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Predicting future trends – responses of beech and fir in the Carpathian region

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European forests are facing enormous threats due to rapid global climate change, affecting the current and future performance of tree species. We focussed on European beech and silver fir, two important tree species for a large part of European forests at medium and higher altitudes. The measured responses from the Carpathian Mountains can serve as a model site with a sufficient geographical and climatic gradient. In addition to physiological and morphological characteristics, radial growth was compared with climate and various indices obtained from satellite images along the investigated geographical gradient. The measured parameters in combination with climate data form the basis for realistic reaction models for both species and enable future reaction scenarios with novel, highly developed algorithms.

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Radek Pokorný¹, Jiří Kadlec¹, Kateřina Novosadová¹

European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill) at the North-Western edge of Carpathians; contributions to ecology and management

KEYWORDS: competition, growth, mixture, water balance

Introduction

European beech is considered as the most widespread tree species in Central Europe. In the past it naturally covered 40 - 60% of the total forested land area in the Czech Republic, while currently it covers only 9 %, despite the fact that it has been used as an amelioration tree species. It has been present in the Czech Republic with silver fir since 3-4 thousand years BC. With fir and yew, it is one of the most shade-tolerant tree species, which does not require a geologically specific substrate. Its competitiveness and growth dominate on calcareous, rich, at least moderately deep, moist and aerated soils. Stagnant water and flooding are not tolerated (Černý et al. 2024). The natural abundance of fir in the Czech Republic reaches 20 % if it were not for its decline and dieback due to emissions, pests, fungal pathogens and severe game damage. Currently in the Czech Republic it is represented only by 1.3 %. Fir is demanding regarding soil moisture and damaged by late or early frosts. Both beech and fir are well anchored in the soil and form mixed stands with spruce and other tree species. Our previous research testing the effect of elevated CO₂ fumigation into the atmosphere (Pokorný et al. 2013a, Pokorný et al. 2013b) to the changes in the amount of the beech biomass of above-ground as well as below-ground part when it grown in individual and groups admixture within the spruce stand (Novosadová et al. – under prep.) showed that under air elevated CO₂, the lowest amount of biomass in beech trees was produced in group-admixture, while the highest biomass amount in trees grown under single-admixture or in pure stand conditions. Therefore, behind pure stands, single admixture of beech could be probably recommended instead of group admixture for beech cultivation in the future.

Global climate change caused by increasing concentrations of greenhouse gases, mainly CO₂, is understood as a deviation of the Earth's climatic parameters, e.g. temperature, precipitation, wind speed, from the averages and trends that have characterised conditions over last 2000 years. The manifestation, frequency and duration of extreme weather events are increasing. Increased atmospheric CO₂ concentrations are likely to make beech more competitive as a deciduous tree species on nutrient rich and calcareous soils (Spinler et al. 2003) Beech is sensitive to drought; increased atmospheric CO₂ concentrations lead to a decrease in stomatal conductance (Hättenschwiler 2001), so the future competitiveness of beech may in turn be declining in its current range (e.g. Gessler et al. 2006) due to susceptibility to cavitation (aeration of conducting vessels; at Vapour Pressure Deficit (VPD) above -1.8 MPa), carbon starvation (McDowell et al. 2008), and strong relationship between soil moisture and increment

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(Lebourgeois et al. 2005). During drought, beech transpiration is reduced, while radial increment persists for further 1-2 years followed by starvation, so drought stress symptoms in beech are delayed. While closed vents and their faster response reduce the probability of cavitation (Lemoine et al. 2002) and the water use efficiency (WUE), it is better compared to spruce (Rötzer et al. 2017). Future predictions for beech are not optimistic (e.g. Hanewinkel et al. 2013, Thurm et al. 2018).

Efforts are made to rehabilitate firs, given its exceptional growth strategy and the possibility of replacing the loss of coniferous timber on the market due to the spruce stands breakdown. Firs benefit by biomass production from increased atmospheric CO₂ concentrations; its light requirements also seem to increase (Hättenschwiler and Körner 2000). Dendrochronological studies demonstrate fir as more resistant to long-term drought compared to Norway spruce and European beech (Vitasse et al. 2019). Preserving fir and beech under shelterwood or in a mixture with more tree species may be promising for the future.

Carpathian Mountains are the second largest mountain system in Europe, covering 210 thousand km². We are presenting several case studies, from two Czech regions in north-western parts of the Carpathians. Studies were focused on: 1) different thinning type on beech, oak and linden in a mixed stand located at low elevations, 2), different thinning intensity on beech tree production and its water regime at low elevations, and 3) fir regeneration and growth at the sites of different micro-climatic conditions.

1. Different thinning effect on dendrometric parameters and subsequent spontaneous growth in a beech-oak-linden stands

Research (see details in Novosadová et al. 2024, devoted to the project) focuses on different types of thinning evaluation performed in mixed stand at the University Forest Enterprise (UFE) Masaryk Forest Křtiny as the edge of the Carpathians dominated by beech and sessile oak after 35 years of continuous monitoring during 5-year intervals; specifically of crown thinning (i.e. thinning from above, intensity of 26 % reduction of Basal area; BA), low thinning (i.e. thinning from below, intensity of 16 % of BA), and heavy crown thinning (intensity of 36 % of BA) realised once in the age of stands about 50 years. As the vertical shift of even two forest vegetation zones upward is predicted in CR (Čermák et al. 2021), the mutual competition of different tree species, especially beech – oak, is under intensive research there nowadays. Results indicate that best results provide heavy crown thinning, i.e. thinning from above with a high intensity (Novosadová et al. 2024).

2. Different thinning measures to improve water balance and beech growth at low altitudes

Repeated dry periods in recent years caused drying of the primary canopy structure, usually from the tree top (Geßler et al. 2006). A set of research plots was established in 2021 at the University Forest Enterprise Masaryk Forest, Křtiny. The area belongs climatically to the warm, moderately dry region with an 8 - 9 °C average annual temperature for the 1961-2008 period and annual precipitation of 550-650 mm (Rožnovský and Litschman 2010). In the research area there are soils developed from the disintegration of carbonate rocks belonging to the rendzina with the subtypes on limestone oak-beech and enriched stony lime oak-beech stands.

High intensity thinning (releasing cut surround the target trees) with small amount of chosen target trees per hectare (50) than recommended (80-110), could be the best solution to enhance

water availability for target trees in stand to support growth and good health status. Selected plots in four neighbouring stands were 50-70 years old, with dominant beech (*Fagus sylvatica*, L.), interspersed Norway maple (*Acer platanoides*, L.), sessile oak (*Quercus petraea*, (Matt.) Liebl.) and ash (*Fraxinus excelsior*, L.). Eight thinning variants (six of which were the target tree method with 50, 80 and 110 target trees per hectare, and with low (LOW; removing of 1-2 nearest competitors in crown, approx. 22 % reduction of BA) and high intensity of thinning (HIGH; 3-4 competitors, approx. 43 % reduction of BA), 1x common management treatment (CMT; 20 % reduction of BA, thinning from Above)) and one control variant without intervention (only sanitary cut) were applied. Each research plot was established as a circle of 2 500 m² (r = 28.2 m).

Trees with a diameter at breast height (DBH) above 5 cm were numbered in all circular plots with basic dendrometric parameters (DBH and H - tree height) measured. Using Field-Map (IFER, Czech Republic), the position and horizontal crown projection of each marked individual was located. Water gate systems were installed under canopies in all plots to quantify through-fall precipitation and interception, and stem surface flow to quantify completely net stand precipitation. Soil moisture (with three replications, in the depth 0-15 cm) was continuously monitored with TMS-4 sensors (TOMST, CR). Only target trees within the variants with 80 target trees and in common management treatment variant were monitored for transpiration flux during the first year after thinning. Sets of transpiration sensors EMS81 and EMS51 (Environmental Measuring Systems, Brno, CR) operating on the principle of stem heat balance method (Čermák et al. 1973) were used for sapflow quantification. Sample trees were determined using the quantile method according to Čermák et al. (2004).

The transpiration measurements during the first growing season (2022) after realisation of thinning show results not fitting hypotheses, but relevant due to possible shock occurrence after realising intensive thinning and opening the target tree's crowns to high solar irradiation, wind movement and low air vapour pressure deficit conditions. In 2022, drought conditions obviously started to manifest at the end of August, when potential atmospheric evapotranspiration demands overcame available water from rain (Fig. 1.)

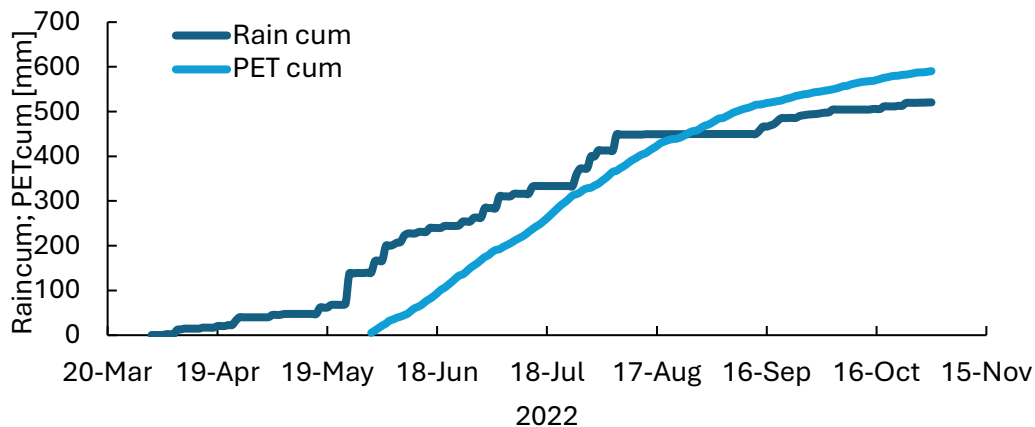


Fig. 1. Cumulative evapotranspiration demands (PETcum) calculated on the base of air humidity and temperature, and the cumulative amount of precipitation (Raincum) during the growing season 2022 at the locality of beech thinning experiments at UFE.

Due to higher canopy reduction also higher water availability for remaining target trees may be presumed. Target trees with high intensity of realising cut surrounding their crowns were stressed and their transpiration shows the lowest values mostly during the whole growing season. Low intensity thinning seems as the best solution for improvement of water regime and supporting growth increment of target trees during the first year after thinning intervention (Fig. 2.).

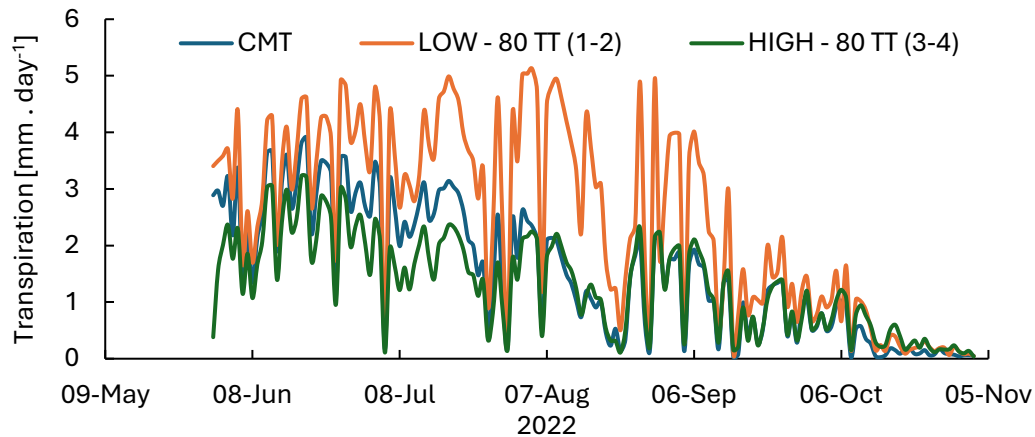


Fig. 2. Average transpiration of target trees from experimental plots with 80 tree per hectare density, when low thinning intensity (LOW TT) with reduction of 1-2 competitors and high intensity of thinning (HIGH TT) with reduction of 3-4 competitors were applied, and common management thinning (CMT).

3. Fir regeneration

Regeneration of fir under different light conditions was studied in the Moravian-Silesian Beskids with average 6-7 °C annual air temperature, 140 - 160 days of growing season and 1353mm annual precipitation (2011-2019 period). The most representative were elevations approximately between 600 - 900 m a.s.l., with mesobasic cambisols and humus podzols. The research was carried out on seventeen young plantations of fir, where two of them reached the stadium “young-growth” with close canopy according to year of establishment (2011). Half of the plots were located at sunny exposed conditions of clear-cut area (with the size of clear cut varying from 0.54 to 4.52 ha) at the parts with the minimal distance from surrounding forest edge of two tree heights, and half of the plots at shaded light conditions of clearing areas with small dimensions (size range from 0.06 ha to 0.29 ha) with the maximum width of plot of one tree height of surrounding stand.

Tree heights (H) young fir plants were estimated for all trees on individual plots, whereas annual height increments, average length of the longest branch (D) and the ratio of height to length of the longest branch were evaluated just for chosen sample trees (n = 30 - 100). The obtained data were evaluated according to light conditions of the plots to compare the fir growth on the sun exposed and shaded conditions. The average total height of the fir trees in a stand, with regard to its year of establishment, was always higher for fir saplings plots under shade than sun exposed conditions. From the measurement of the longest branches, very variable results were found out. Morphological H/D ratio was mostly higher for shade-grown conditions. Small size clear-cut plots (gaps) with prevailing shade conditions provide more

suitable conditions for the growth of fir young plantations, especially after the regeneration or establishment of stand up to the stage of the thicket stand with close canopy cover (Fig. 3).

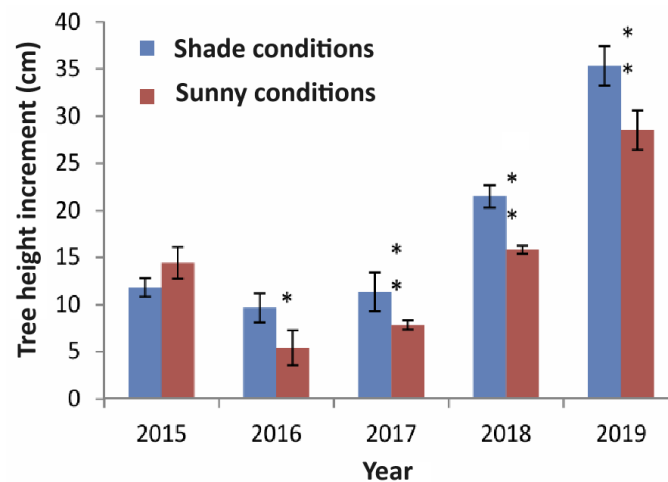


Fig. 3. Results from plot established in 2015, fir tree height increment under shade and sunny conditions of forest stand. Stars note statistically significant difference (* - $P < 0.05$, ** - $P < 0.01$) (after Konvičný 2020).

Artificial planting or natural regeneration on larger open areas with high proportion of direct light (i.e. gaps or clear-cuts over 0.5 ha) does not favour fir. Best site conditions for fir are under shelter of mature stand within gaps up to 0.3 ha or at large clear-cuts (or calamity sites) in near border (up to one tree height due to still prevailing shade conditions with just shortly temporal occurrence of direct sun). Recommendations refer to the current situation at research forest sites in the Czech Republic (Konvičný 2020).

Acknowledgement

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Calamities: A chance to increase proportion of silver fir

KEYWORDS: disturbance, pioneer species, nurse crop

Introduction

Central European forestry has been strongly influenced by traditional German (Saxony) forest school, which leads to a change in species composition. The present proportion of silver fir in the Czech Republic is around 1 %, whereas the natural should reach 20 % (Zpráva 2021). The traditional way to increase the proportion of this species is associated with the conversion of Norway spruce stands, where fir is artificially regenerated (planted and seeded) under the shelter of Norway spruce trees (Spiecker et al. 2004; Huth et al. 2017). On the other hand, for the process of reforestation of large clearings, silver fir is not so not well-adapted (Korpel' and Vinš 1964), as it is slowly growing, shade tolerant, and very sensitive species to climatic extremes (Korpel' and Vinš 1964). On the other hand, Volařík and Hédľ (2013) found a high proportion of silver fir in the regions that were strongly deforested and where forest nature expansion occurs.

We discuss the use of silver birch as a preparatory species in the artificial regeneration of silver fir. Some results of experiments established in 2015 in the Czech Republic are presented.

Material and Methods

All experiments were performed in the plots that are located in the eastern part of the Czech Republic. In total, 10 experimental plots – Padělky, Mokřinky, Krůtí, Bílá, Rakovec, Tornádo, Stará Ves, Hlubočec I, II, Skrchov represented middle rich and rich soil of oak-beech, beech and fir-beech vegetation zone. In these plots we observed the spontaneous regeneration of silver fir (Padělky, Mokřinky); evaluated the seeding experiment (Krůtí, Bílá, Hlubočec I) and analysed the nurse crop method with pioneer and silver fir. Height increment was calculated from the heights of all 70 initially planted silver firs measured between 2016 and 2018 in Skrchov. Shoot water potential in Skrchov was measured on 6-7 firs per treatment during midday on 23 August 2018 and before predawn on 24 August 2018. Light response curves of photosynthesis were measured in Stará Ves during 21 August 2023 on 7 firs per treatment and radial increment of Silver fir stems was measured during the vegetation season of 2023 on three firs per treatment.

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Results

In the first experiment, we try to understand the “pioneer behavior” strategies of silver fir. We established the seeding experiment in two clearings: one represented the optimum (Bílá: fir-beech vegetation zone) and the second sub-optimum (Krútí: oak-beech zone) for silver fir introduction. The germination was similar at both sites. Higher survival rates were on the optimum site, but due to strong weed competition, the success of Silver fir was low, at 2 % (Fig. 1). We found higher regeneration success under the canopy of nurse trees than at the clearing. In the other experiment, where seeding of Silver fir was carried out in about 15-year-old pioneer silver birch dominant stand, the yield of seed exceeded 7 % after 5 years (Hlubočec I).

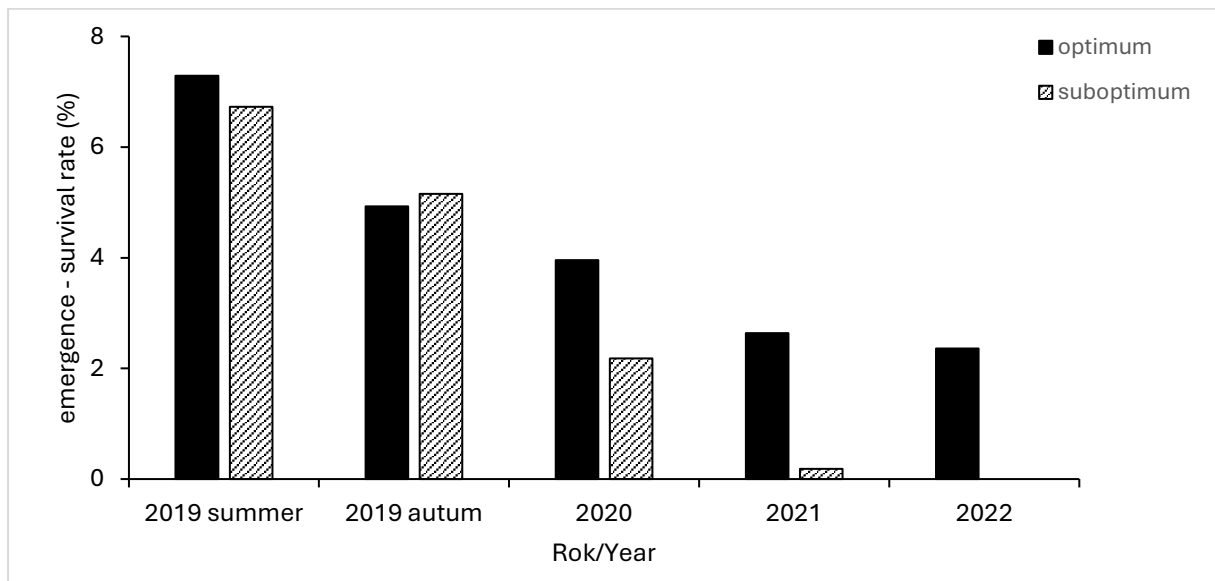


Fig 1. Emergence rate and survival rate of silver fir seed (seedlings); optimal site: fir-beech vegetation zone, suboptimal site: oak-beech vegetation zone.

To support the presumption that silver fir prospers well in pioneer stands, we analyzed the structure of naturally regenerated silver fir in 20 year old pioneer aspen-dominant stands, which emerged after Norway spruce dieback (Mokřinky, Padělky – Martiník, Krásenský 2023). The presence of mature silver fir around these stands led to spontaneous and continuous regeneration (Fig. 2).

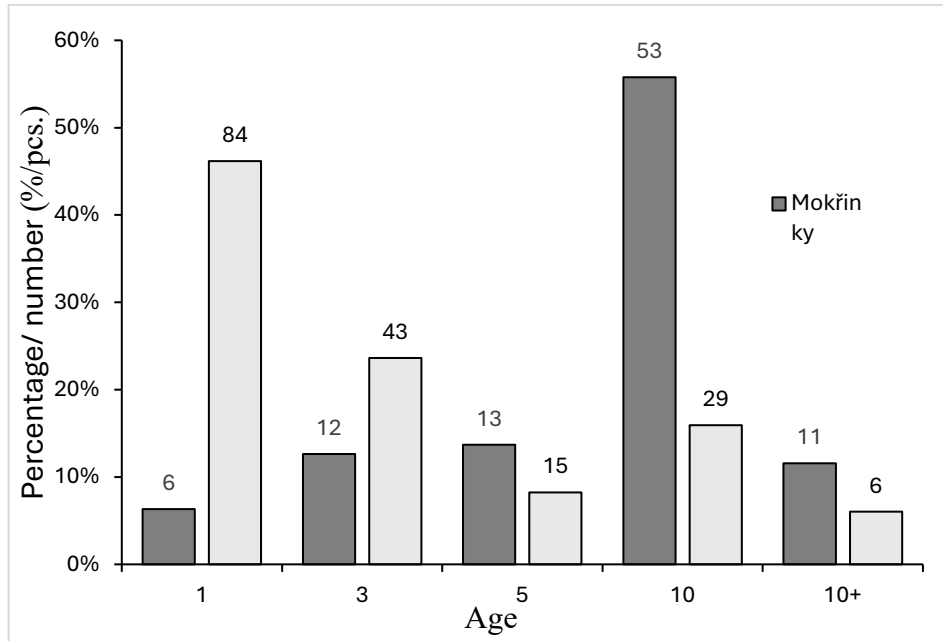


Fig. 2. Age structure of silver fir regeneration, growing in aspen pioneer stands (the numbers above the columns indicate the number of fir seedlings)

The timing of planting of silver fir relative to the age of the nurse crop was crucial. One approach considered planting the silver fir in row spacing with pioneer species immediately after clearing emergence, both species at the same time. In the second approach, silver fir was planted into preparatory pioneer stands of different ages and silvicultural regimes.

