deviance (Type III Wald chi-square tests) for the linear mixed-effects model evaluating the baseline influence of local site conditions on basal area increment (BAI) across the entire study period (1864–2025), excluding Sites E and P.

Fixed effect	Chi-Square	Degrees of freedom	p-value
(Intercept)	45.30	1	< 0.001
Moisture	0.20	1	0.66
Slope	0.08	1	0.78
Cambial age	60.41	1	< 0.001

Table A9: Estimated marginal means (EMMs) of basal area increment (BAI) across topographic classifications for the full study period (1864–2025), excluding Sites E and P. The 95% confidence intervals are asymptotic.

Slope	Moisture	Estimated mean BAI (mm ²)	Standard error (SE)	Lower confidence level	Upper confidence level
flat	dry	3205	799	1639	4772
	wet	3582	633	2342	4822
steep	dry	2986	799	1420	4552
	wet	3363	632	2124	4602

Table A10: Analysis of deviance (Type III Wald chi-square tests) for the linear mixed-effects model evaluating the influence of local site conditions on basal area increment (BAI) across the historical (1864-1979) and modern (1980-2025) eras, excluding Sites E and P.

Fixed effect	Chi-Square	Degrees of freedom	p-value
(Intercept)	42.42	1	< 0.001
Moisture	0.23	1	0.63
Slope	0.00	1	0.97
Era	6.07	1	0.01
Cambial age	57.31	1	< 0.001
Moisture:Slope	1.94	1	0.16
Moisture:Era	30.97	1	< 0.001
Slope:Era	125.89	1	< 0.001
Moisture:Slope:Era	62.87	1	< 0.001

Table A11: Estimated marginal means (EMMs) of basal area increment (BAI) across topographic classifications for the historical (1864-1979) and modern (1980-2025) eras, excluding Sites E and P. The 95% confidence intervals are asymptotic.

Era	Slope	Moisture	Estimated mean BAI (mm ²)	Standard error (SE)	Lower confidence level	Upper confidence level
Historical (1864-1979)	Flat	Dry	2686	899	923	4448
		Wet	3643	642	2385	4902
	Steep	Dry	3922	898	2162	5683
		Wet	3298	636	2051	4544
Modern (1980-2025)	Flat	Dry	2304	900	540	4068
		Wet	4251	637	3003	5500
	Steep	Dry	3295	901	1529	5061
		Wet	2497	640	1242	3751

Personal declaration

I hereby declare that the submitted thesis is the result of my own, independent work. All external sources are explicitly acknowledged in the thesis.

DeepL was used to translate German sources into English, and Google Gemini was used for coding assistance in R. Grammarly and Google Gemini were used for grammar and text refinement.

A handwritten signature in black ink, reading "Shelby Peyton". The signature is written in a cursive style with a horizontal line extending from the end of the name.

Shelby Peyton

Zürich, 24 April 2026