We found success in regeneration approaches, but only where soil moisture was sufficient (Tornádo). Pioneer stands stimulate early fast growth of silver fir, reduce seedling mortality and regeneration costs. At the same sites, silver fir planted without a mixture of pioneers was exposed to climatic extremes and weed competition. In clearings with a high level of soil moisture (Rakovec), direct planting of silver fir with (or without) pioneer was not successful (Martiník et al. 2018). On the site with sufficient soil moisture (Krnov), the pioneer height of about 4 m closed the canopy and covered silver fir with height of about 1 m after five years; thus, the stimulation effect of the pioneer stopped and started competition. To reduce competition for light and moisture frequent thinning is recommended (Fig. 3).

At water-affected soils (pseudogley - Stara Ves), the highest radial stem growth increment was recorded at the narrow gap (i.e. three rows of silver firs) but seedlings had to compete with grasses. Shelter of frequently thinned stand of silver birch suppressed the weed but still allowed high radial growth of silver fir. The dense unthinned canopy of silver birch suppressed the growth of both grass and silver fir. The photosynthesis of needles increased already the first year after thinning of the dense stand (Fig. 3). However, the increased carbon assimilation did not reflect in the stem radial growth, which remained in the first year after thinning same as in the dense stand (Fig. 4).

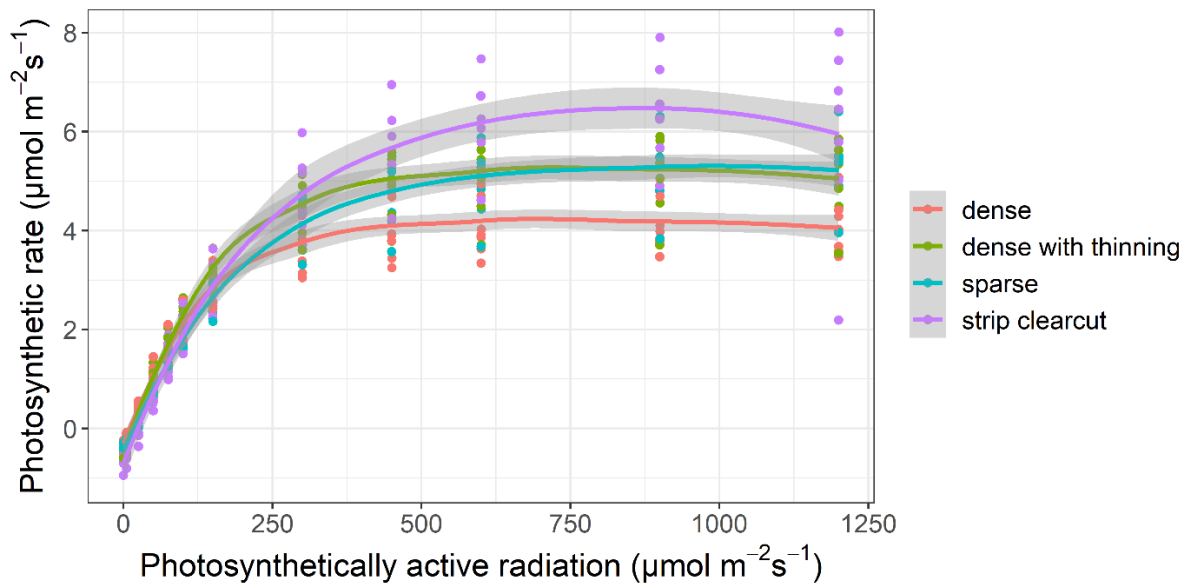


Fig. 3. Light response curves of Silver fir current year needles which developed under the birch canopy of different densities. Thinning of the dense overstory of formerly dense silver birch canopy resulted in the photosynthesis of new needles comparable to the one under a frequently thinned stand.

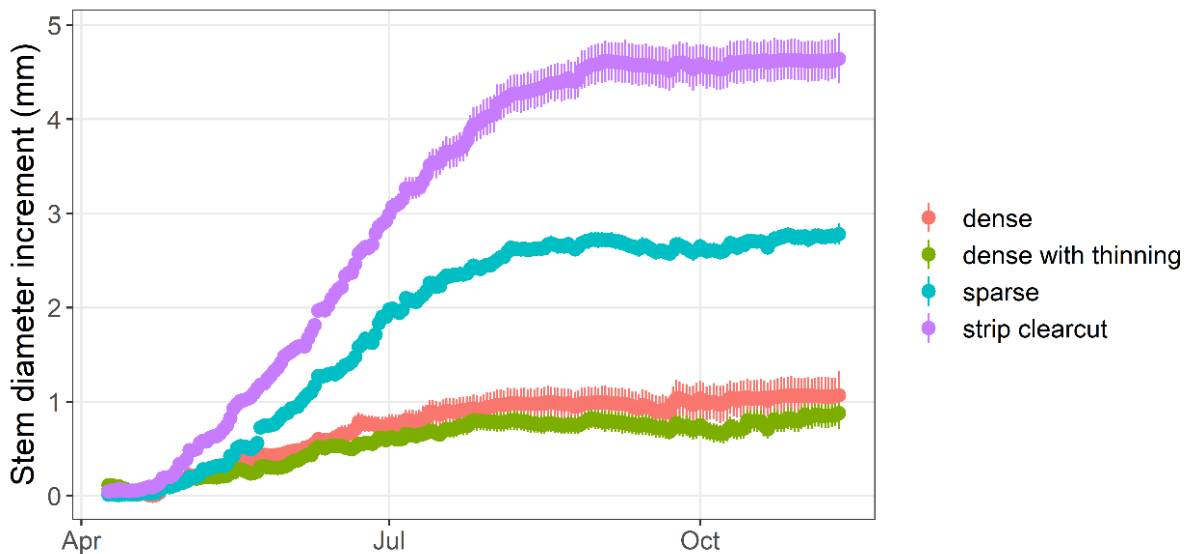


Fig. 4. Radial increment of silver fir plants growing under the shelter of sparse and dense birch, at a strip clearcut, and the response of silver fir that grew under the dense canopy to thinning.

The introduction of silver fir into preparatory (pioneer) stands optimizes structure of pioneer stands and reduces competition for light and moisture; to keep less cover of weeds and to balance the total forest ecosystem radial increment with pioneer trees included. At the suboptimal sites with drought-prone sites (Skrchov) the water stress of silver fir was evaluated. The silver fir was planted in different stands situations of about 20 years old silver birch stands: gaps (20x20 m), control no unthinned plots (density 3 000 trees per ha), strongly thinned plot (density 1 050 trees per ha). During summer drought, trees growing in the gap had the least

negative water potential, indicating no water stress (Fig. 5). On the contrary, both predawn and midday water potential of silver fir under the birch plummeted below -3 MPa, indicating the risk of drought-induced mortality (Nourtier et al. 2014). The water potential of birch was less negative than of the underplanted silver fir which indicates that deep roots can access water. Water stress and light availability jointly resulted in the highest height increment of Silver fir growth in the gap and lower under the tree canopy

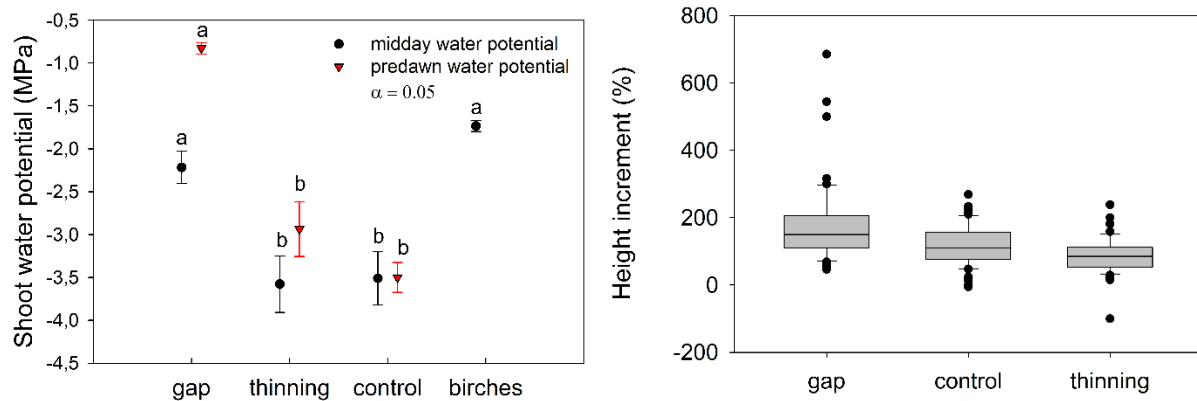


Fig. 5. Left: The water potential of the silver fir under the various densities of silver birch canopy and in the gap. Right: The height increment of the silver fir in the gap and under two densities of silver birch overstory.

Calamities and clearing may offer an opportunity to increase the proportion of silver fir in forest stands in the Czech Republic. Nurse crop methods, where fir is cultivated with the pioneers in variable time and space scale may provide a basic silvicultural tool for preservation and the increase of silver fir at exposed sites after large scale disturbances.

Acknowledgement

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Effect of temperature, water availability, and soil properties on soil CO₂ efflux in beech-fir forests along the Carpathian Mts.

KEYWORDS: Canopy gap, carbon content, nitrogen content, soil respiration, soil water content

Introduction

Carpathian Mountain beech-fir forests are exposed to severe pressures related to climate change. Soil CO₂ efflux contributes substantially to ecosystem carbon flux and affects the forests' carbon storage due to its climate sensitivity, especially temperature and precipitation (Rodrigues et al. 2023). Forest gaps are an integral part of forest ecosystems and play a crucial role in the regeneration of mixed beech-conifer forests (Čater and Diaci 2017) but they also alter the microclimate (Londo et al. 1999, Čater et al. 2021), new carbon input (Hukić et al. 2021) and soil CO₂ efflux (Han et al. 2020).

Soils are a big carbon pool but increased CO₂ emissions from soil respiration due to climate change can decrease these carbon reserves (Rodrigues et al. 2023). Within the terrestrial carbon cycle, soil respiration is the largest carbon efflux into the atmosphere (IPCC, 2021) and, therefore, it plays a crucial role in the response of the ecosystems to climate change. Soil can either be a net source or a net sink of CO₂. This depends on which flux prevails, the input of carbon into the soil due to plant growth, or the losses of carbon, i.e. soil respiration.

The objective of this study was to assess soil CO₂ efflux in beech-fir forests along the Carpathian Mountains, to determine potential topographical, biological, and climatic factors driving soil CO₂ efflux variability, and to evaluate the effect of forest gaps on soil CO₂ efflux and soil properties.

Methods

The study was conducted on eight experimental sites along the Carpathian Mountains during two-week campaigns in 2022 and 2023. The sites were numbered from 1 (the southernmost site in Romania) to 8 (the northernmost site in the Czech Republic). At each site, we found a medium gap size (100–200 m²) according to Han et al. (2020) or Lyu et al. (2022) where three plots were selected: forest with closed canopy cover (closed), forest adjacent to the gap (edge),

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and the gap without canopy (open). On each plot, we measured soil CO₂ efflux at nine positions using a portable infrared gas analyzer Li-8100 (LI-COR, USA) and a 20cm-survey chamber, soil temperature (TPD32 penetrate thermometer, Omega, Stamford, CT, USA), and soil water content (ThetaProbe ML2x, DeltaT Devices, Cambridge, UK). Moreover, the top 10 cm of soil (containing organic and mineral horizons) was sampled in each plot using a portable stainless steel soil core sampler with a diameter of 5 cm. The samples were dried and sieved through a 2-mm sieve and analyzed in the laboratory for pH (H₂O), carbon, and nitrogen content (%).

Results

Mean soil temperature at 1.5 cm (T_s) under the closed canopy ranged between 13.5 and 17.4 °C in 2022 and between 9.8 and 15.8 °C in 2023. Soil water content (SWC) under the closed canopy exceeded 20% at all sites, except for site 5 in 2023 (Fig. 1).

Soil C content ranged between 4.4 and 12.9% (Fig. 1). The highest C content of 12.9% was found at site 2 and highly exceeded C content at other sites. The second highest C content was found at site 6 and the lowest at site 7. The same trend was observed also for soil N content and C:N ratio. N content ranged between 0.32 and 0.58%, while C:N ranged between 13.6 and 22.2. The soil was mostly strongly acidic with a pH below 5.5. Exceptions were site 3 with a pH of 5.6 (acid soil) and site 4 having neutral soil with a pH of 7.0.

Mean soil CO₂ efflux (R_s) under the closed canopy ranged between 2.5 and 7.8 μmol m⁻² s⁻¹ (Fig. 1). The differences in R_s between 2023 and 2022 depended significantly on soil water content but not on temperature. Correlations of R_s with different climatic and topographical variables, and soil properties were analyzed to evaluate, which factors drive the R_s spatial variation along the Carpathians. In 2022, R_s significantly decreased with latitude and increased with C:N, while in 2023, R_s significantly increased with both C and N content (Fig. 2).

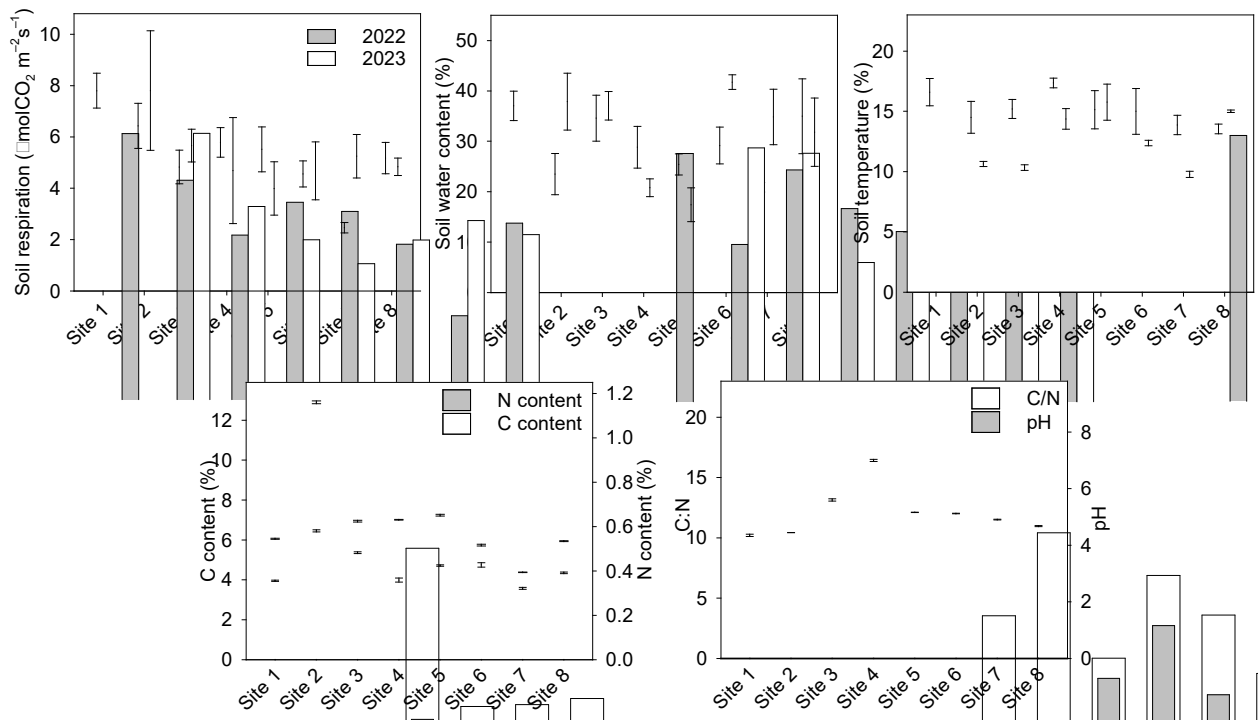


Fig. 1. Mean (\pm SD) soil CO₂ efflux, and soil properties on the plots with closed canopy at eight study sites along the Carpathians.

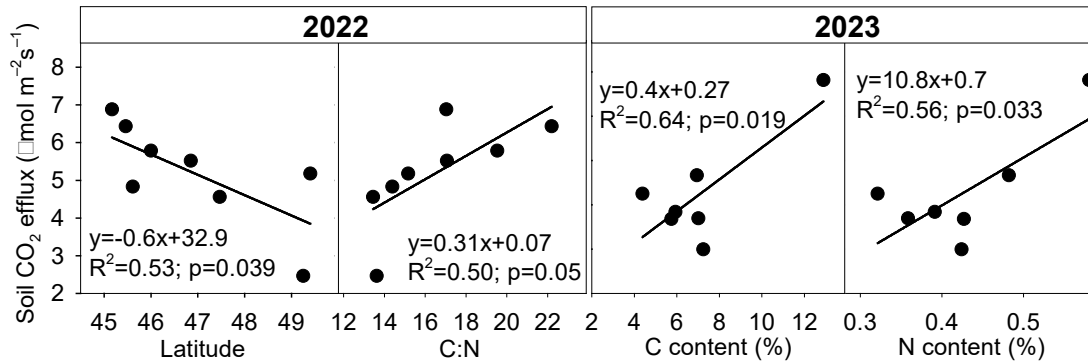


Fig. 2. Statistically significant linear regressions between different site characteristics and parameters measured on plots with the closed canopy during the campaigns in 2022 and 2023.

Canopy openness did not have any uniform effect on soil CO₂ efflux and soil properties. However, when analyzing the effect of soil properties and microclimatic conditions on the overall variability over all sites and plots, the effect of the soil C and N content was substantial, while soil temperature, SWC, and pH affected soil CO₂ efflux variability negligibly (Fig. 3).

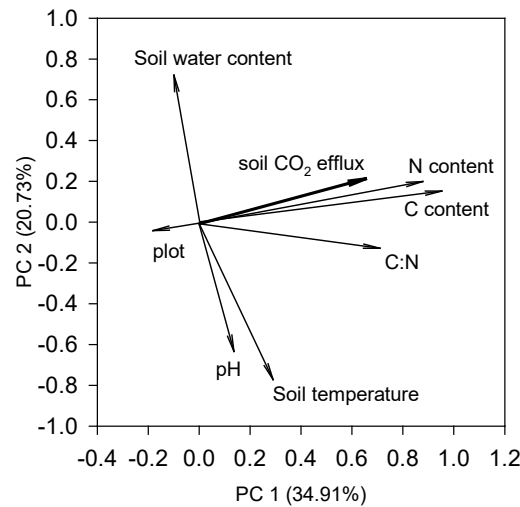


Fig. 3. The Loading Plots of Principal Component Analysis (PCA) of soil CO₂ efflux, soil microclimatic parameters, and soil properties of all sites, plots (with the closed canopy, at the forest edge, and with the open canopy), and years (2022 and 2023). The angle between arrows indicates the direction of the relationship (acute angle positive relationship, obtuse angle – negative relationship, right angle – no relationship).

Conclusions

On eight experimental plots along the Carpathian Mountains within beech-fir forests, the soil CO₂ variability efflux among the plots was driven by soil properties such as carbon and nitrogen content rather than by climatic conditions. Therefore, we may assume that climate effect on new organic matter input through forest productivity and species composition will have a big effect on soil organic matter decomposition and storage. The changes in climate can be attributed to changes in air temperature and precipitation. Air temperature at the studied sites

has gradually increased for several decades, while annual precipitation showed no trend (Darenova et al. 2024). Nevertheless, there was a substantial decrease in summer precipitation during the last decade at all sites except for the two northernmost. Canopy gaps bring uncertainty to the estimation of the forest carbon balance as we did not find any uniform effect of the canopy openness on soil CO₂ efflux or soil properties. That could be a result of the different ages of these gaps, which we were not able to estimate.

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Soil microbiome along the carpathian mountains

KEYWORDS: soil microbiome, next-generation sequencing, climate change, soil, fungi, bacteria

Introduction

The Carpathian Mountains represent one of the largest mountain forest chains in Central Europe, characterized by diverse forest types predominantly composed of beech (*Fagus sylvatica* L.) and mixed conifer stands (*Picea abies* Karst and/or *Abies alba* Mill.) at altitudes ranging from 500 to 1450 meters (Dinca et al., 2022; Knorn et al., 2013). This forest zone has been significantly impacted by human activities and climate change over centuries. Numerous studies have focused on the adverse effects of climate change on the radial increment of beech stems (Levanič et al., 2023) and the regeneration potential of silver fir (Čater and Levanič, 2019). Despite these studies, the Carpathian arc, like many other European mountain chains, remains underexplored, particularly in terms of soil-related parameters such as soil biodiversity, ecosystem services, and functions (Guerra et al., 2020). Recent large-scale soil sampling initiatives, such as the LUCAS survey, have largely excluded this region as well (Labouyrie et al., 2023). Motivated by the study of Darenova et al. (2024), which investigated topographical, biological, and climatic drivers of soil CO₂ efflux in beech-silver fir forests, we aimed to analyse the alpha diversity of bacterial and fungal communities along the Carpathian arc. Using the same experimental setup as Darenova et al. (2024), we employed highly informative metabarcoding of soil environmental DNA to estimate the diversity of selected taxonomic groups (Vasar et al., 2023).

Methods

Following the sampling scheme of Darenova et al. (2024), we collected soil samples from eight locations along the Carpathian arc. At each location, samples were taken from "open canopy", "forest edge," and "closed canopy" positions, including bulk soil and samples from the vicinity of roots. Soil samples were collected using a standardized soil probe (Grebenc et al., 2007). Molecular barcoding of bacteria was performed using the primer pair 341f/805r and fungi using the primer pair gITS7/ITS4, as described in Unuk et al. (2019). Bioinformatics and statistical analyses were conducted in R (v. 4.3.2) using RStudio (v. 2024.04.2) with the following libraries: phyloseq, vegan, ggplot2, data.table, parallel, multcomp, devtools, ggpubr, stringr, tibble, tidyverse, dplyr, indicpecies, and pairwiseAdonis.

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Results

ANOVA and subsequent Tukey HSD tests revealed a statistically significant effect of sampling location on the alpha diversity indexes (richness, evenness, and Shannon index) of bacterial communities. For fungal communities, sampling location significantly affected species richness. The alpha diversity of fungal communities was significantly influenced by soil sample type (bulk soil vs. rhizosphere soil). Species richness of fungal communities was significantly different between locations Buzau and Gorj versus Neamt. Conversely, bacterial diversity indexes showed consistent differences between Beskidy and Neamt, Suceava, and Vrancea.

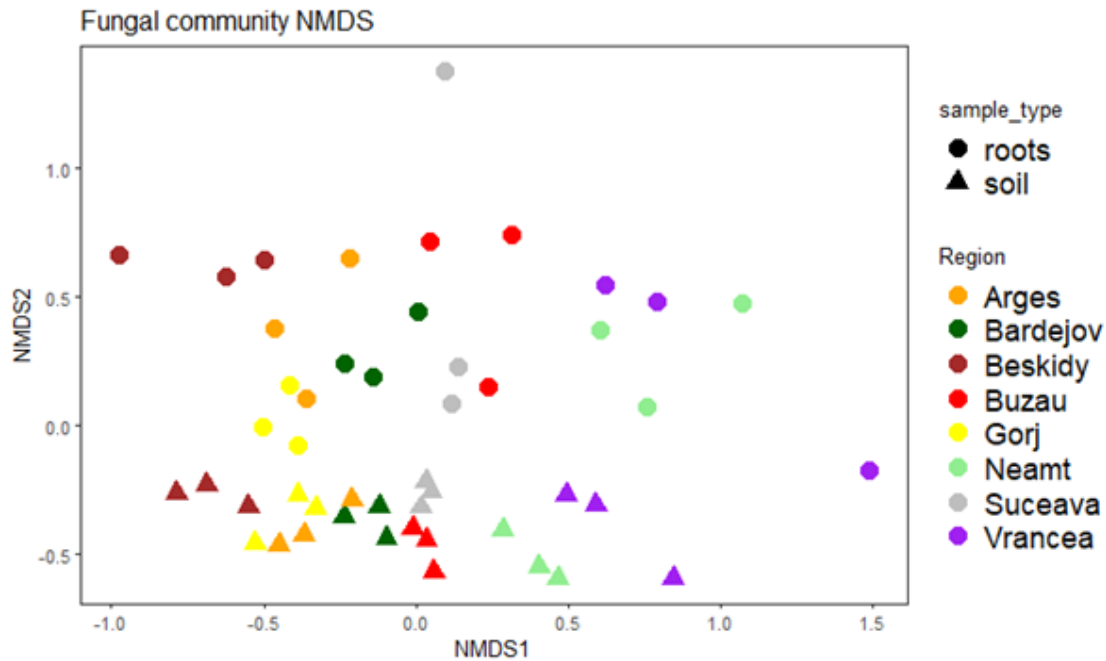


Fig. 1. Fungal community for roots and soil collected along the Carpathian Mountains analysis and analysed by the non-metric multidimensional scaling (NMDS) with Bray-Curtis dissimilarity.

We visualized differences in bacterial and fungal communities using non-metric multidimensional scaling (NMDS) with Bray-Curtis dissimilarity. Community data were standardized using Hellinger transformation. Pairwise PERMANOVA with Bonferroni correction was used to test community differences between locations and environmental factors. NMDS stress values indicated reliable dissimilarity matrix representation. PERMANOVA analysis showed that 31.29% of bacterial community variation was explained by sampling location, while sample type explained 5.24%. Similarly, 28.6% of fungal community variance was significantly influenced by sampling location, followed by sample type (11.7%) (Figure 1).

The Figure 2 summarizes the relative abundance plot of bacterial taxonomic groups revealed *Actinobacteriota* as the predominant phylum, followed by *Proteobacteria*, except at Agres, where *Planctomycetota* were slightly more abundant. Other represented phyla included *Verrucomicrobiota*, *Firmicutes*, *Chloroflexi*, *Acidobacteriota*, *Myxococcota*, *Gemmatimonadota*, and *Bacteroidota*.

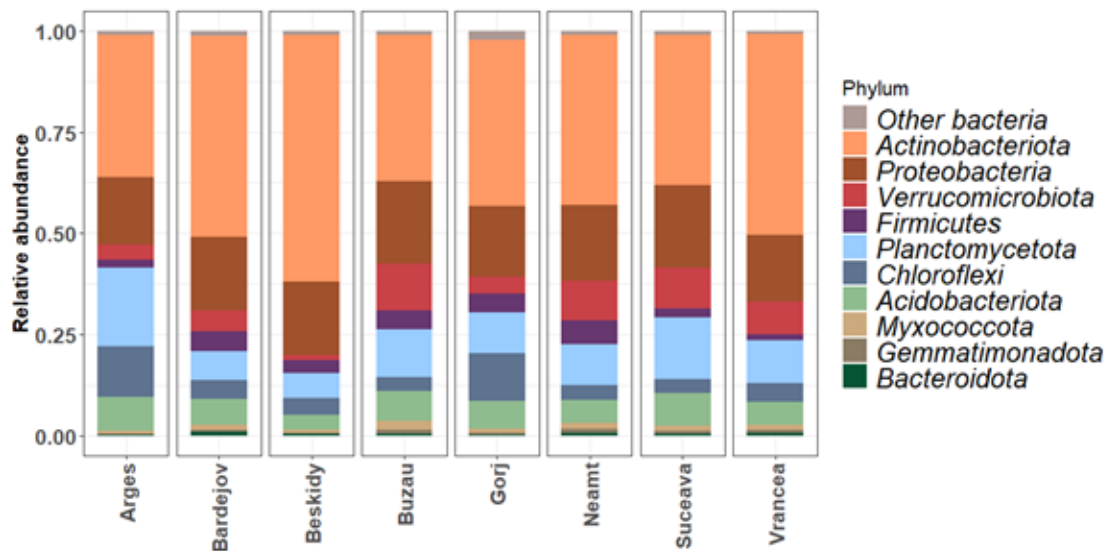


Fig. 2. Relative abundance of the dominant bacterial phyla identified from roots and soils collected along the Carpathian Mountains analysis. Communities were assessed by a metabarcoding of the hypervariable region of the 16S rRNA gene.

Fungal taxonomic group abundance, identified to the genus level with a 92% similarity threshold, showed diverse compositions at each location. Some genera were unique to rhizosphere samples at specific locations (e.g., *Tomentella* and *Ganoderma*) or predominantly present at few locations (e.g., *Cladophialophora*, *Sistotrema*, *Podila*) (Figure 3). Ectomycorrhizal fungi (Figure 4) were mainly attributed to 15 genera, with all but *Tuber* (Ascomycota) belonging to Basidiomycota. *Tuber* and *Melanogaster* were notably present at Neamt. Other genera, such as *Laccaria*, were widespread, while some, like *Amphinema*, *Tylospora*, and *Xerocomellus*, were location specific.

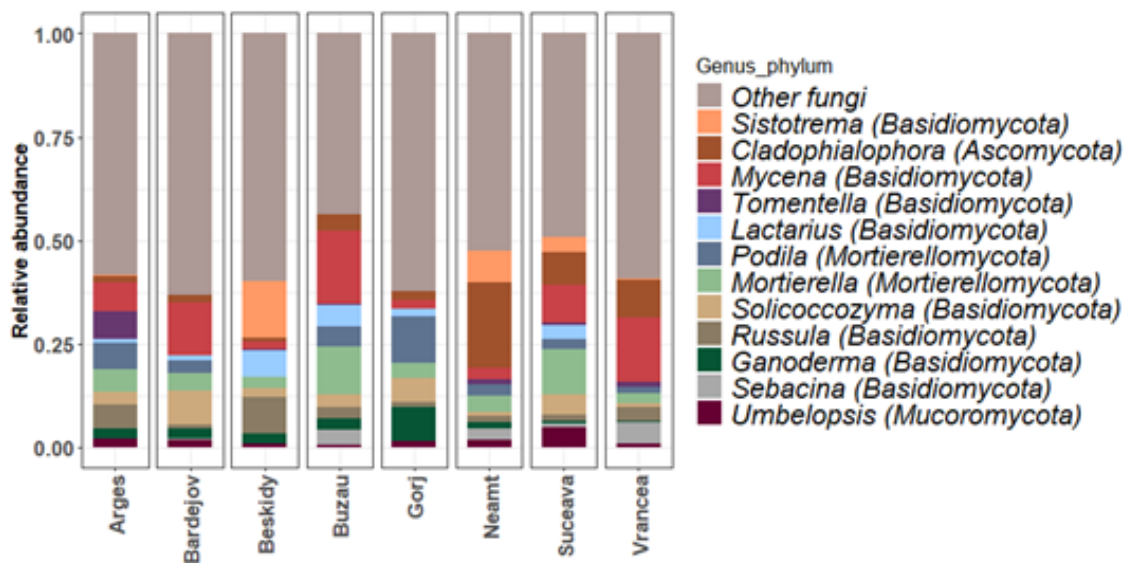


Fig. 3. Fungal community composition at analysed locations along the Carpathian Mountains. Rhizosphere communities were identified based on a 92% similarity threshold for an identification at the genus level.

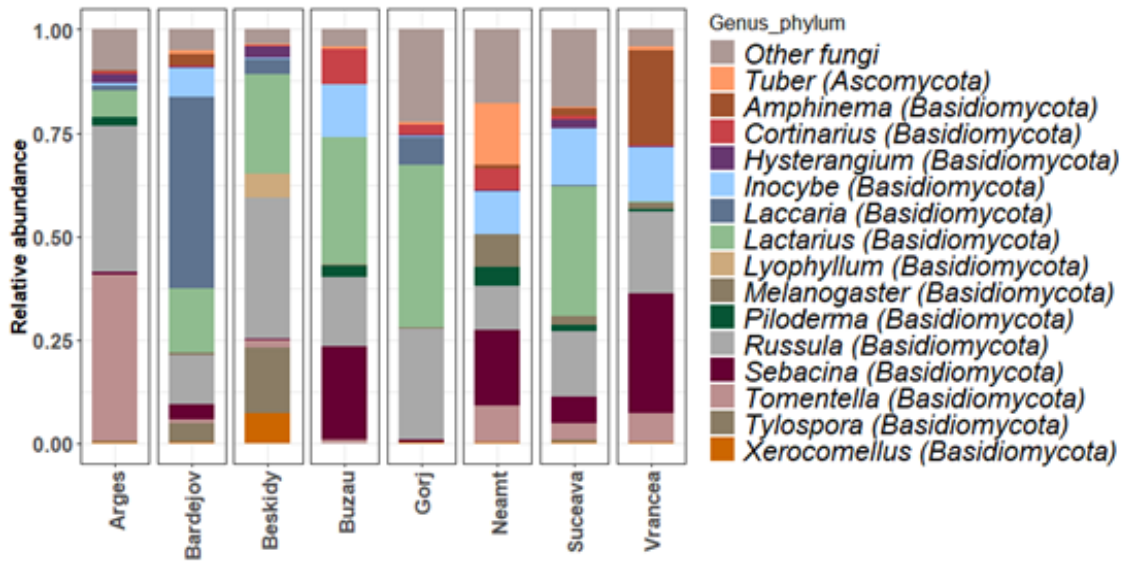


Fig. 4. Fungal community composition at analysed locations along the Carpathian Mountains. Ectomycorrhizal fine roots associated communities were identified based on a 92% similarity threshold for an identification at the genus level.

Functional group analysis based on the total rhizosphere samples revealed higher abundances of soil saprotroph fungi in bulk soil samples (29.5%) compared to rhizosphere samples (14.3%) (Figure 5). Conversely, rhizosphere samples had higher abundances of litter saprotrophs (27.7%) compared to bulk soil (4.9%). Bulk soil also showed a higher presence of plant pathogen fungi (6.72%) compared to rhizosphere samples (1.6%).

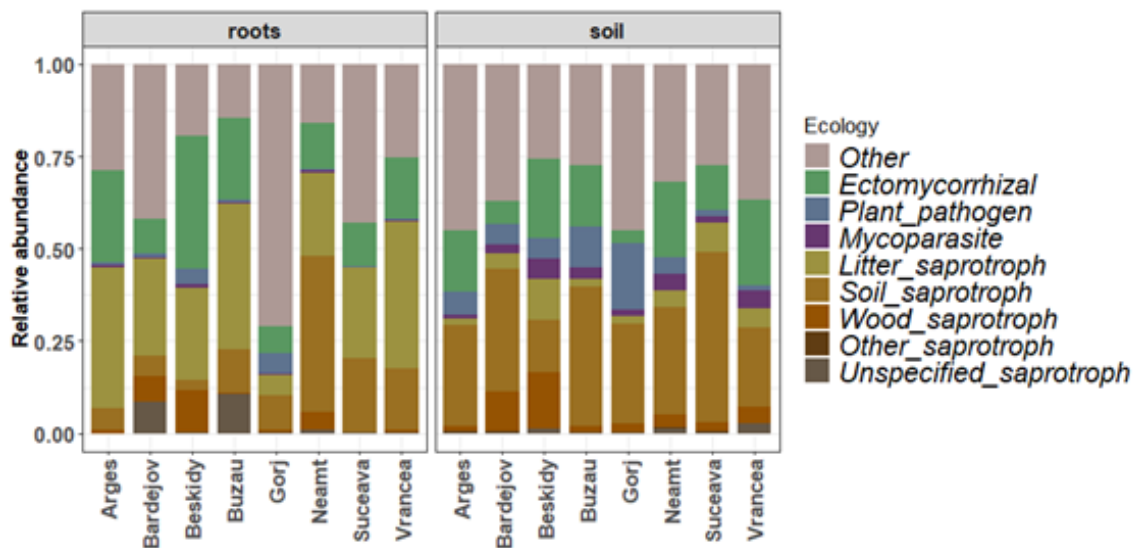


Fig. 5. Relative abundance of the fungal community functional groups based on the total rhizosphere samples composition analysed in soil samples collected along the Carpathian Mountains.

Conclusions

The analysis of soil microbial communities along the Carpathian Mountains revealed variations in diversity indexes and taxonomic compositions across different sampling locations and soil types (bulk soil vs. rhizosphere). However, no significant effects were found related to the sampling point's position relative to tree canopies. The composition of fungal communities indicated some widely present groups, with some taxa showing specific location preferences, likely due to soil properties, vegetation, or environmental conditions. The differing compositions of saprotrophs in bulk soil and rhizosphere samples align with substrate availability.

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Response of beech and fir in the Carpathians and Dinarides

KEYWORDS: silver fir, beech, light response, Carpathians, Dinarides

Introduction

Mixed fir-beech forests are an essential component of Central and South-Eastern European Forest ecosystems and landscapes (Bledy *et al.*, 2024). Vegetation changes in the Carpathian forests can be attributed to various processes (Šamonil and Vrška, 2007), such as air pollution and the competitive influence of tree seedlings (Łysik, 2009). Of particular interest is how silver fir will cope with recent climate trends (Maiorano *et al.*, 2013). Adamič *et al.* (2023) already confirmed different stem radial growth in beech and fir since 1950s and their response to climate conditions along the Carpathians, while Darenova *et al.* (2024) related soil respiration spatial variability with soil water content, soil carbon and nitrogen content with no significant effect connected with canopy gaps.

On the Balkan Peninsula, the response of beech and fir from the southern, sites already served as a future prediction for less extreme sites in the north (Čater and Levanič, 2019), while Carpathian Mountains are more complex and exhibit a sufficient latitudinal and longitudinal gradient associated with significant differences in temperature/precipitation as well as differences in seasonal patterns (Micu *et al.*, 2016). Quantum yield (Φ) in various light microsites proved beech as more efficient in exploiting direct radiation in sun exposed parts of the gap, compared to silver fir (Čater *et al.*, 2024).

Our aim was to compare the light responses of beech and fir in the Carpathian and Dinaric Mountains (1), and to verify the relationship between climatic parameters and light response along both complexes (2).

Material and methods

19 permanent research plots were located above an altitude of 800 m a.s.l., with abundant natural regeneration of both tree species. Eight plots were established in the Carpathians, and eleven in the Dinarides. Two old growth reserves were selected in the Carpathians (plots 3 and 8) and three in the Dinarides (plots 3, 7 and 8, Fig. 1).

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- Three light intensity categories were defined on each plot based on the analysis of hemispherical photographs (Čater et al. 2024).
- Monthly mean temperatures (°C) and monthly total precipitation data were interpolated for the 0.5° grids from the ‘Climate Explorer’ website (<http://cliexp.knmi.nl>). Data from the last 50-year average period (1981-2020) were used.
- Total leaf nitrogen concentration (N_{tot}) [mg/g] was determined from leaves and needles taken from the upper canopy position (Čater et al., 2014). Leaves were dried to constant weight at 105 °C for 24 hours and weighed in the laboratory to determine leaf mass per area (LMA) [g/m²].

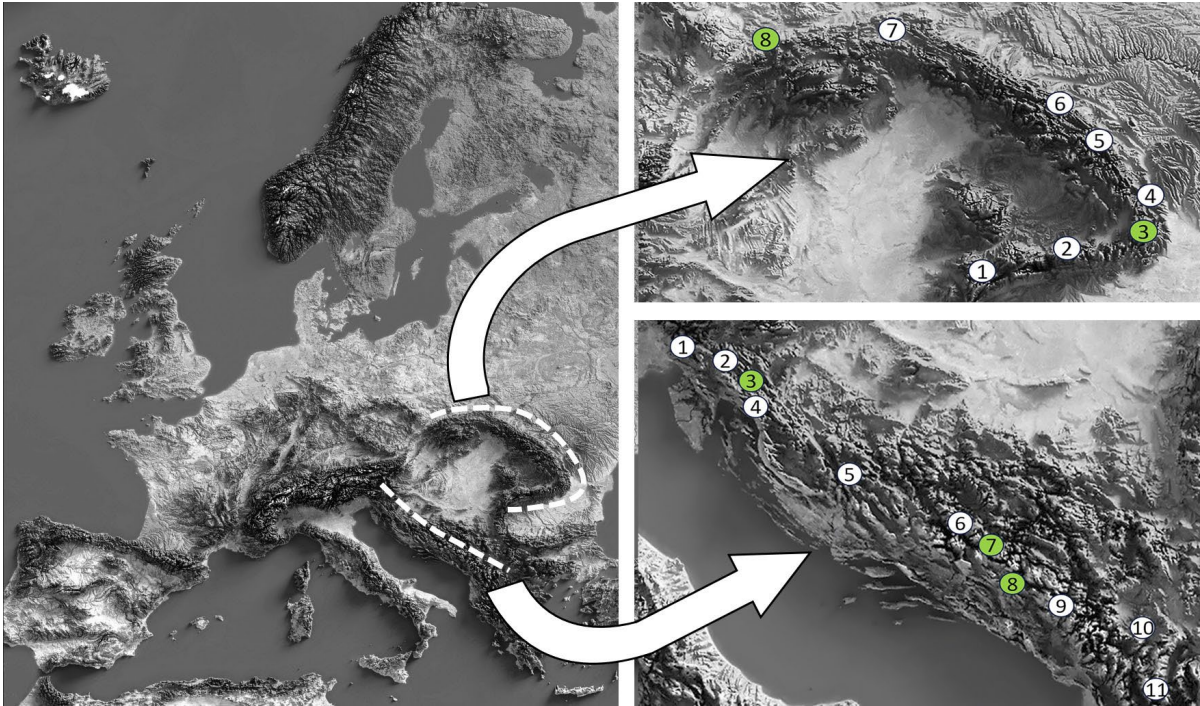


Fig. 1. Research plot location

- Light saturation measurements were carried out in June and July in three consecutive growing seasons, at least 8 young trees with a portable LI-6400 (Li-Cor, USA) system (Čater et al. 2024).
- The maximum quantum yield (Φ), defined as the maximum amount of fixed CO₂ per amount of absorbed light quanta (Lambers et al., 1998) measured as the initial slope of the light response curve of CO₂ fixation, were determined for each light category, species and plot, as described in Čater et al. (2024).
- Differences between the same years for the LMA, N_{tot} , A_{max} and Φ were tested using two-way ANOVA with tree species (beech and fir) and light (open, edge, canopy) as dependent variables. HSD Tuckey post-hoc test was performed after testing data to meet conditions of normality. Probability values of $p < 0.05$ (*), $p < 0.01$ (**) and $p < 0.001$ (***) were considered significant. Data analyses were performed using Statistica Data Analysis Software System (2011).

Results

Long-term average temperatures show homogeneous conditions over Dinarides and more variable conditions in Carpathians. The average annual precipitation in the Carpathians is lower.

Foliar nitrogen (N_{tot}) in all plots was highest for both beech and fir in the open and lowest in the closed canopy, without significant differences between light categories and years. On all studied plots N_{tot} was within the optimal thresholds (Yang et al., 2022; Bachofen et al., 2020). The same trend was observed for LMA. N_{tot} and LMA were non significantly lower in all categories of Carpathians compared to Dinarides.

Quantum yield (Φ) followed the pattern of precipitation and temperature; it was highest for beech in the open light and under closed canopies for fir. In old growth reserves of the Dinarides, Φ was shifted towards the response of open light and the absolute values were higher in all light categories than in the neighbouring managed forest stands (data not shown). Areas with the highest Φ for both species and complexes were defined for beech in the central Dinarides and western Carpathians and for fir in Northern Dinarides and also western Carpathians. With post-hoc analyses significant differences between light categories for Φ in Dinarides were confirmed. In Carpathians differences between light categories were not so pronounced.

Table 1. ANOVA for beech and fir in different light conditions and complexes.

Complex	Df 1;2	Species		Df 1;2	Light category		Df 1;2	Species X Light category	
		F	p		F	p		F	p
Carpathians	1; 1096	622.2	2e-17***	2; 1096	214.9	2e-17***	2; 1096	2869.5	2e-17***
Dinarides	1; 1578	73.0	2e-16***	2; 1578	231.0	2e-16***	2; 1578	775.4	2e-15***

Positive correlation between Φ and annual precipitation increased with the light intensity for beech in all light categories in Carpathians and Dinarides. The correlation for fir decreased with increasing light and was highest when the canopy was closed. Φ of beech in both complexes decreased with increasing annual temperature. Φ for fir in the Carpathians decreased with increasing annual temperature, while in the Dinarides, it increased (Fig. 2).

The average annual temperatures at the selected Carpathian sites ranged between 12 and 14 °C with the exception of sites 4 and 1, while the average annual temperatures at the Dinaric sites showed more homogeneous conditions (13 to 14 °C). The average precipitation in the Dinarides decreased evenly from the north-west to south-east, while the amount of precipitation in the Carpathians decreased from west to east. Φ in Dinarides was highest for beech in the central area, for fir in the north-western part, while in the Carpathians it was highest at the beginning and end of the studied transect. In both complexes, Φ were higher for beech in the open, and for fir highest under shaded conditions. Differences between old-growth forests and neighbouring managed forests were less pronounced in the Carpathians than in the Dinarides (Čater et al., 2024).

Variability of Φ and between light categories were higher for both species in the Dinarides, possibly reflecting the more diverse growing conditions and more abundant water availability compared to the Carpathians (Micu et al., 2016). We believe water to be the most important limiting parameter, as the response of both species at all study sites in the Carpathians, except the first two, corresponded to sites in Dinarides with annual precipitation below 500 mm.

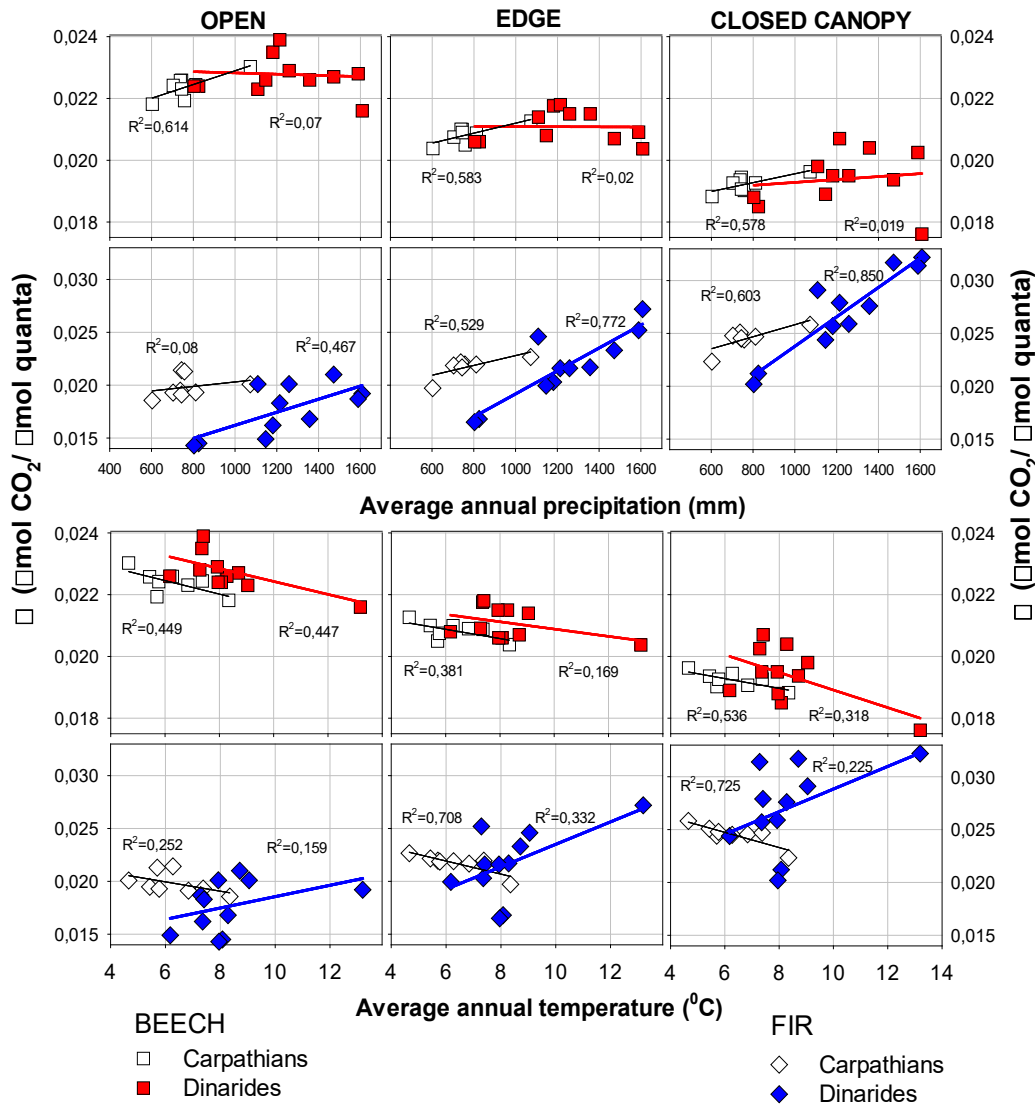


Fig. 2. Quantum yield (Φ) vs. precipitation and temperature

The assimilation response in young beech and fir trees was in good agreement with the growth response in adult trees (Čater and Levanič, 2019); study of Adamič et al. (2023) confirmed clear differences in the growth response to climate (temperature and precipitation) between southern, eastern and northern locations on the same study plots. Accordingly, the quantum yield of beech and fir showed the lowest values in the eastern part and the highest values in the west.

In the Dinaric Mountains growth of fir responded more strongly to climate than that of beech in the same study plots. Both temperature and precipitation had a stronger influence on the growth of fir. The climate signal of fir became weaker from NW to SE, with only the drought indices remaining significant, while the response of beech to climate was weaker in all plots and decreased from NW to SE, similar to fir (Čater and Levanič, 2019).

Short-term ecophysiological responses of beech and fir provided information on the behaviour at three different light intensity categories compared to long-term radial growth observations, which were consistent. The main difference between the two larger areas was the response of

young fir to increasing temperatures, which correlated positively with increasing temperatures in the Dinarides and negatively in the Carpathians. In our opinion, this difference is related to the high precipitation in the Dinaric Mountains and the low precipitation in the Carpathians.

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Growth response of European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) on climate factors along the Carpathian massive

KEYWORDS: climate change; dendrochronology; radial growth response; meteorological parameters.

Introduction

We focused on beech (*Fagus sylvatica* L.) and fir (*Abies alba* Mill.), which are likely to be the two most important tree species for a large part of Europe's mid- and high-altitude forests in the future (Dobrowolska et al., 2017). In study at the Balkan Peninsula along the Dinaric high karst, where different and well-expressed ecological factors intertwine at relatively short geographical distance (approx. 1000 km) (Bohn et al., 2000), response of beech and fir from the southern, warmer and dryer sites already served successfully as a most probable future prediction for the same species response on currently less-extreme sites northward (Čater and Levanič, 2019). Carpathians as more complex site comprise sufficient latitudinal and longitudinal gradient connected with significant differences in temperature/precipitation as well as differences in their seasonal pattern (Micu et al., 2016). The quality and future of fir-beech forests is in tight connection with our understanding of tree-response to environmental parameters. Dendrochronological analysis of stand growth provides a historical retrospective of the response to climatic factors in different time series of mature trees (González et al., 2003). In predicting the consequences of climate change on tree species, studying the response of species on a geographic gradient may highlight the crucial parameters important for tree growth on a larger scale, help to predict future response and optimize future forest management. In the presented study, we were interested if there is a similar response between tree species along the Carpathian arc. The aim was to determine the influence of climate on the growth of beech and fir along the geographical gradient (a), to find similarities or differences between the two species (b) and to compare response in time for eventual change in the growth response (c).

Methods

Along the Carpathian Mountains, seven sites with mature fir-beech stands located between 820 and 1038 m above sea level were selected and analyzed (Figure 1 and Table 1). At the study sites, the average temperature is 7.3 °C and the average temperature in the growing season

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(from May to August) is 15.8 °C. The average precipitation is 60.7 mm per month and 91.5 mm per month from May to August. The meteorological data were calculated for the years 1950 to 2020. At each site, 15 mature dominant healthy fir and beech trees were double cored, which gave in total 105 sampled trees for fir and 105 sampled trees for beech. Tree cores were packed into plastic straws, marked, and transported to the dendrochronology laboratory. The cores were dried, mounted and glued on a wooden support and sanded with progressively finer sandpaper. The cores were then scanned with an ATRICS (Levanič, 2007) image capturing system, and annual radial increments were measured to within 0.01 mm using CooRecorder and CDendro software, which also served as quality control for the measured tree-ring width (TRW) sequences. TRW sequences were visually and statistically synchronized with PAST-5. Quality control was also performed by checking and correction. We calculated correlations between trees in CDendro and created a plot chronology that we compared to individual trees. Any tree ring width sequence that did not fit well into the plot chronology were corrected in CooRecorder and returned into data pool. Individual TRW were standardized to remove long-term trends using a cubic smoothing spline of 67 % with a frequency cutoff of 50 % in R program's dplR library (Bunn, 2008). Indexed TRW chronologies were compared to monthly mean temperatures, maximum temperatures, monthly sum of precipitation, and two drought indexes using the boot-strapped resampling method and calculating the correlation coefficient in the Treeclim library (Zang and Biondi, 2015) of the R program. Temporal correlation between tree-ring proxies and combinations of monthly and seasonal variables was examined using monthly gridded temperature, precipitation, and drought data ($0.5 \times 0.5^\circ$ grids) from the CRU TS and CSIC database, available online in KNMI Climate Explorer (<http://climexp.knmi.nl>). Each tree-ring proxy was tested against monthly meteorological data or different combinations of seasonal variables to find the best possible combination of influencing climate variables. We analyzed the period from 1950 to 2016. To show whether trees along the Carpathians respond similarly to meteorological data, correlation coefficients above 0.2 and below -0.2 were considered. If such a value was confirmed in at least three studied sites, we marked a particular month with a climate parameter as important for certain species. The sites on different sides of the Carpathians were grouped into three clusters: southern group - sites 1, 2, 3; eastern group - sites 4, 5, 6 and northern site number 7. We calculated the average TRW for fir and beech by decades from 1950 on.

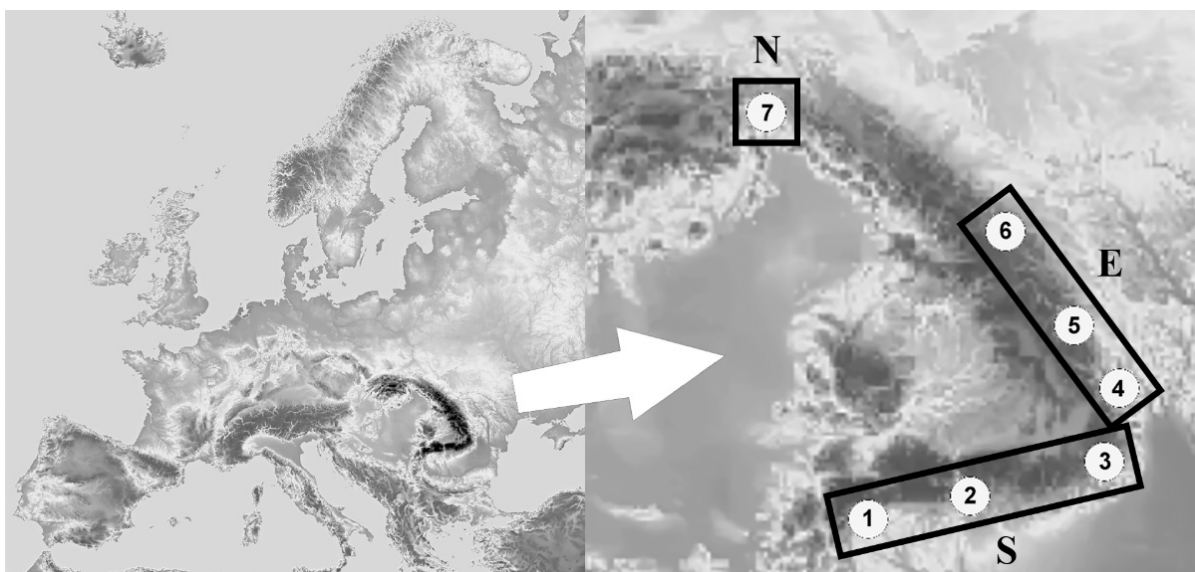


Fig. 1. Research site location.

Table 1. Locations, forest label, altitude, and coordinates of research site locations.

	County	Plot	Managed/old growth forest	Altitude (m)	E (DMS)	N (DMS)
1	Gorj	Tismana	managed	985	22°55'1.00"	45°10'10.00"
2	Arges	Arefu	managed	995	24°39'4.00"	45°27'37.00"
3	Buzau	Zagon	old growth	1038	26°13'44.00"	45°36'51.00"
4	Vrancea	Soveja	managed	830	26°36'14.00"	46° 0'5.00"
5	Neamt	Tarcau	managed	950	26°10'6.00"	46°51'15.00"
6	Suceava	Frumosu	managed	850	25°40'60.00"	47°28'6.00"
7	Bardejov	Livovska huta	managed	880	21°0'59.62"	49°15'17.06"

Results

The study showed a more significant correlation between tree growth and seasonal variables was observed on the eastern side of the Carpathian arc, while it was less evident or absent at sites on the southern side (sites 1,2,3). In comparable studies, the response to different climatic variables was decreasing or was absent in the south side of the studied transect due to genetic adaptability, phenotypic plasticity, or both (Čater and Levanič, 2019). The reason for the different response could also be that the eastern side of the Carpathians is affected by a climate with continental nuances and Baltic influences (Nechita et al., 2017). Fir and beech on northern sites react differently to meteorological parameters. Above-average precipitation in July had a positive effect on radial growth in both species, and in beech also in June. In the course of climate change, we don't expect above-average precipitation in summer; on the contrary, we expect more summer drought. In the study, we showed that fir responds negatively to above-average temperatures in June and in September of the preceding tree ring formation, with above-average summer temperatures likely to become more frequent under climate change, while warmer winters increase fir radial growth. Above average maximum winter temperatures from January to March have an even more significant positive influence on fir growth than above average temperatures. Fir, as an evergreen tree species, enjoys warm winters, while beech, as a deciduous tree species, is not as affected by warm winter temperatures. Mihai et al. (2018) showed high genetic variability within the silver fir studied in the Carpathians. They confirm that climate change could increase fir productivity at higher elevations while climatically marginal environments and low elevations, such as edges of the Eastern Carpathians and the Banat region may be exposed to higher risk (Mihai et al., 2018), due to higher temperatures and lack of moisture. Current fir populations have well-preserved genetic resources and relatively high genetic variability (Konnert and Bergmann, 1995) but are threatened by pressure from herbivores, large-scale reforestation of old fir stands, inappropriate management practices (Dobrowolska et al., 2017), reductions in population density that can lead to fragmentation, self-pollination, and genetic drift (Jump et al., 2006), and predicted climate change, particularly increases in temperature and lack of precipitation (Cailleret et al., 2013). Beech does not like too hot summers during the active growth phase, while this is not so pronounced in fir. Above-average temperature in the summer months had a negative effect on radial growth, so the higher summer temperatures may cause disturbances in beech growth. In the Eastern Carpathian region, changes in beech forests have been noted in recent decades (Durak, 2010), while old-growth beech forests in the Northwestern Carpathians were considered stable (Kucbel et al., 2011). Martinez del Castillo et al. (2022) predicted a substantial decline in beech growth across Europe, ranging from -20% to more than -50% by 2090, depending on the region and climate change scenario (CMIP6 SSP1-2.6 and SSP5-8.5). A comparison of average TRW over decades shows better growth of fir at the northern and eastern sites and slight decrease at the southern sites. Beech demonstrates more consistent

radial growth in the south; but growth increases less than in fir on the eastern and northern studied sites. The effects of global warming becomes evident in comparison of fir and beech response in time. Since we wanted to know the recent growth trend due to climate change, we calculated the average TRW for fir and beech by decades from 1950 on. Fir on the southern side shows a decreasing trend in TRW over time, signaling that these sites are gradually becoming unfavorable for fir. At the same time, the eastern and especially the northern sites are becoming more favorable for growth of both species. Of particular concern is the negative effect of above-average summer temperatures on beech growth, which is becoming more significant over the years, while July precipitation indicates an increasingly positive effect radial growth of fir. We may expect more frequent above-average summer temperatures and the absence of summer (July) precipitation, reflecting along both latitude and longitude, so also future differences in seasonal responsiveness of beech and fir may be expected. Extreme weather events and increasing average temperatures will influence future demographics of fir, as mentioned by Tinner et al. (2013) and Klopčič et al. (2017) to higher elevations and northward. At the same time a similar response of beech at the expense of fir and its general spread in Central Europe was observed by Šamonil (2008), Vrška (2009) and Janík (2014). Our results confirm increasing dependence of trees on precipitation over the past century and coincide with the increasing drought events after 1951. The likely response of species to climate change will vary, affecting their competitiveness, their existence, and consequently forest management decisions and measures (Brang et al., 2014). In southwestern Europe fir is more resilient to climatic extremes compared to other tree species (Bošela et al., 2018). At the same time, two fir populations have been distinguished in the Carpathian region: the eastern one, which is similar to the Balkan population, and the western one, which is less sensitive to summer droughts (Bošela et al., 2018). In the south-exposed areas of Eastern Carpathians, fir was the least sensitive of studied tree species (Bouriaud and Popa, 2008); its growth rate increased continuously and remained at a high level even in old individuals compared to Scots pine or Norway spruce. Firs growth was significantly and positively correlated with December temperatures and spring precipitation in April and May (Bouriaud and Popa, 2008). Although growing under the same conditions, European beech and silver fir have shown remarkably different growth patterns over the past half century. While fir has responded positively to recent warming, beech growth has declined at all examined sites, suggesting that fir is less susceptible to warmer and drier conditions than beech (Bošela et al., 2018). Long-term growth patterns and growth-climate sensitivity of fir and beech did not differ significantly between managed and unmanaged forests.

Conclusions

Predicted forest productivity loss is mostly pronounced at the southern limit of beech natural distribution, where drought intensity is expected to increase (Martinez Del Castillo, 2022). Our study confirmed different responses depending on species and location. A more pronounced response of tree growth to climate was observed on the eastern side of the Carpathians, while it was less pronounced or absent at the southern sites. Both beech and fir show better radial growth with higher precipitation in July and slower growth with higher average and maximum temperatures in June of the current year. Fir shows a positive correlation between radial growth and temperature in winter, while beech shows a negative correlation between radial growth and temperature in summer. In 1950, average tree ring widths for fir and beech were largest at southern sites compared to other sites, but after 2016, the increase is smallest at southern sites while it is greatest at northern sites. Despite the adaptive diversity of beech populations, the survival of beech and other temperate tree species in the future is uncertain, as the rate, uniformity, and intensity of climate change vary among different sites. We may expect strong climate future variability in southern forest ecoregion, while northern sites still exhibit stability and structural resistance. Temporal changes in species composition led to minor fluctuations in

stand parameters that do not threaten the long-term coexistence of beech and fir (Petritan et al., 2015). Beech populations at the edge of the species range have great adaptive potential, and their persistence appears to contribute to forest stability throughout Europe, requiring adaptation of forest management and conservation policies (Mátyás et al., 2009; Lefèvre et al., 2014; Fady et al., 2016).

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Climate growth limitations of European beech and silver fir along the Carpathian arc – the recent state and future prospects

KEYWORDS: climate-growth limitation; VS model; Carpathians; climate change; silver fir; European beech

Introduction

Changing temperature and precipitation patterns are shaping tree climate-growth limitations. The influence of climate change affects individual tree species differently (Zang *et al.*, 2014; Kašpar *et al.*, 2021), and varies across extensive geographical regions (Gazol *et al.*, 2015). The Carpathians, a vast mountainous area of Europe, host significant numbers of silver fir (*Abies alba* Mill.) and European beech (*Fagus sylvatica* L.; Kholiavchuk *et al.*, 2024), both of which exhibit distinct climate-growth responses despite sharing similar ecological niches (Paluch, 2007). Our study aims to discern the climate growth limitations of silver fir and European beech, identify the effects of climate change on their growth, and forecast the future growth trajectories of silver fir and European beech across Carpathians. To achieve this, we (i) calculated climate-growth limitations of beech and fir based on recent data, and then (ii) extended the simulations based on a future climate scenario to identify potential effects of climate change on long-term growth trends and climate limitations of both species.

Methods

We selected eight sites along the Carpathian arc at similar elevations and edaphic conditions (Figure 1A), where 14 to 17 mature canopy trees of both species were dendrochronologically sampled and measured. Using the purely climate-driven process-based model (Vaganov-Shashkin process-based model, hereafter VS model, Vaganov *et al.*, 2006), we simulated radial growth and computed growing season variables as well as temperature and moisture limitations (the entire process is schematically captured in Figure 1B-H). Model calibration covered the period from 1985 to 2015. E-OBS data were then used to simulate the period from 1985 to 2022 (Cornes *et al.*, 2018), while the bias-corrected prediction of the RCP 4.5 scenario was utilized for predictions from 2023 to 2050 (Berg *et al.*, 2021).

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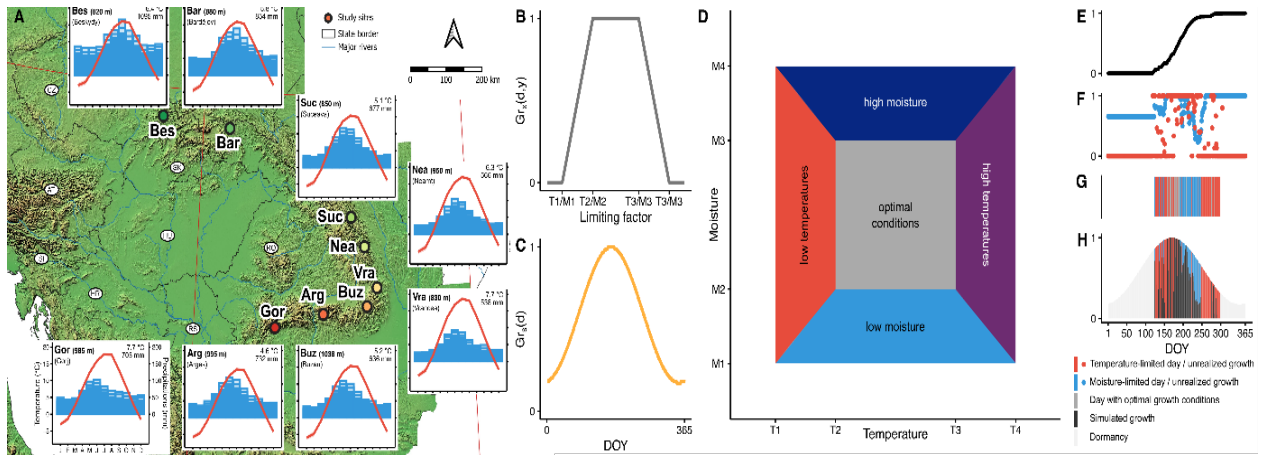


Fig. 1. *A – The study area and climate characteristics of individual study sites. And the methodological approach used in this study for simulating climate-growth limitations. B – the response function's shape depicting the relationship between temperature/precipitation and partial growth response; C – the response function's shape illustrating the relationship between growth rate and day duration; D – computation of specific daily growth rates; E – daily growth rates with emphasis on the predominant limiting factor (low moisture and/or low temperatures; F – representation of the growing season's progression categorized by the dominant limiting factor; G – visualization of tree-ring formation throughout the growing season; H – simulation of realized growth and growth not realized due to insufficient temperature and moisture conditions.*

Results

VS model predicts earlier, but statistically non-significant start of the growing season (Figure 2A) in the future period (2020-2050). However, together with the later cessation of the growing season, the growing season lengths will be significantly ($p < 0.05$) longer in the future (Figure 2B). The proportion of the growing season limited by low temperatures will generally decrease (except sites Vra, Nea and Suc; Figure 2C) in favour of an increase in moisture limitations (Figure 2D), which will significantly ($p < 0.05$) increase at most of the sites. Suppression of the main limiting factor at individual sites will result in the preservation of current growth rates or growth acceleration (Figure 2E).

The observed non-significant change in the growing season's start over both periods, estimated at 1-2 days per decade (Figure 3A). Combined with later cessation, this resulted in a prolongation of the growing season by 3-5 days per decade, with statistically significant trends for both species at all sites ($p < 0.05$; Figure 4B). These trends are mirrored in reductions of the proportion of temperature-limited growing season days (at south-western and northern sites;

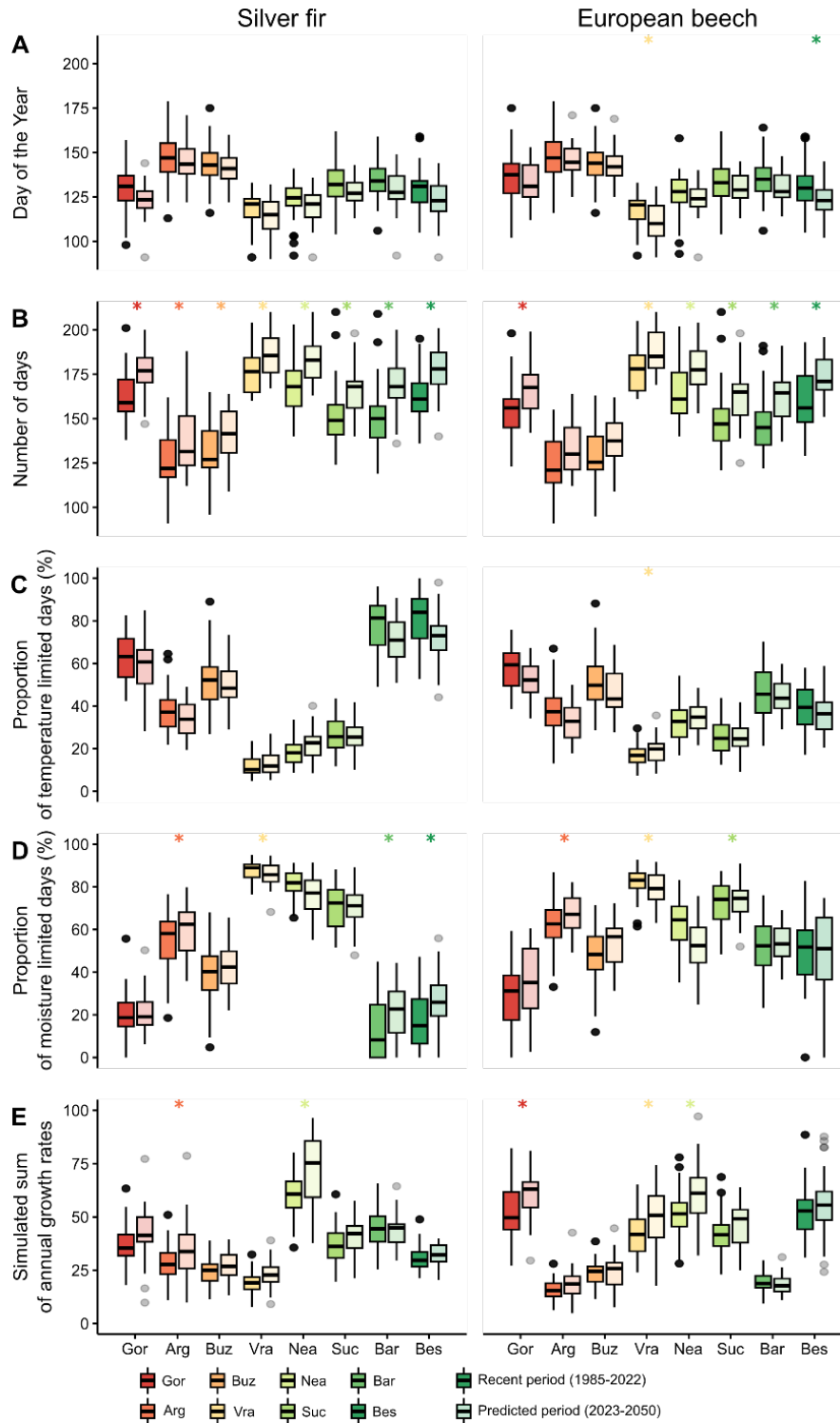


Fig. 2. Growing season parameters and climate growth limitations at individual sites and tree species in the recent and predicted periods. A – start of the growing season; B – duration of the growing season; C – percentage of the growing season limited by temperatures; D – percentage of the growing season limited by moisture conditions; E – simulated growth rates. The boxplots denote 25th, 50th and 75th percentiles. Whiskers illustrate “reasonable” minimum and maximum, and dots represents outliers. For each site, the boxplot with the darker colour depicts the recent period (1985-2022) and the boxplot with the lighter colour the predicted period (2023-2050). Asterisks denote statistically significant differences ($p < 0.05$) between recent and future periods.

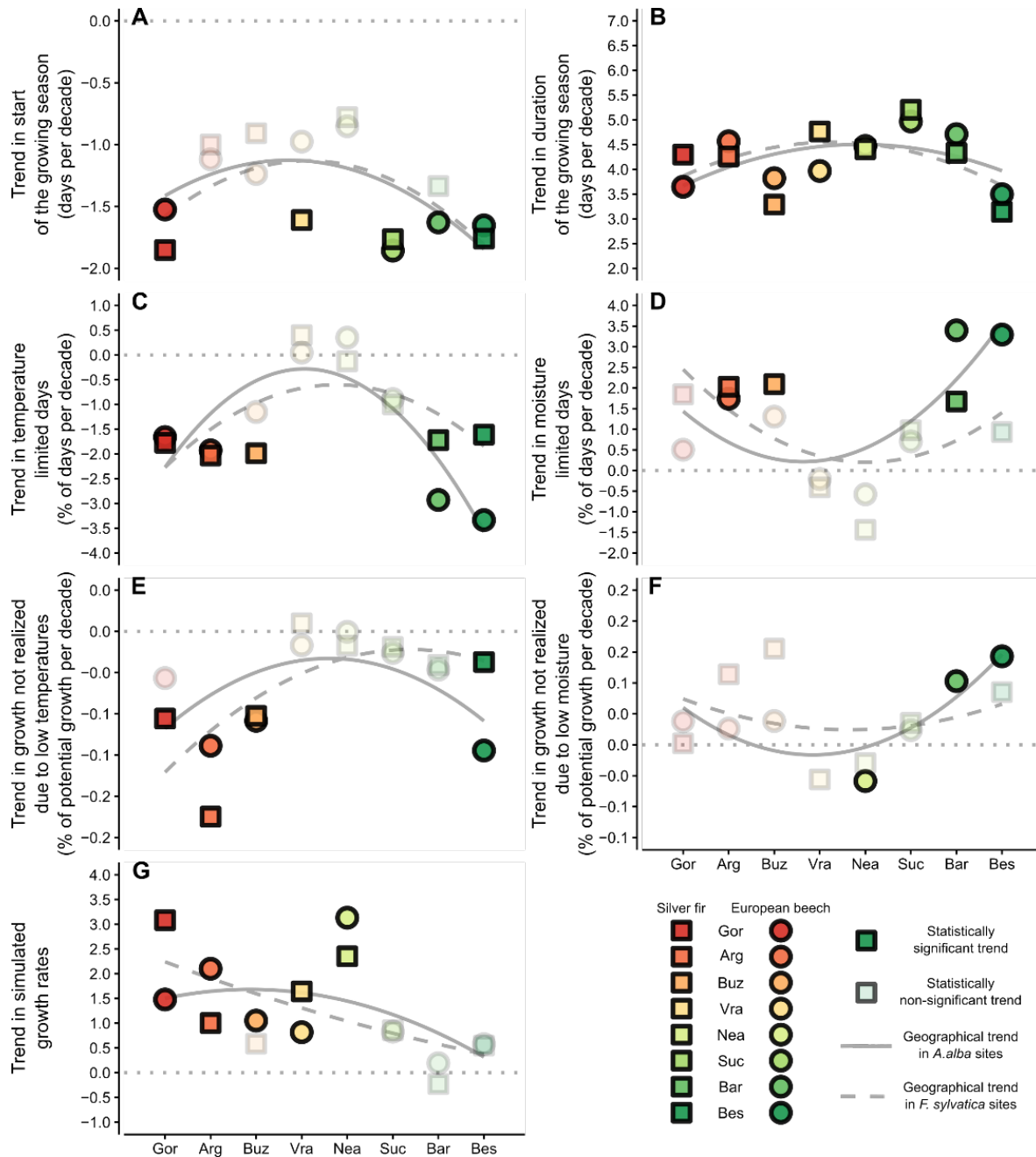


Fig. 3. Trends (slopes of linear regressions in the study period) in growing season parameters and climate-growth limitations of fir and beech at individual sites. A – start of the growing season; B – length of the growing season; C – proportion of the growing season limited by temperatures; D – proportion of the growing season limited by moisture; E – growth not realized due to temperature conditions; F – growth not realized due to moisture conditions; G – simulated growth rates.

Figure 3C). Conversely, limitations caused by insufficient moisture conditions showed a significant increase in the proportion of moisture-limited days (Figure 3D). Similar patterns were detected for growth not realized due to insufficient temperature (Figure 3E) and moisture (Figure 3D) conditions. The highest increase in simulated growth was observed at southern sites, with a gradual decrease towards the north (Figure 4G).

Based on the PCA, individual sites were clustered according to their common climate-growth limitations. For both species, we found (Figure 5A and A8): (i) sites mainly limited by low

temperatures (for fir at the northern sites - Bes, Bar, plus Gor and for *F. sylvatica* Bes and Gor); (ii) sites mainly limited by low moisture (south-eastern sites - Suc, Nea, and Vra); and (iii) sites with mixed limitations (sites close to 0 at both PC axes; mainly southern sites; for fir Arg and Buz and for beech Arg, Buz and Bar. The results of the PCA also confirmed a gradual shift from temperature-limited growth towards limitation by low moisture at the expense of temperature limitation. Finally, the results of the PCA demonstrated that the period 2011-2020 was the driest in the recent period.

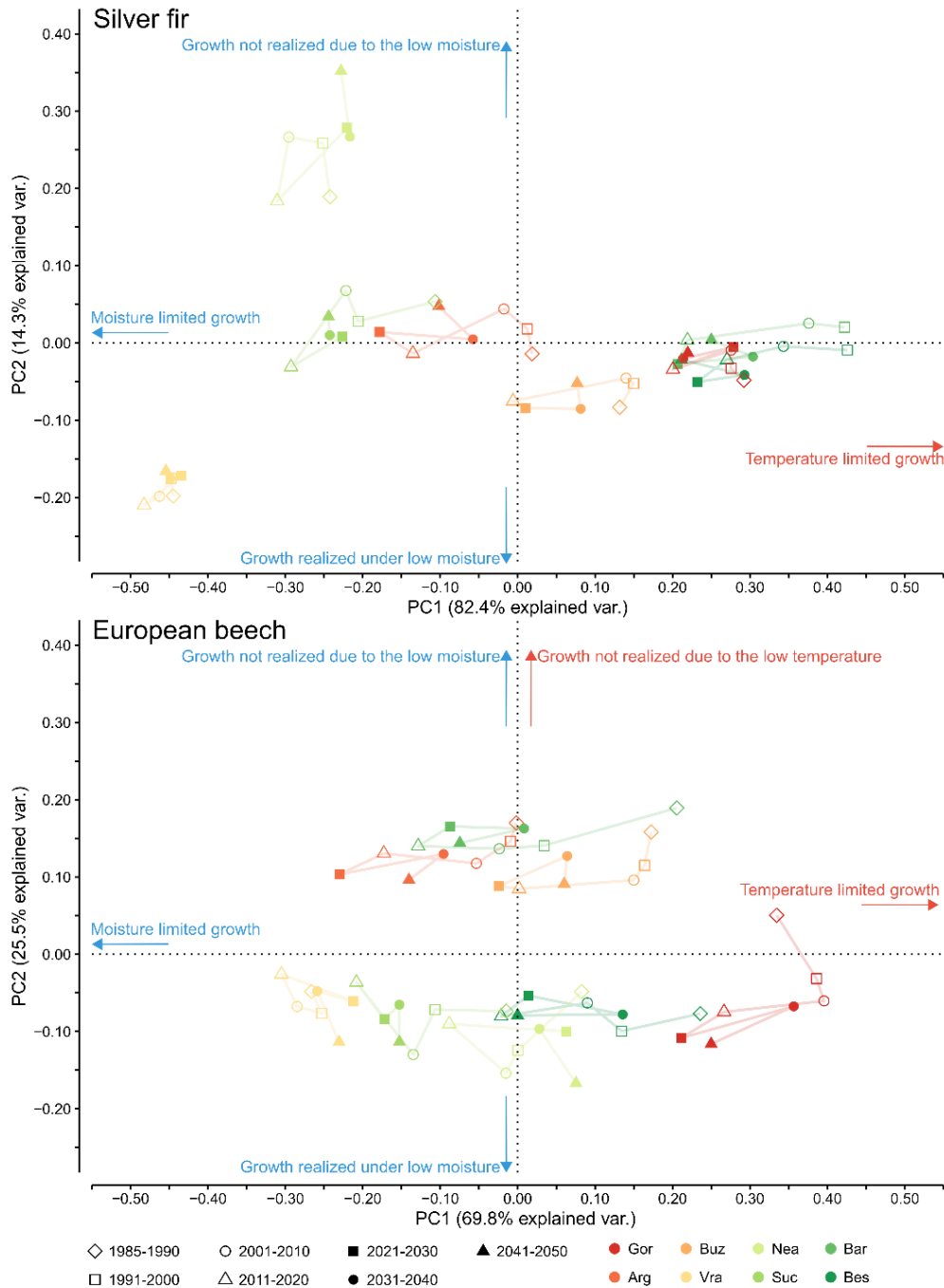


Fig. 4. Principal Component Analysis of growth limitations at investigated sites A – fir and B – beech.

Conclusions

In summary, our results confirmed three distinct regions in the Carpathians, with varying climate-growth limitations: the northern, south-western, and south-eastern areas (Adamič *et al.*, 2023). Northern sites are primarily limited by cold temperatures, southern sites by insufficient moisture, intensifying eastward. The gradual decrease in the main limiting factor results into increased growth rates, suggesting improved growth conditions of silver fir and European beech under RCP 4.5 scenario at elevations above 800 m (Klesse *et al.*, 2024). Nonetheless, under the RCP 4.5 scenario, distinctions among these clusters are anticipated to persist into the future. Our findings highlight site-specific variations in simulated annual growth between the recent and future periods beech consistently exhibited more pronounced moisture limitations across the entire Carpathian gradient (Zang *et al.*, 2014; Kašpar *et al.*, 2021), indicating a potentially heightened susceptibility to future droughts due to its limited growth plasticity compared to fir, which appears to show better adaptability to future conditions, particularly in the northern Carpathians.

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Variability in wood anatomical characteristics in silver fir and European beech at three different sites in the Carpathian Mountains

KEYWORDS: climate change; dendrochronology; radial growth response; wood anatomy.

Introduction

Although the general anatomical features are species-specific and thus genetically determined, their actual characteristics vary in different parts of xylem rings within internally determined limits due to various external factors (Rathgeber 2017). The structural adjustments of wood to environmental cues play a decisive role in defining wood's hydraulic and mechanical properties and, consequently, in tree performance and survival (Chave et al. 2009). In addition to dendrochronology, quantitative wood anatomy has been shown to provide valuable information on how trees adjust their anatomical structure in response to changing environmental conditions (von Arx et al. 2016).

Variability in wood anatomical traits and their relationships with environmental factors have not been analysed in silver fir. However, similar studies have been carried out on other conifer species; Ziaco et al. (2014) investigated the effect of drought on different pine species and found significant effect of precipitation on cell enlargement and thus on the final size of tracheids. Furthermore, Castagneri et al. (2017) found that the effect of temperature and precipitation on cell morphology (i.e. cell lumen size and wall thickness) changes during the growing season. Variability in beech anatomical characteristics has recently been investigated using data from beech provenance trials (Eilmann et al. 2014; Hajek et al. 2016). Eilmann et al. (2014) confirmed that southern beech proveniences respond differently to drought conditions compared to northern proveniences, suggesting genetic control of xylem performance in beech. Hajek et al. (2016) observed that beech responded to drought by adjusting vessel number, but not vessel diameter. Similarly, Prislan et al. (2018) recorded differences in vessel density between sites with different weather conditions, while differences in vessel dimensions were not significant. Arnič et al. (2021) found differences in growth and wood anatomical characteristics of beech growing in different forest sites in Slovenia. They concluded that changes in temperature and precipitation regimes, as predicted by most climate change scenarios, will affect tree ring growth and wood structure in beech.

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The aim of the study was to evaluate the effect of site conditions at three different sites in the Carpathian Mountains on wood anatomical characteristics of European beech and silver fir. We hypothesised that wood anatomical characteristics (i.e. cell size, cell wall thickness, density and distribution of water conducting cells) would differ between the eastern and western populations of fir and beech. The assessment of variability in radial growth and wood anatomical characteristics at the selected sites may be crucial in assessing the range of plasticity in the species under different environmental conditions as a first step in predicting their responses to future climate scenarios.

Material and methods

Site description

In the Carpathians, three sites with mature fir-beech stands located between 830 and 985 m above sea level were selected and analyzed (Table 1). The selected sites were part of seven sites along the Carpathians that we recently studied as part of a dendrochronological analysis (Adamič et al., 2023). Table 2 shows the meteorological data of the selected sites.

Table 1. Locations, forest label, altitude, and coordinates of research site locations.

No.	County	Plot	Altitude (m)	E (DMS)	N (DMS)
A2	Suceava	Frumosu	850	25°40'60.00"	47°28'6.00"
A4	Vrancea	Soveja	830	26°36'14.00"	46° 0'5.00"
A7	Gorj	Tismana	985	22°55'1.00"	45°10'10.00"

Table 2. Average annual air temperature, average air temperature from April to September, total annual precipitation and total precipitation from April to September for selected locations.

No.	County	Average annual air temperature (°C)	Average air temp. April-Sept. (°C)	Total annual precipitation (mm)	Total Apr.-Sept. precipitation (mm)
A2	Suceava	5.4	12.0	738	501
A4	Vrancea	8.3	15.6	603	412
A7	Gorj	4.7	10.7	1073	695

Sample collection and preparation

Samples (cores) of beech and fir were collected for quantitative wood anatomy analysis at the selected locations. All sampled trees were healthy trees with no visible signs of stem damage or any kind of declining tree vitality. The samples were prepared for observations under a light microscope according to the protocol suggested by von Arx et al. (2016); i.e. each core was split into sub-samples of similar length to fit on the object glass. From each sub-sample 15 to 20 μm thick transverse sections were cut with a sledge-microtome and then stained with safranin. High-resolution images of the sections were prepared using a light microscope and digital camera. The measurements of the sections were performed with image analysis software Image Pro Plus and ROXAS (Prendin et al. 2017; von Arx et al. 2016), which provide cell dimensions (e.g. lumen size, cell wall thickness) and relative position within the dated growth ring for all selected cells (Castagneri et al., 2017). Chronologies of the following parameters were then established; for European beech and silver fir (1) mean lumen area of

vessels/tracheids (MLA), (2) tracheid or vessel density (CD) as the number of tracheids/vessels per squared mm, and (3) relative conductive area (RCTA) representing the percentage of cumulative tracheid/vessel lumen area within the measured area. In addition to the above-mentioned wood anatomical characteristics, chronologies of mean thickness of tangential cell walls (CWTTAN) were also established for silver fir.

Statistical analysis

Raw chronologies were used to assess differences in wood anatomical characteristics between sites. The quality of site chronologies was described with common descriptive statistics, such as expressed population signal (EPS), mean inter-series correlation (\bar{r}), and Gleichlaufigkeit (%GLK) (Cook and Kairiukstis, 1990). To test the hypothesis of equal means of tree-ring characteristics, i.e., TRW, MLA, CD, RCTA, MLA and CWTTAN we used parametric and non-parametric statistical tests. Repeated measures (rm) ANOVA was used when assumptions for parametric tests were met, while in other cases, the nonparametric Friedman test was applied.

Results and discussion

For silver fir and European beech, the local chronologies of wood anatomical characteristics at sites A2, A4 and A7 ranged from 40 to 49 and 39 to 42 years, respectively (Table 3). The widest mean TRW in silver fir for the 1976–2016 period was measured at A2 ($4654.9 \pm 916.3 \mu\text{m}$), followed by A4 ($2262.8 \pm 913.0 \mu\text{m}$) and A7 ($1159.4 \pm 322.5 \mu\text{m}$); the differences were statistically significant (Figure 1A, Figure 2A). Mean TRW for European beech was significantly lower at A2 ($2638.5 \pm 518.1 \mu\text{m}$) compared to silver fir while at A4 ($2301.6 \pm 780.9 \mu\text{m}$) and A7 ($1340.8 \pm 600.1 \mu\text{m}$), they were slightly wider (Figure 1B, Figure 3A).

MLA values in silver fir were similar at A2 and A7, but significantly lower at site A4 (Figure 2B). Similar observations were also made for European beech, where similar MLA values were observed at A2 and A7, while the values at A4 were significantly higher (Figure 3B).

The measured wood anatomical features CD and RCTA were significantly different between all sites in case of European beech (Figures 3C–D); the highest values were observed at site A7 and the lowest at site A2 (Figure 1H–F, Figures 3C–D). In the case of silver fir, different values between sites were observed for CD; the highest values at A4 and the lowest at A7. RCTA values in silver fir were similar at site A4 and A7, yet significantly higher at A2. Mean tangential cell wall thickness (CWTTAN) in silver fir was highest at A7, and significantly lower at A2 and A4 (Figure 2E).

Our results show differences in wood anatomical characteristics (e.g. TRW, CD, RCTA and MLA) at the selected sites for both analysed species, thus confirming our hypothesis.

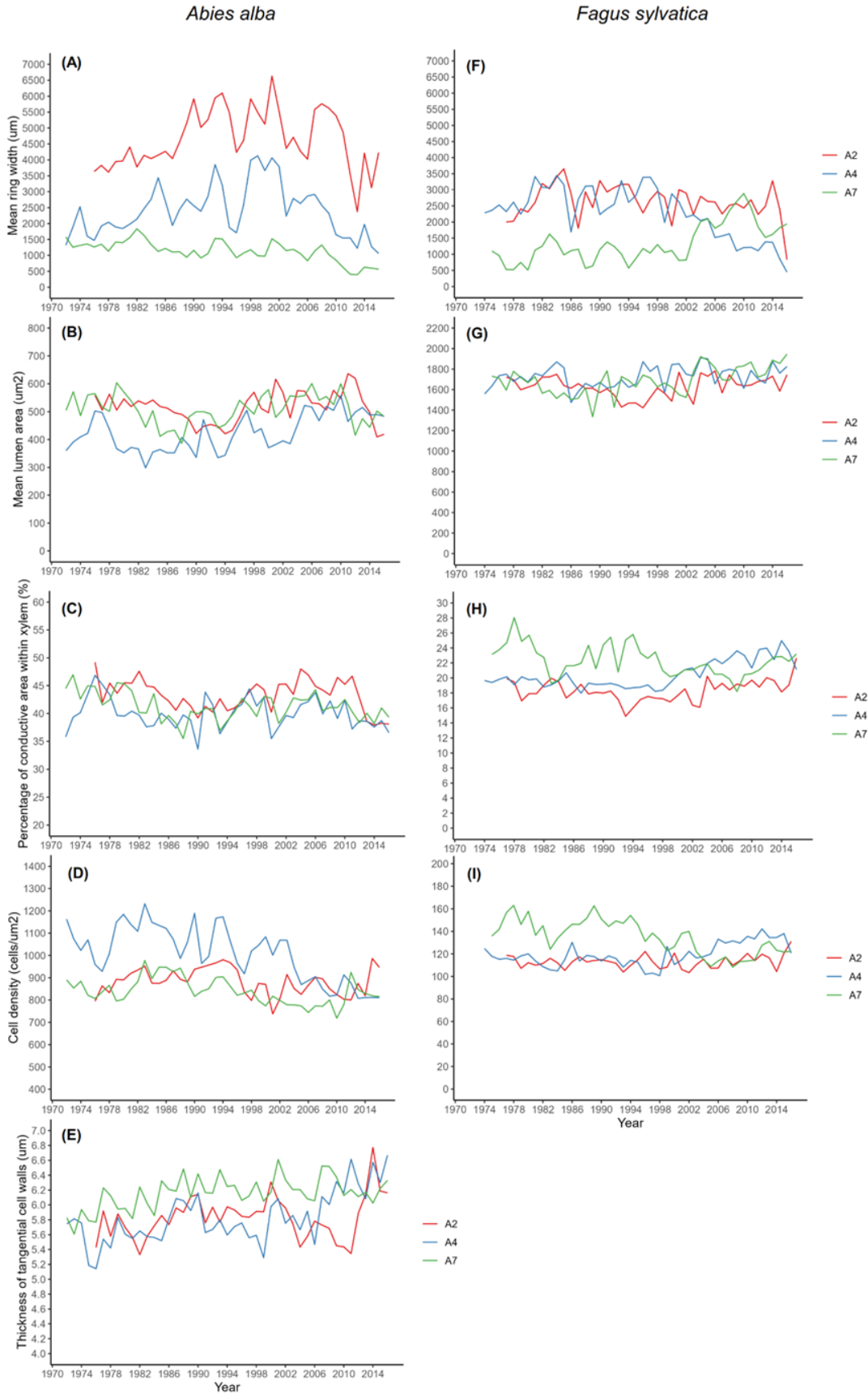


Fig. 1. Chronologies of wood anatomical characteristics in silver fir and European beech at sites Suceava (A2), Vrancea (A4) and Gorj (A7).

Table 3. Tree ring width and wood anatomy chronologies and descriptive statistics: mean values, standard deviation (SD), first-order autocorrelation (AC1), Gleichläufigkeit coefficient (%GLK), mean interseries correlation (rbar), and expressed population signal (EPS) for silver fir (ABAL) and European beech (FASY) at the selected sites; Suceava (A2), Vrancea (A4) and Gorj (A7).

Species	Site	Parameter	Start year	End year	Mean	SD	AC1	%GLK	rbar	EPS
ABAL	A2	TRW	1976	2016	4654,9	916,3	0.706	63	0.146	0.406
		RCTA	1976	2016	43,3	2,8	0.556	53	0.066	0.22
		CD	1976	2016	882,9	59,3	0.510	51	0.037	0.169
		MLA	1976	2016	515,5	56,1	0.568	51	0.019	0.072
		CWTTAN	1976	2016	5,8	0,3	0.520	50	0.09	0.285
A4	A4	TRW	1967	2016	2262,8	913,0	0.764	65	0.308	0.727
		RCTA	1967	2016	39,5	3,5	0.485	59	0.131	0.475
		CD	1967	2016	1017,1	121,3	0.680	57	0.381	0.787
		MLA	1967	2016	417,5	69,2	0.583	59	0.295	0.715
		CWTTAN	1967	2016	5,8	0,4	0.535	53	0.251	0.626
A7	A7	TRW	1968	2016	1159,4	322,5	0.751	65	0.333	0.749
		RCTA	1968	2016	41,7	2,8	0.365	55	0.229	0.598
		CD	1968	2016	836,5	59,4	0.548	47	0.115	0.395
		MLA	1968	2016	517,1	59,5	0.475	53	0.23	0.599
		CWTTAN	1968	2016	6,1	0,3	0.329	55	0.082	0.31
FASY	A2	TRW	1977	2016	2638,5	518,1	0.421	67	0.252	0.628
		RCTA	1977	2016	18,3	1,4	0.493	57	0.176	0.516
		CD	1977	2016	113,1	5,8	0.344	58	0.07	0.272
		MLA	1977	2016	1627,4	98,8	0.439	51	0.084	0.314
A4	A4	TRW	1974	2016	2301,6	780,9	0.662	58	0.553	0.881
		RCTA	1974	2016	20,5	1,8	0.532	47	0.194	0.59
		CD	1974	2016	119,4	10,3	0.545	55	0.317	0.736
		MLA	1974	2016	1726,8	102,7	0.396	57	0.106	0.415
A7	A7	TRW	1975	2016	1340,8	600,1	0.698	60	0.527	0.87
		RCTA	1975	2016	22,3	2,1	0.577	53	0.127	0.467
		CD	1975	2016	134,8	15,3	0.581	59	0.509	0.861
		MLA	1975	2016	1689,5	135,5	0.461	58	0.232	0.644

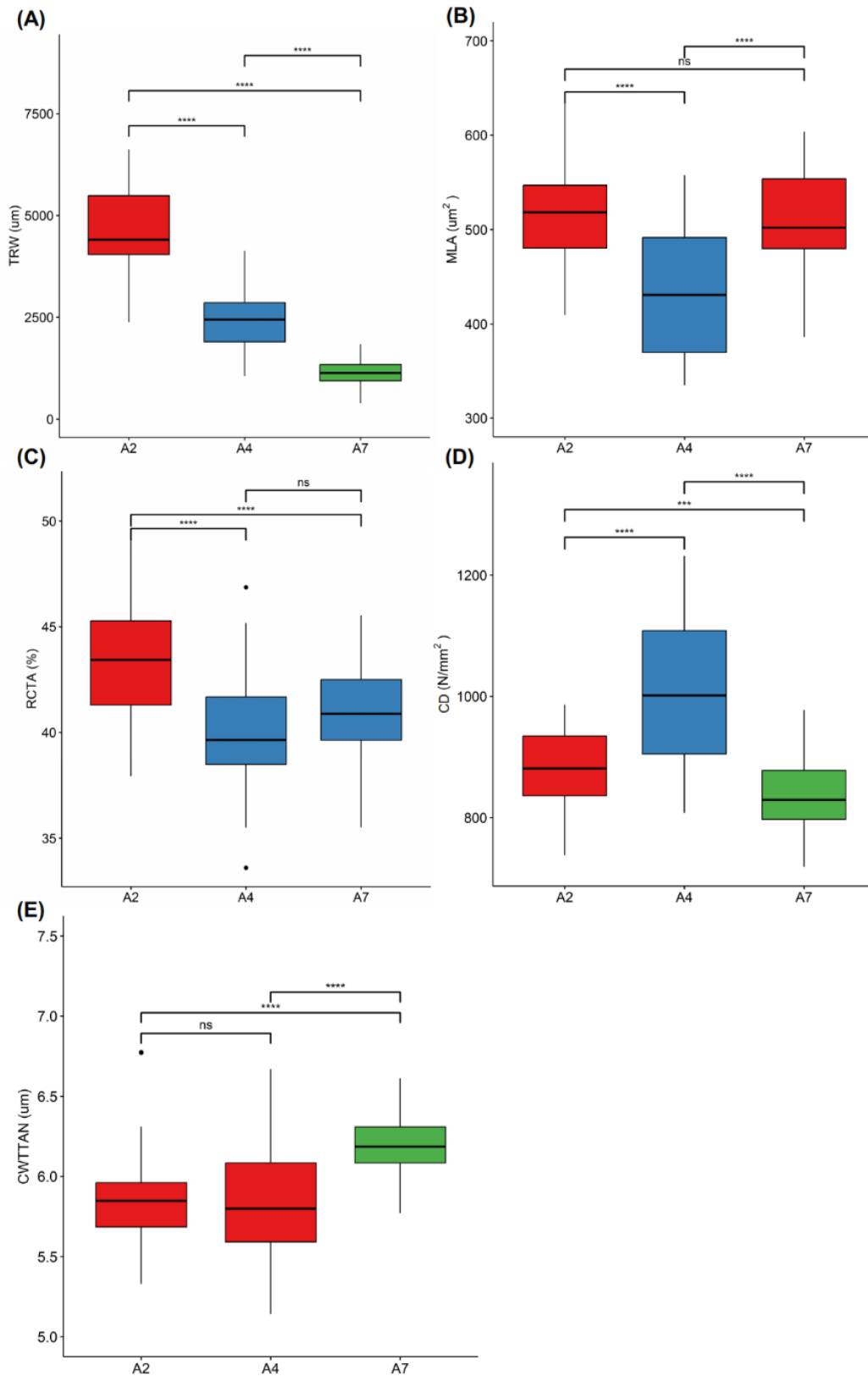


Fig. 2. Differences among the sites Suceava (A2), Vrancea (A4) and Gorj (A7) in (A) tree ring width (MRW), (B) mean vessel area (MVA), (C) relative conductive area (RCTA), (D) cell density (CD) and (E) tangential cell wall thickness (CWTTAN) in silver fir analyzed by rm-ANOVA or the Friedman test. The significance of differences in tree ring characteristics between sites is marked by ns-not significant. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, and **** $p < 0.0001$.

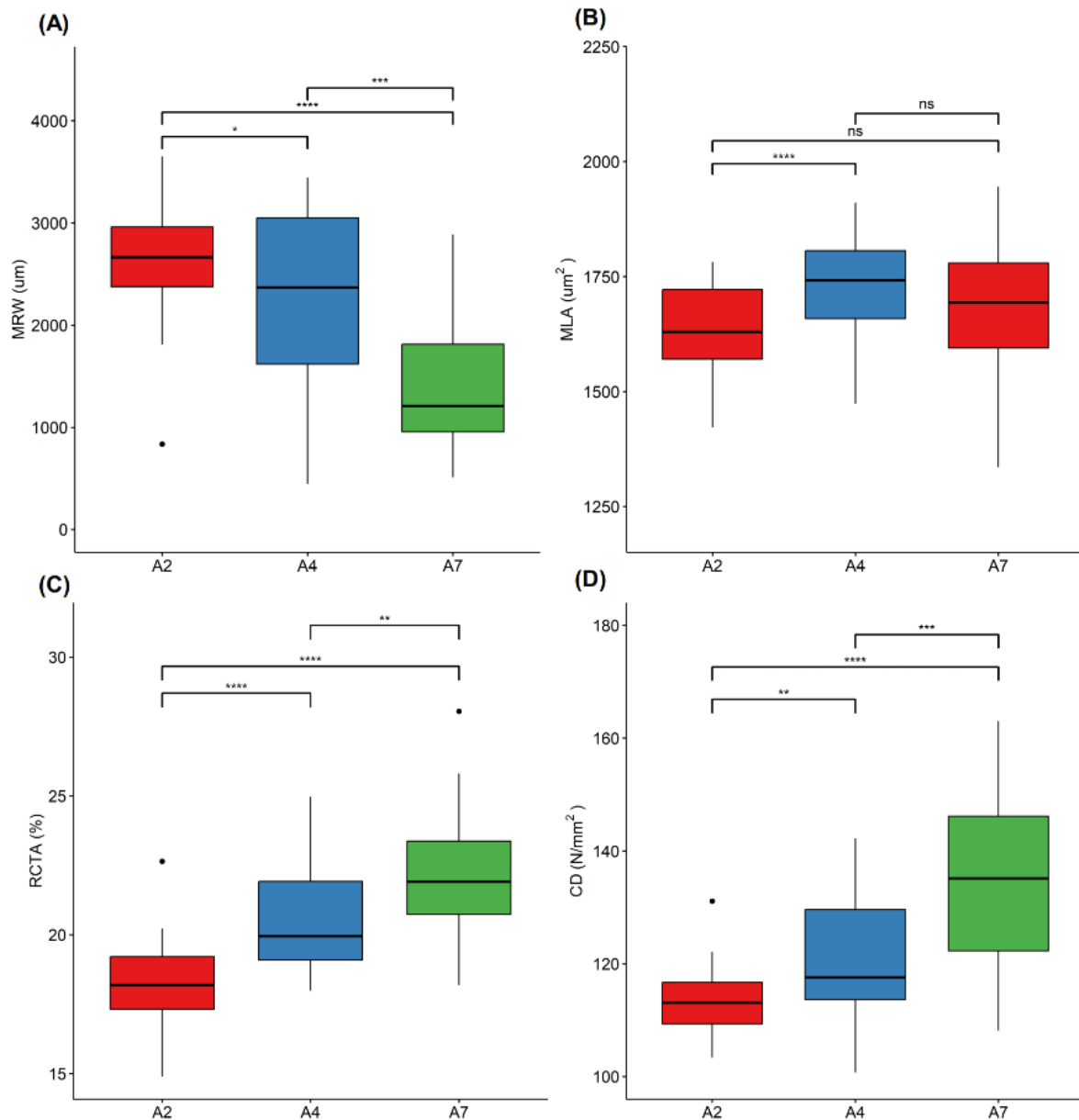


Fig. 3. Differences among the sites Suceava (A2), Vrancea (A4) and Gorj (A7) in (A) mean ring width (MRW), (B) mean vessel area (MVA), (C) relative conductive area (RCTA) and vessel density (CD) in European beech analyzed by *rm*-ANOVA or the Friedman test. The significance of differences in tree ring characteristics between sites is marked by *ns*-not significant. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, and **** $p < 0.0001$.

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Monitoring forest response using Sentinel-2 observations to climatic factors along the Carpathian Mountains

KEYWORDS: Sentinel-2 time-series, forest canopy, precipitation, temperature, lagging effects

Introduction

Vegetation is often seen as a biological indicator of climate change. Although various factors such as temperature, water, light and nutrients influence vegetation dynamics and affect plant physiology, phenology, growth rates and water availability, the study of the direct and indirect effects of climatic conditions on vegetation development is complex (Mehmood, 2024). Forests disturbed by climate-related changes or disturbances, such as drought and frost-related stress, affect the susceptibility of trees to pests and diseases and also influence species competition and their adaptive strategies – processes that are essential for effective understanding and management of ecosystems (Čater, 2024; Adamič, 2023).

Satellite-based vegetation observation enables continuous monitoring of forest dynamics, ecosystem transitions and changes in composition. By analysing long-term satellite data together with climate variables, we can gain valuable insights into spatio-temporal vegetation patterns and their relationship to climate factors (Mehmood, 2024).

In this study, we examine the Sentinel-2 satellite vegetation indicators to observe satellite signal responses from eight selected observation plots along the Carpathian Mountains gradient for similarities and differences. We compare the satellite-based vegetation responses using six vegetation indicators (NDVI, S2REP, kNDVI, EVI, MSAVI, NDWI) from 2017 to 2022 with meteorological data on precipitation and temperature, paying particular attention to possible time-delayed effects in the observed Sentinel-2 time series.

Material and methods

Study area. The Carpathian Mountains sweep in a wide, crescent-shaped arc about 1,450 kilometers in a north-south direction, have a difference of almost 300 kilometers between their western and eastern stretch and cover about 200,000 square kilometers. The Carpathians are geologically diverse in their vast area and consist of several mountain ranges with different relief forms and include several different ecosystems such as mixed forests, alpine meadows

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and wetlands. The climate in the Carpathians is diverse and is characterised by cool, humid conditions in the higher altitudes and a warmer, continental climate in the foothills, which contributes to the rich biodiversity and pronounced seasonal variations in the region. Precipitation patterns and mean annual and monthly air temperatures vary mainly according to altitude above sea level, but not to the same extent and patterns (Kondracki, 2024).

The study analyzed eight forest sites, distributed along the Carpathian arc. These sites are permanent research plots, situated at elevations between 820 and 1038 meters above sea level, consisted of mature beech and fir trees (Čater et al., 2024). Two sites are old-grown reserves (Zagon and Salajka), while the other sites are considered managed forests (Figure 1).



Fig. 1. Location of research sites. Eight sites (shown in yellow color) with mature fir–beech forest stands at an altitude between 820 and 1038 m above sea level were selected and analysed along the Carpathian Mountains at a north-south distance of more than 1500 km and an east-west distance of 300 km. The southern locations, Tismana, Arefu and Zagon, are situated at higher altitudes. Bing aerial imagery in the background.

Satellite-based vegetation indicators. Sentinel-2 time series for six vegetation indicators (NDVI – Normalised Difference Vegetation Index, S2REP – Sentinel-2 Red Edge Position, kNDVI – kernel NDVI, EVI – Enhanced Vegetation Index, MSAVI – Modified Soil Adjusted VI, NDWI – Normalised Difference Water Index) from 2017 to 2022 were created for each observation site with surroundings. The preparation included the elimination of clouds, shadows and non-valid observations using the s2cloudless algorithm. The data sets were also smoothed using the Savitzky-Golay temporal filter to reduce noise while preserving the satellite signal trend.

Sentinel-2 spectral bands have spatial resolution of 10, 20 and 60 m, time series were prepared in 10 m resolution, and have a revisit frequency of 5 days at the Equator.

Meteo datasets. Daily gridded meteorological temperature and precipitation data from Copernicus E-OBS were used. The time series were processed at a spatial resolution of 1 km (Harris, 2020). Different time intervals for precipitation summaries and temperature averages were used in the analyses.

Time-lagging analyses. Time-delayed effects occur when an event at one point in time impacts a variable of interest later (Nicolau, 2024). For example, persistent drought in spring or heavy rain during the flowering period can severely affect tree development in later stages or influence their condition in the next season. While seasonal comparisons reveal trend development, understanding forest responses through satellite observations requires exploring how precipitation and temperature influence seasonal forest growth and how these patterns appear in satellite vegetation indicators.

In the study, we focused on the spatio-temporal dynamics of various vegetation indicators. NDVI, kNDVI, EVI and S2REP are indicators of vegetation vigour, condition and chlorophyll content. They were selected because they consist of the inclusion of different spectral bands so that the variability of response in different spectral regions can be observed (Govender, 2009). MSAVI is an alternative to assess the state of vegetation when the soil surface is not completely covered with vegetation. NDWI is used to monitor changes in water content and estimates the amount of moisture in the vegetation, which is used to monitor changes in water content in the leaves.

The research methodology involves the analysis of satellite imagery and meteorological datasets to investigate the interactions between selected vegetation indicators (VIs), total precipitation (P) and temperature (T). We created several time-lagged collections, where different time periods of the meteorological summaries are taken prior to the date of satellite acquisition. The previous P and T values (*lag*) that are within a certain time difference (in days, $t - lag$) from each VI (in time t), were linked to the current VI value and correlation coefficients were calculated. To assess the possibility that perhaps precipitation in the month(s) prior to the observed VI is relevant, we introduce further lagged periods in the interpretation of the vegetation response observed in the VI time series by introducing progressively longer lags back up to 200 days.

Since the meteorological datasets are available at a raw resolution of 1 km, we have also investigated the strength of these relationships using the different extent areas around the site in the VIs time series averages, i.e. 30, 50, 100, 210, 250 and 1010 m² respectively. Higher positive values indicate higher correlation between the elements of the dataset, and lower negative values indicate the opposite.

The aim of this approach was:

- to value seasonal forest stand satellite based observation with regard to meteorological parameters and geographical location,
- to explore the potential of Sentinel-2 data to detect spatio-temporal differences in forest response between site locations and tree species.

Results

Comparison of annual VIs time series, monthly precipitation summaries and temperature for each study site revealed years or locations with some deviations (Figure 2).

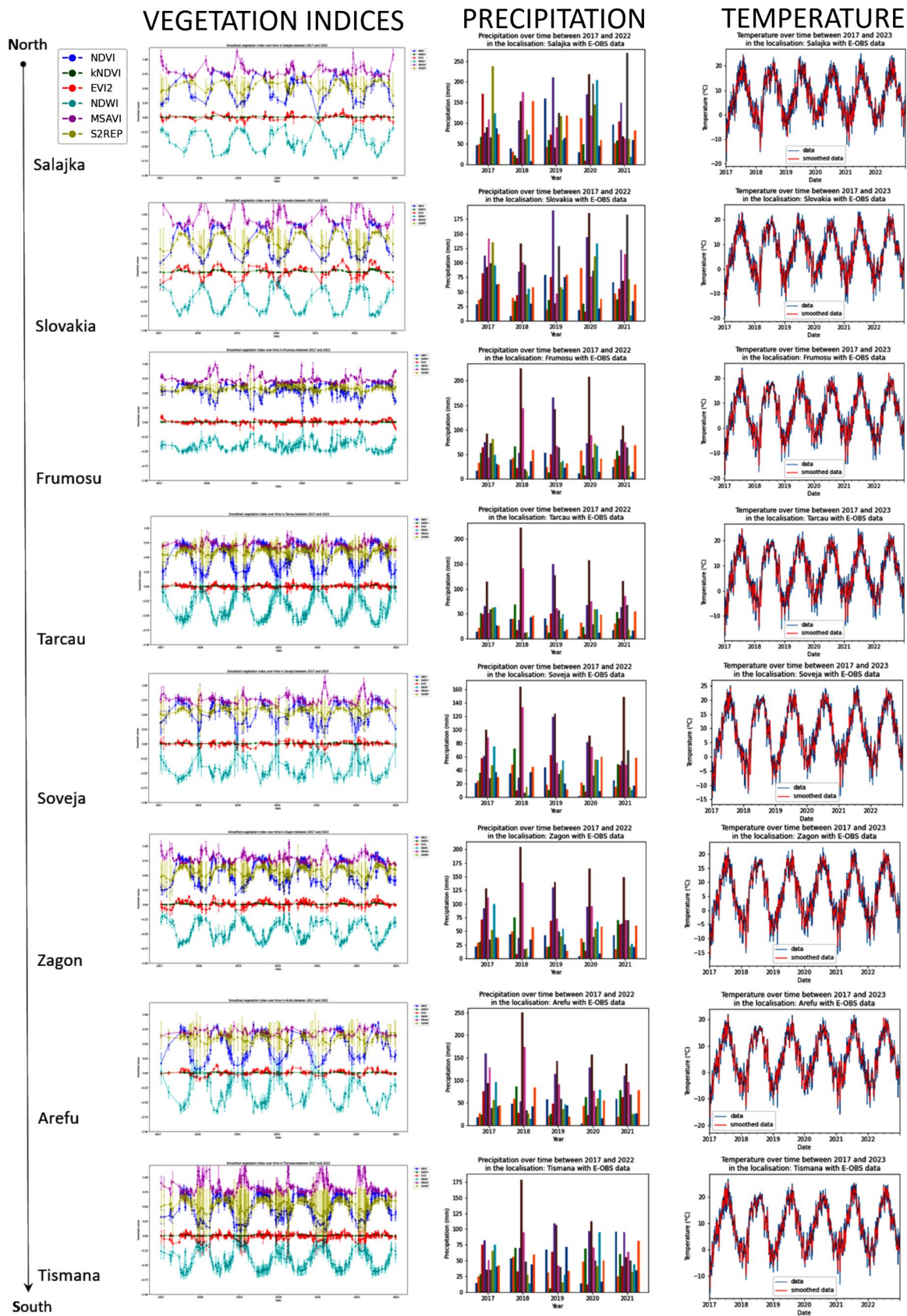


Fig. 2. Sentinel-2 vegetation indices (VIs) time series, precipitation (P) and temperature (T) regime obtained with Copernicus E-OBS meteorological data at research sites for the period 2017 – 2022 in columns. Research sites locations from north to south are presented in rows.

The year with the highest summer precipitation and lower average temperatures is 2018; this observation is slightly less pronounced for the two northernmost locations, Salajka and Slovakia. Different amounts and seasonal precipitation regimes are expressed between the research sites, decreasing slightly towards the south and also over time until 2021.

The preprocessing of Sentinel-2 time series reduced the frequency or density of vegetation indices to some degree. On average half of satellite observations are eliminated due to cloud and cloud shadow masking and limiting the time-series to vegetation season between April to November. The density of valid observations for selected study sites varies between sites and years, but likely as there is no association between precipitation amount and VI density (see year 2017 for Arefu and Tismana compared to other years).

There is a different response in vegetation indicators between sites. Larger differences are observed for MSAVI and NDWI, while the vegetation condition-orientated NDVI and kNDVI are more stable and comparable across the seasons.

Direct correlations between VIs and precipitation and temperature were rather insignificant to allow a meaningful interpretation of forest response. Nevertheless, stronger correlations between VIs and temperature and weaker correlations between VIs and precipitation were generally observed. There are no significant differences in these correlations (sign and strength) between the eight locations observed (Figure 3).

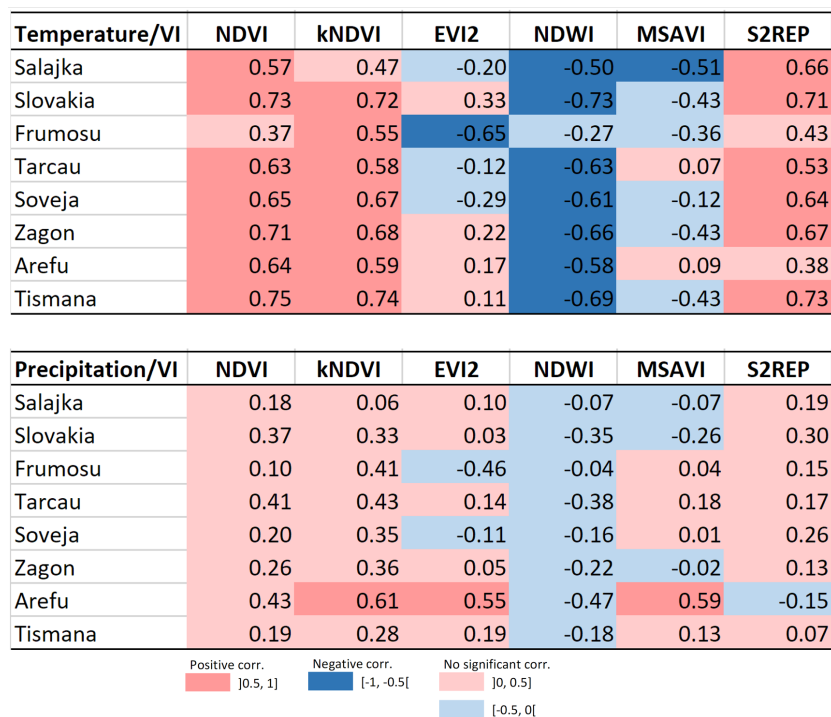


Fig. 3. Correlation coefficients between vegetation indices and temperature and precipitation during the growing season. The monthly precipitation total, the monthly mean temperature and the monthly mean vegetation index were used to calculate the correlation, taking into account the period from April to November.

T and VIs: A strong positive correlation was found for NDVI, kNDVI, S2REP, indicating that these VIs tend to increase with increasing T, suggesting that temperature influences the improvement of forest health, greenness, vigour and chlorophyll. For NDWI, there is a strong negative correlation, suggesting that NDWI decreases with increasing T, which is due to

decreased water availability and increased evapotranspiration. For MSAVI and EVI2, the correlation signs are mixed and less significant.

P and VIs: A mostly weak positive correlation was found for NDVI, kNDVI and S2REP, indicating that a higher P value generally leads to a higher VI value and thus to an improvement in the health and greenness of the forest. For NDWI, there is a moderately negative correlation, suggesting that NDWI decreases rather unusually with increasing P value, indicating that the water cycle of a forest is a complex system. For MSAVI, EVI2, similar to T, the correlation signs are mixed and less significant.

The inclusion of different intervals of previous precipitation summaries and temperature average in correlation analyses with VIs revealed several interesting relationships. To illustrate this on temperature examination, for each data set for which we know the value of the vegetation indices, we take the temperature on the same day and calculate the correlation and the average temperature on the same day + 9 days before (i.e. a total of a 10-day window) and then the same for 20, 30, 40... and 90 days and calculate the correlations. The results for the previous temperature conditions (Table 1) indicate that the NDVI correlates strongly positively and EVI2 strongly negatively with previous temperature conditions of up to one month. Shorter previous temperature conditions of one to three weeks seem to correlate well with the NDWI. For other VIs, a greater diversity is observed and the correlations are weaker.

Table 1. Maximum correlation and associated prior temporal window size in days between temperature and VIs for each index and location.

Site location	NDVI		kNDVI		EVI2		S2REP		MSAVI		NDWI	
	Corr.	Days	Corr.	Days	Corr.	Days	Corr.	Days	Corr.	Days	Corr.	Days
Salajka	0.88	24	0.78	40	-0.82	24	0.47	31	-0.66	7	0.74	15
Slovakia	0.93	29	0.90	51	-0.91	29	0.77	16	-0.78	16	0.79	20
Frumosu	0.67	1	0.68	90	-0.60	1	-0.34	22	-0.62	2	0.79	20
Tarcau	0.88	17	0.56	90	-0.86	7	0.38	20	-0.41	90	0.73	6
Soveja	0.86	31	0.62	90	-0.82	17	0.20	66	-0.40	90	0.77	6
Zagon	0.90	27	0.77	71	-0.88	27	0.68	48	-0.59	90	0.77	16
Arefu	0.88	9	0.61	90	-0.84	8	0.63	16	-0.39	90	0.74	8
Tismana	0.91	27	0.80	53	-0.87	10	0.65	48	-0.65	84	0.80	14

Various intervals of previous precipitation summaries in correlation analyses with VIs are shown in Figure 4. For NDVI, kNDVI and S2REP, the correlation increases with the size of the time window, consistently in all cases and at all locations. This suggests that moisture conditions up to three months in the past may have an influence on the state of the vegetation canopy condition as was observed for these satellite vegetation indicators. EVI also follows this correlation dynamic, but less consistently and also varies between sites. NDWI and MSAVI seem to have an opposite relationship. Both show a negative correlation with increasing strength up to a period of three months or even longer, and are moderately consistent at all sites.

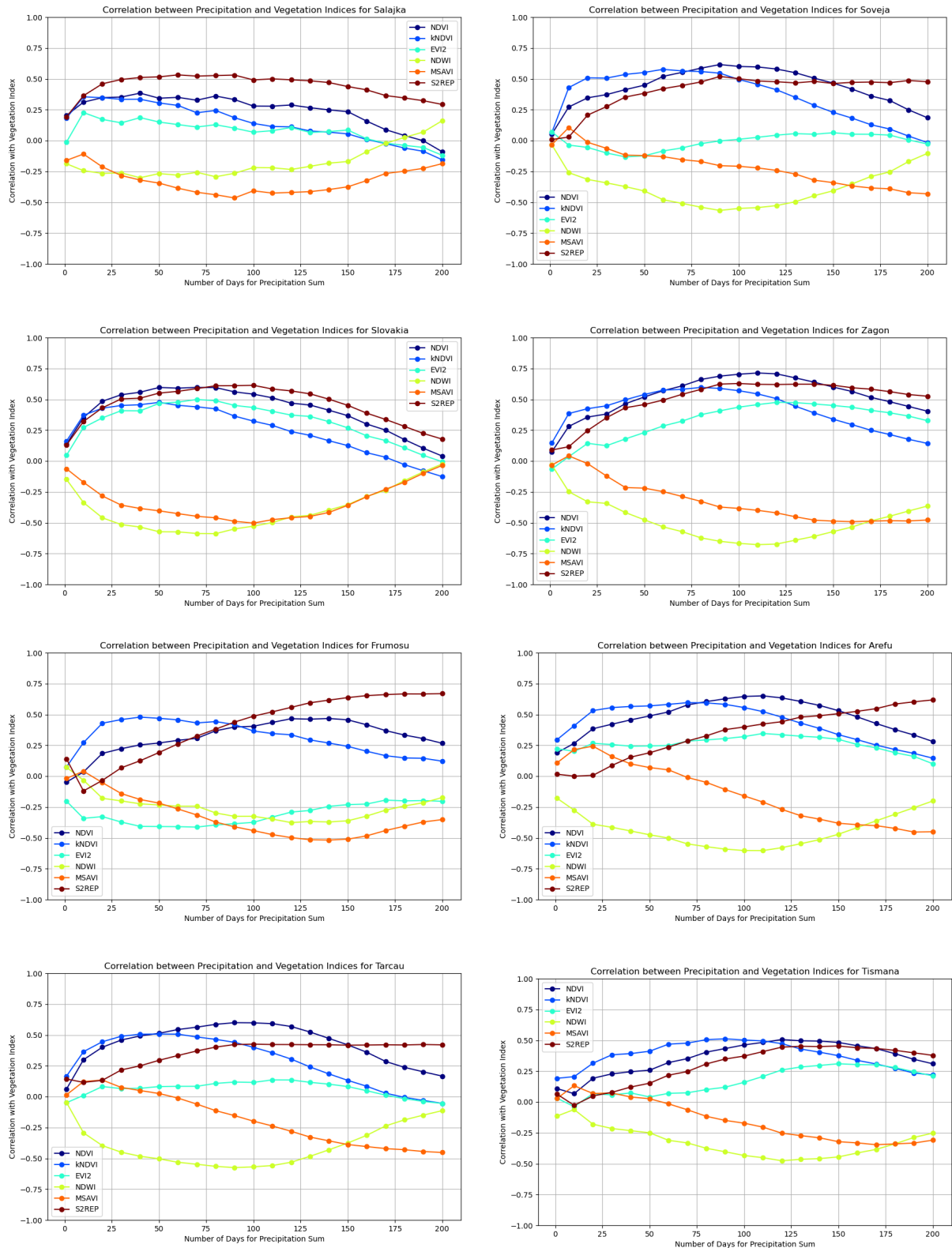


Fig. 4. Correlation (vertically) and associated size of the previous time window in days (horizontally) between the precipitation summary and the VIs for each index (colored lines). Eight charts represent eight study locations from north to south, continuing in two columns.

Since the spatial resolution of the meteorological data is rather coarse (1 km) and the satellite vegetation indicators have a resolution of 10 m, we were also interested in how the size of the area influences these correlations. The larger the area, the greater the mix of tree species and forest stand structures is averaged into correlation analyses. In general, the correlations between precipitation and VIs were lowest at larger extents of 1 km². This was true for the NDVI for most locations except Frumosu, Soveja and Tismana. We had expected the correlations to be more pronounced for smaller areas where forest cover is more homogeneous, but the results are not clearly substantiated and consistent between locations.

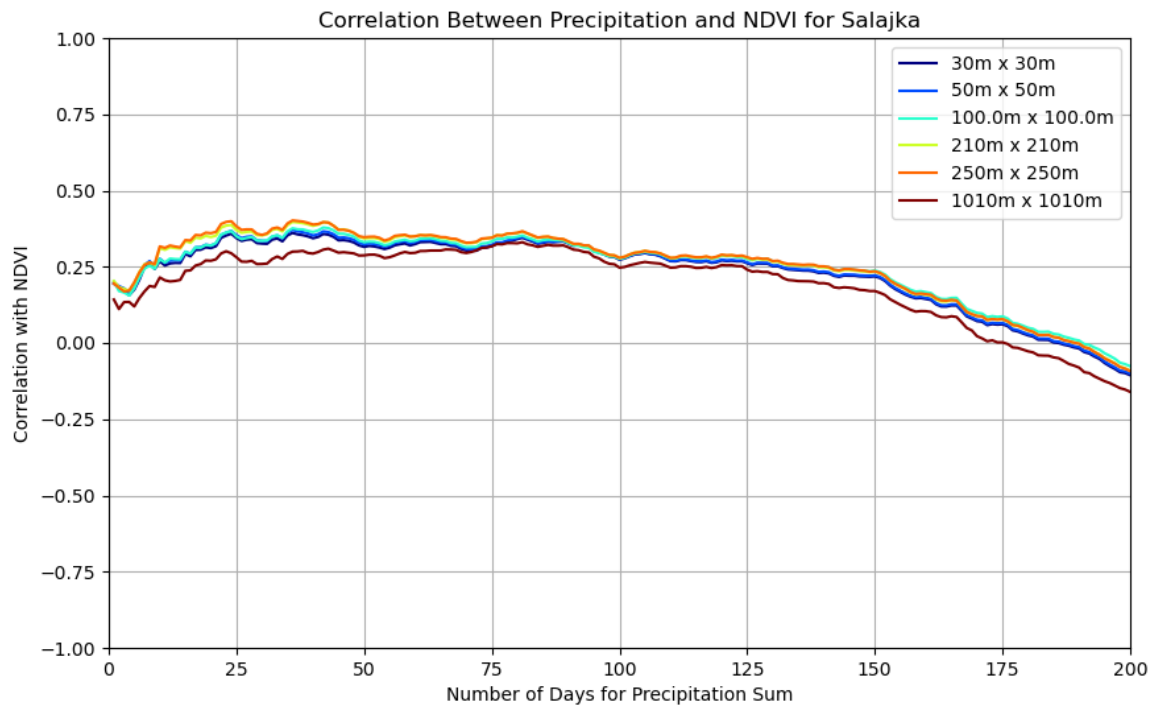


Fig. 5 Study of different area sizes in precipitation and VI correlation analysis. The example is shown for the Salajka site and the previous moisture condition on canopy response in the NDVI development.

Conclusion

Understanding the intricate relationship between climate variables and satellite-derived vegetation indices is essential for effective ecosystem understanding and management. Our experiments were designed to address the question of whether trees as observed with satellite vegetation indicators along the Carpathian Mountains respond similarly to meteorological data. Therefore, the correlation coefficients between Sentinel-2 satellite derived vegetation indicators (VIs) and precipitation and temperature were analysed. Direct (date to date) correlations indicate that the correlation between VIs and temperature is more pronounced and that the correlation between VIs and precipitation is weak and less significant. However, since forest parameters observed using vegetation/soil/moisture indices might respond with delay to meteorological parameters, we also explored the relationship between Sentinel-2 satellite vegetation indicators and precipitation and temperature at multiple time steps using a correlation coefficients providing association strengths and tested for possible time-lagged effects. By analysing the time series lag, we found that the preceding precipitation can contribute to the correlation of vegetation indicators up to three months, while the preceding average temperature contributes in a shorter time, for example for the NDVI within one month.

The interpretation of the various vegetation indicators in comparison to meteorological parameters requires further testing in which field data and phenological characteristics of the site as well as canopy structure and other environmental parameters should be examined and considered. The dependence of the satellite-derived vegetation response on meteorological factors should also be tested with other metrics and models, e.g. time-warping models, before drawing firm conclusions for locations along the Carpathian gradient.

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Analysis of forest canopy land surface temperature along the Carpathian Mountains over the last two decades

KEYWORDS: thermal remote sensing, Landsat, forest canopy

Introduction

The application of satellite thermal remote sensing to the analysis of forest canopies can provide valuable insights into forest health and dynamics. By measuring temperature variations within forest canopies, satellite thermal imagery can help identify stressed areas caused by factors such as disease, drought, canopy moisture levels, or pest infestations. Forest canopy temperature is closely correlated with air temperature and follows similar seasonal trends (Guo et al. 2023), thereby complementing forest phenology analysis (Smigaj et al. 2024).

The Carpathian Mountains, spanning Central and Eastern Europe, play a crucial role in maintaining regional biodiversity, regulating climate, and providing ecological services. This study utilizes Landsat satellite (NASA) thermal time-series data to enhance the current analysis of Carpathian forest phenology from the project with observational data, offering reliable information on land surface temperature (LST) trends in the forest canopy.

Methods

The study examined eight forest sites with the area of 25 ha each, distributed along the Carpathian arc to allow for meaningful space-time substitution. These sites, ranging in elevation from 830 to 1038 meters above sea level, predominantly feature beech trees mixed with mature fir and spruce (see Adamič et al. (2023) and Čater et al. (2024)). The sites were listed from south to north, and named as Tismana, Arefu, Zagon, Soveja, Tarcau, Frumosu, Livovská Huta, and Salajka (Fig. 1).

The LST values were derived from thermal bands of Landsat satellites (5, 7, 8, 9) for each forest site, covering the period from 2003 to 2022. The number of LST averages available for each forest site varied monthly and yearly due to the extensive distribution of the sites, the arrangement of the satellite data collected, and cloud cover. LST values were estimated using the statistical mono-window algorithm developed by the Climate Monitoring Satellite Application Facility and the Google Earth Engine (GEE) online platform, which enables the analysis of extensive thermal satellite time series (Ermida et al. 2020).

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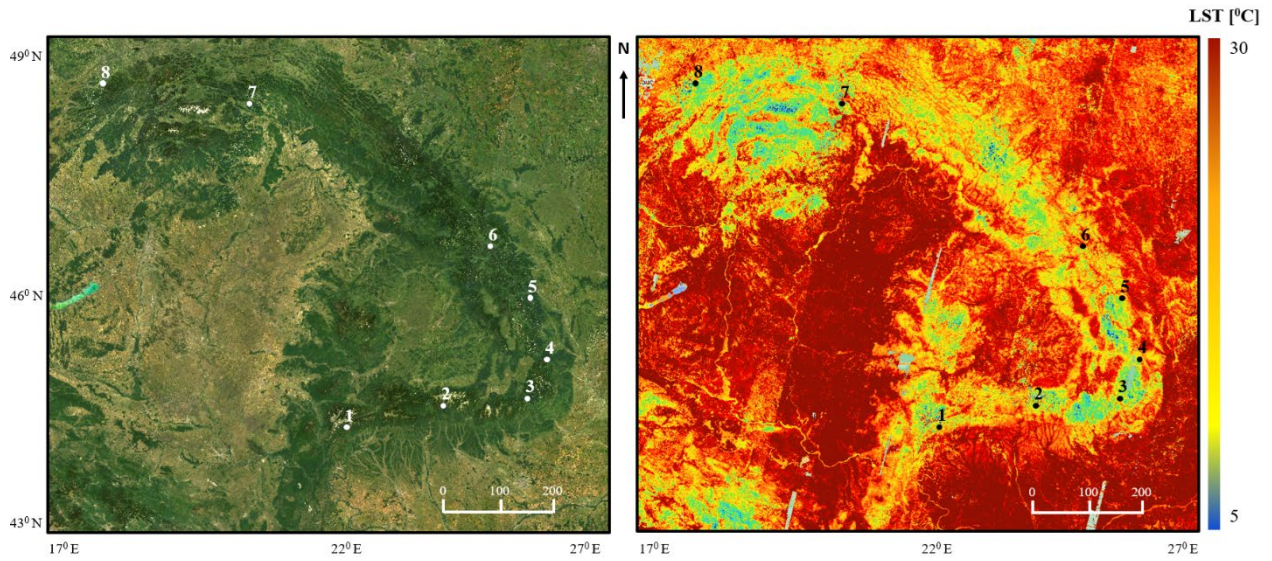


Fig. 1. Carpathian Mountains RGB composite (left), and Land Surface Temperature (LST) map (right) from Landsat 8 data (mosaic of cloudless images from 2021-05-01 to 2021-08-30) The study sites are numbered from south to north: 1 - Tismana, 2 - Arefu, 3 - Zagon, 4 - Soveja, 5 - Tarcau, 6 - Frumosu, 7 - Livovská Huta, and 8 - Salajka.

Results and Conclusions

Mean LST from Landsat time series revealed years with maximum and minimum canopy surface temperature for each study site (Table 1).

Table 1. Mean LST for study sites. Bold values are maximum and minimum mean LST

Mean LST [°C]	Tismana	Arefu	Zagon	Soveja	Tarcau	Frumosu	Livovska Huta	Salajka
2003	4.1	7.2	3.4	7.5	8.9	3.6	4.8	11.9
2004	9.7	11.6	13.3	15.0	12.7	6.6	11.8	13.0
2005	4.2	6.2	1.4	8.9	11.3	5.8	12.3	3.2
2006	8.0	9.7	9.8	11.9	7.2	5.3	15.3	9.4
2007	11.4	15.0	11.5	11.7	9.5	12.5	15.7	10.9
2008	12.8	15.3	14.9	14.9	16.3	13.8	12.3	12.2
2009	11.0	13.4	12.1	13.3	10.2	9.1	16.0	11.9
2010	9.7	8.6	10.0	12.3	6.2	2.3	11.2	11.2
2011	6.1	12.9	11.5	7.9	7.4	9.1	14.9	12.0
2012	12.1	13.3	9.7	11.5	16.3	12.1	12.8	10.1
2013	9.5	15.7	13.5	4.1	9.4	9.2	11.3	13.4
2014	9.7	10.8	7.9	4.0	4.8	8.4	9.9	6.2
2015	9.8	11.8	16.1	13.5	16.5	8.1	16.1	10.3
2016	5.6	10.0	12.5	3.1	9.9	4.4	13.7	10.7
2017	7.8	12.6	16.0	7.4	13.2	6.8	7.9	9.9
2018	9.2	11.4	13.3	13.7	7.8	8.4	15.8	13.5
2019	8.1	11.5	12.8	15.1	8.9	8.3	11.8	12.1
2020	9.2	13.9	15.3	10.4	4.6	9.5	12.5	9.9
2021	8.6	13.0	12.2	4.7	6.8	6.5	11.6	3.7
2022	7.7	7.1	5.5	10.2	5.1	4.9	6.6	10.3

The analysis of the forest canopy LST trend (Fig. 2) revealed a statistically significant increasing trend for Zagon and a significant decreasing trend for Soveja ($p < 0.1$). A non-significant increasing trend was observed for Arefu, while no trends could be confirmed for the other sites. Over the past 20 years, the canopy surface temperature in Zagon has increased by 3 °C, whereas it has decreased by 2 °C in Soveja. The highest canopy surface temperatures were recorded at Livovská Huta, Arefu, and Zagon, with mean LSTs over the 20-year period being 13.5 °C, 11.3 °C, and 11.2 °C, respectively. The coldest site was Frumosu, with a mean LST of 7.6 °C for the same period.

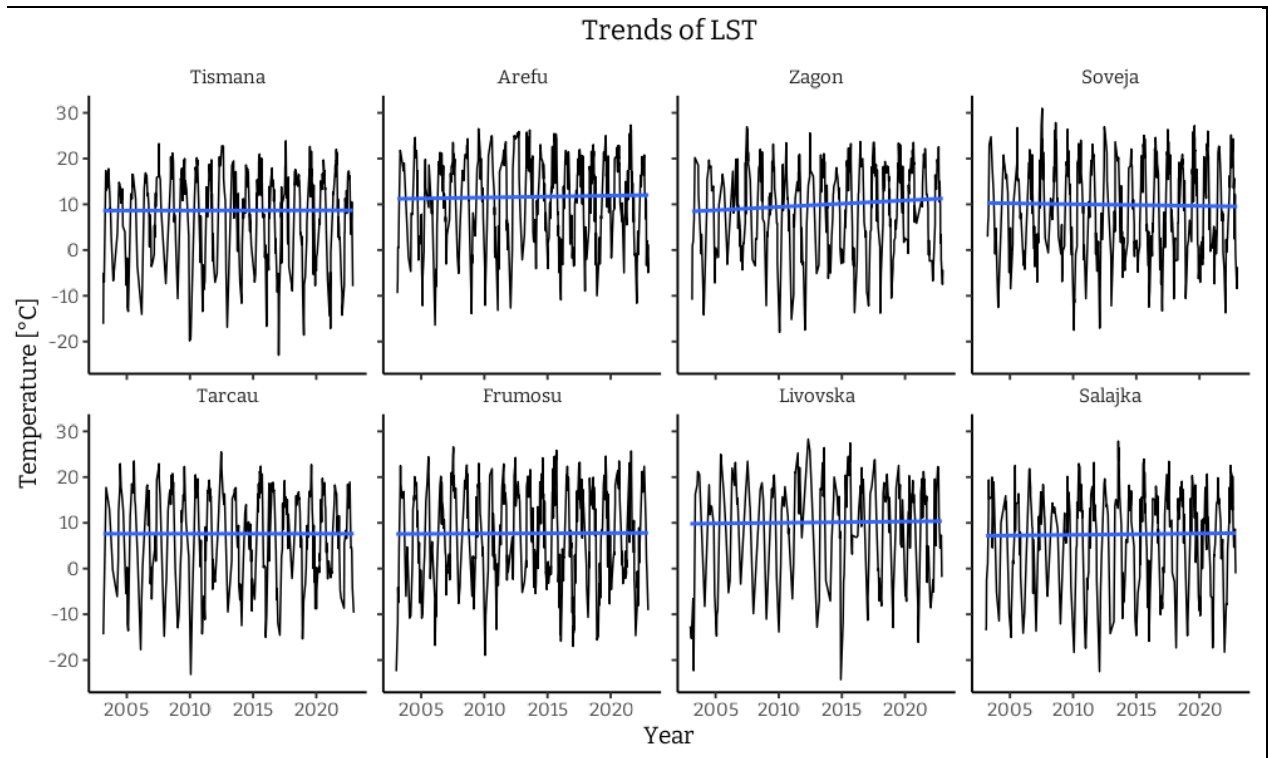


Fig. 2. Canopy land surface temperature (LST) trends for studied sites

Analysing maximum and minimum mean LST for each study site (Table 1) can provide the information about potentially extreme years, such as 2003, 2008 and 2015. Tismana, Zagon and Livovská Huta had a minimum mean LST in 2003. Tismana, Arefu and Frumosu had a maximum mean LST in 2008. Zagon, Tarcau and Livovská Huta had a maximum mean LST in 2015.

The increase in forest canopy surface temperature to 3 °C on Zagon did not lead to an earlier start of the growing season as might be expected, but may have contributed to the longer duration and late end of the growing season on Zagon's during the 20-year period studied. Schieber et al. (2017) reported that the growing season of European beech was extended by more than two weeks over the 21-year period within the increasing mean monthly air temperature.

Although the surface temperature of the forest in Soveja decreased by 2 °C, this site had one of the highest surface temperatures, which is consistent with the highest air temperature among the study sites (Table 1). The decreasing trend in canopy surface temperature in Soveja can be

attributed to the influence of colder winter months observed in the period from 2010 to 2015 (Figure 2). The lower LST in Soveja may also indicate cooling due to phenological shift. Park & Jeong (2023) demonstrated the sensitivity of LST to advanced phenological SOS (start of season) and delayed EOS (end of season) over northern deciduous forests and explained the cooling effect of the phenological shift by the reduced aerodynamic resistance of trees.

The LST of the canopy can be influenced by the intensity and duration of sunlight (Li et al. 2023), which affects the balance between absorbed and reflected solar radiation as well as ecophysiological processes such as evapotranspiration and shading. This aspect was not considered in our study and is suggested as an additional factor to be investigated in future research on canopy LST and forest phenology in the Carpathians. Using a Digital Elevation Model can be estimated the amount of solar radiation taking into account the slope, aspect, and shadows.

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Phenological trends of European beech stands along the Carpathian arc: A 20-year MODIS based analysis

KEYWORDS: European beech, phenology, remote sensing, time series, vegetation index

Introduction

Phenology, the study of biological life cycle events and their climate relationships, is vital in the context of global environmental change. Forest phenology provides insights into tree events and their environmental responses. The Carpathian Mountains offer significant ecological services, and understanding their forest phenology is essential for managing ecosystem services under changing conditions.

Personal visual observations and local ground stations are typically used to study forest phenology, but these methods can be time- and resource-intensive. Satellite remote sensing (RS) offers a valuable alternative for long-term phenological studies at larger scales. Recent satellite-based studies have observed phenological shifts in Carpathian forests, such as delayed leaf unfolding and extended growing seasons, linked to increased air temperatures. Air and soil temperatures significantly influence the growing season's start and duration. Beech trees, for instance, begin leaf unfolding when mean daily temperatures exceed 10 °C.

Further research is needed to explain spatial phenological variations, especially in the less-studied regions of the Carpathians. Geographic gradients may help predict climate change impacts on tree species. Previous studies have shown different growth responses of beech and fir to climatic conditions and spatial variability of soil respiration.

This study uses MODIS satellite data to analyze phenology metrics for European beech forests from 2003 to 2022. It aims to assess seasonal and inter-annual changes and examine the relationship between phenological metrics, precipitation and air temperature to better understand phenological responses to climate change in the Carpathians.

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Methods

The study focused on eight forest sites dominated by European beech (*Fagus sylvatica* L.) along the Carpathian Arc, covering various altitudes (830 to 1038 meters above sea level) and climatic conditions. These sites were selected to represent a geographical gradient with minimal human intervention, ensuring a consistent ecological context.

We utilized MODIS Terra and Aqua vegetation indices product for the period 2003-2022 to derive the Enhanced Vegetation Index (EVI). Meteorological data, including monthly mean temperatures and total precipitation, were obtained from the CRU TS 4.01 dataset.

The phenofit software package for R was employed to extract key phenological metrics, namely the start (SOS), length (LOS), and end (EOS) of the growing season. The time series of EVI were split into individual growing seasons, followed by curve fitting and extraction of phenological indicators. The derivative method was used for determining these metrics.

Results

The analysis revealed varied responses across the sites, with significant site-specific differences in the start, length, and end of the growing season (Figure 1). Salajka exhibited the earliest mean SOS (DOY 105), while Livovska Huta and Zagon had the latest mean SOS (DOY 119). Trends in SOS showed delays in some sites like Zagon, whereas Salajka experienced earlier SOS over the years.

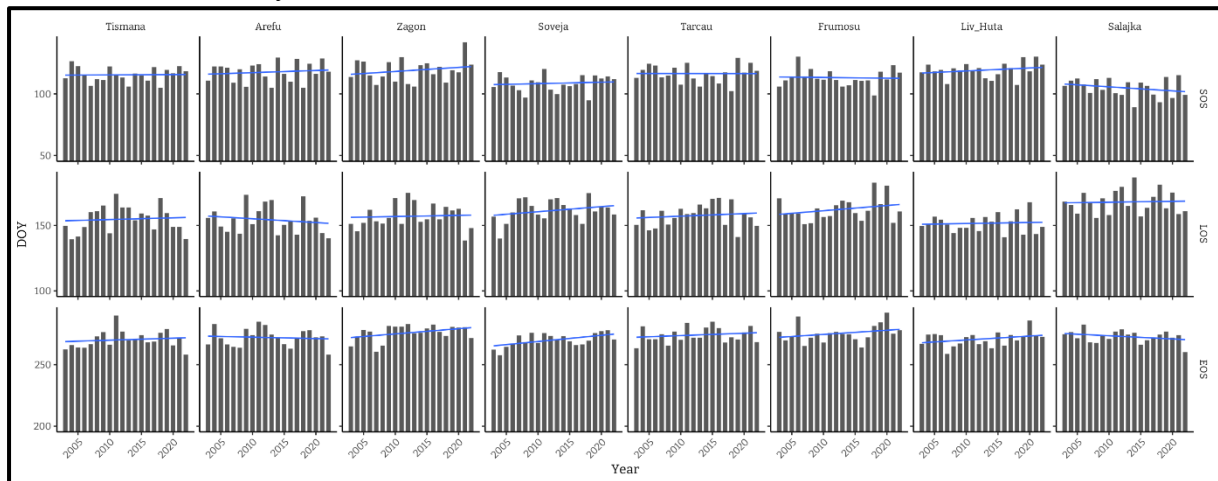


Fig. 1. Day of year of start, end and length of season on eight research sites between the years 2003 and 2022 with linear trend (blue line)

The EOS varied, with Zagon and Soveja having later EOS compared to other sites. Soveja showed a statistically significant extension of the growing season by approximately half a day each year. The LOS was longest at Salajka (168 days) and shortest at Livovska Huta (152 days), indicating spatial variability in phenological responses.

April and May temperatures had a strong influence on SOS, with warmer temperatures leading to earlier starts (Figure 2). Precipitation in April correlated positively with SOS and negatively

with LOS, suggesting that increased spring precipitation may delay the onset of the growing season but shorten its length. September temperatures showed a positive correlation with EOS, indicating extended growing seasons in warmer early autumn conditions.

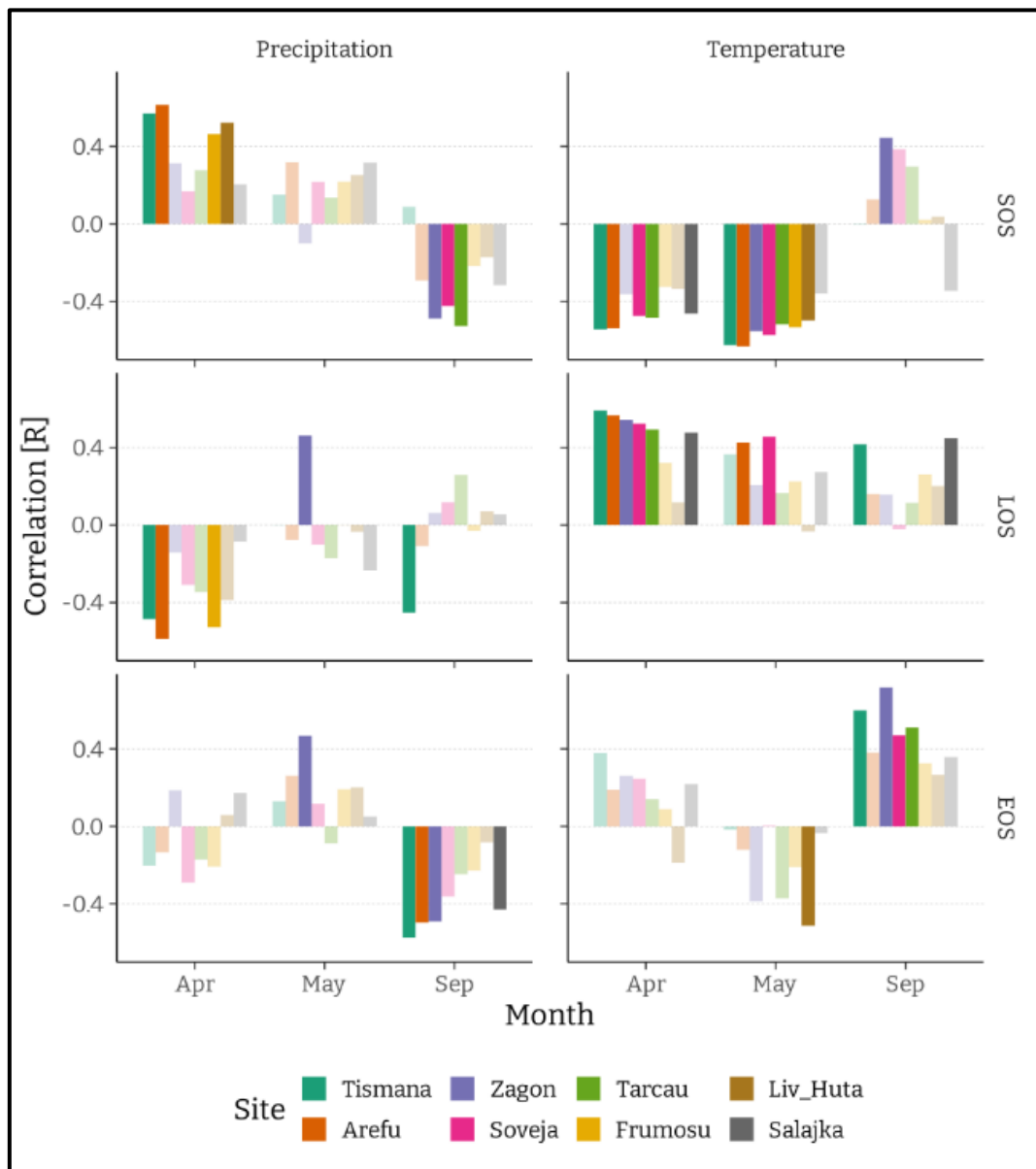


Fig. 2. Correlation between each phenological indicator and precipitation/temperature for individual sites for April, May and September. Darker color indicates significant correlation ($p < 0.1$)

Conclusions

This study highlights the complex interactions between climate variables and phenological responses of European beech forests in the Carpathian region. The observed phenological shifts are influenced significantly by both temperature and precipitation, with notable site-specific variations. The use of MODIS data combined with the phenofit R package provided a robust framework for long-term phenological monitoring. The findings underscore the need for

continued long-term research and the integration of advanced remote sensing technologies to better understand and predict the impacts of climate change on forest ecosystems.

Future research should focus on refining data integration techniques and expanding the temporal and spatial scope of phenological studies to develop more accurate predictive models for forest management and conservation strategies in the face of global climate change.

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Predicting GPP in Carpathian Beech Forests: Uncovering spatial and temporal patterns using a regression model with climatic, topographic and additional features

KEYWORDS: Gross primary product, remote sensing, regression model, temperature, precipitation, digital elevation model

Introduction

Climate change impact ecosystems globally, including the mixed forests of the Carpathian Mountains (Kruhlov et al. 2017). The primary manifestations of climate change are shifts in temperature and precipitation regimes, which undoubtedly affect biomass growth in complex ways. Since direct observations of the future are impossible, we rely on various modeling methods. Machine learning is the most popular contemporary approach for addressing such tasks.

The aim of our study is to develop a regression model that predicts the behavior of Gross Primary Product (GPP) based on a range of climatic, topographic, and other variables. We use this model to forecast the growth of beech forests over the next 20 years under different climate scenarios.

Methods

GPP values were derived from the NASA Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua satellite imagery database (Justice et al. 2002). GPP data aggregated annually from biweekly intervals over 500m resolution. The study period spans from 2003 to 2020.

We utilized NASA Shuttle Radar Topography Mission (SRTM) Digital Elevation Model (DEM) (van Zyl. 2001) data with a 30 meter-level resolution, focusing on topographic variables such as elevation, slope, and aspect. Statistical measures (median, mean, and standard deviation) are computed at scales of 500m and 5km.

Climatic variables were sourced from the E-OBS gridded dataset, limited to temperature and precipitation data collected daily with a spatial resolution of 0.25 degree (Cornes et al. 2018). Monthly averages and variations for both temperature and precipitation were calculated.

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Latitude and longitude were included as separate variables, as they can indirectly influence GPP growth through variations in day length.

We also introduced categorical variables derived from visual analysis of GPP data patterns. These include:

- 1) Size Class: GPP values range from 8000 g C/m²/year to 18000 g C/m²/year. Annual GPP distribution across the Carpathian basin can be unimodal or bimodal. Considering the maximum GPP values from 2003-2020, we distinguished two size classes based on which peak of the distribution the maximum GPP values belong to. (see Fig. 1)

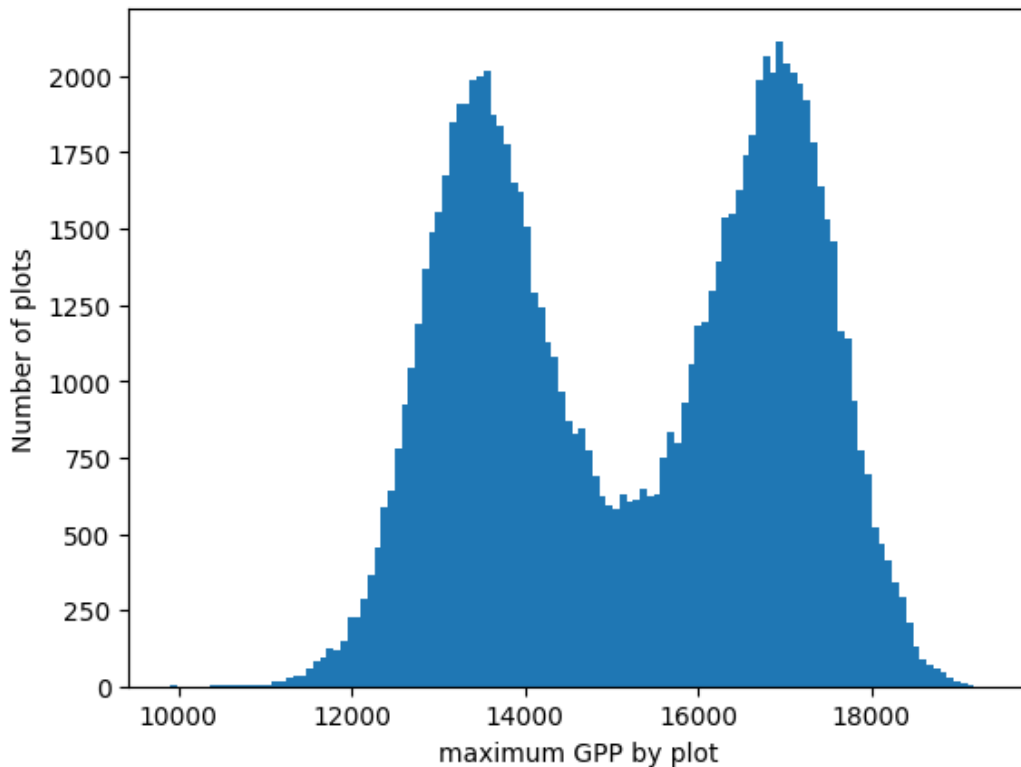


Fig. 1. Maximum GPP distribution

- 2) Masting Index: Temporal analysis shows GPP fluctuations, with low GPP years followed by high GPP years, suggesting a masting cycle. The Masting Index (whether a site is in a masting year) is used to assess its importance, but cannot be used directly in regression due to future uncertainty. We used 7-year cycle proxy for the Masting Index. (see Fig.2)

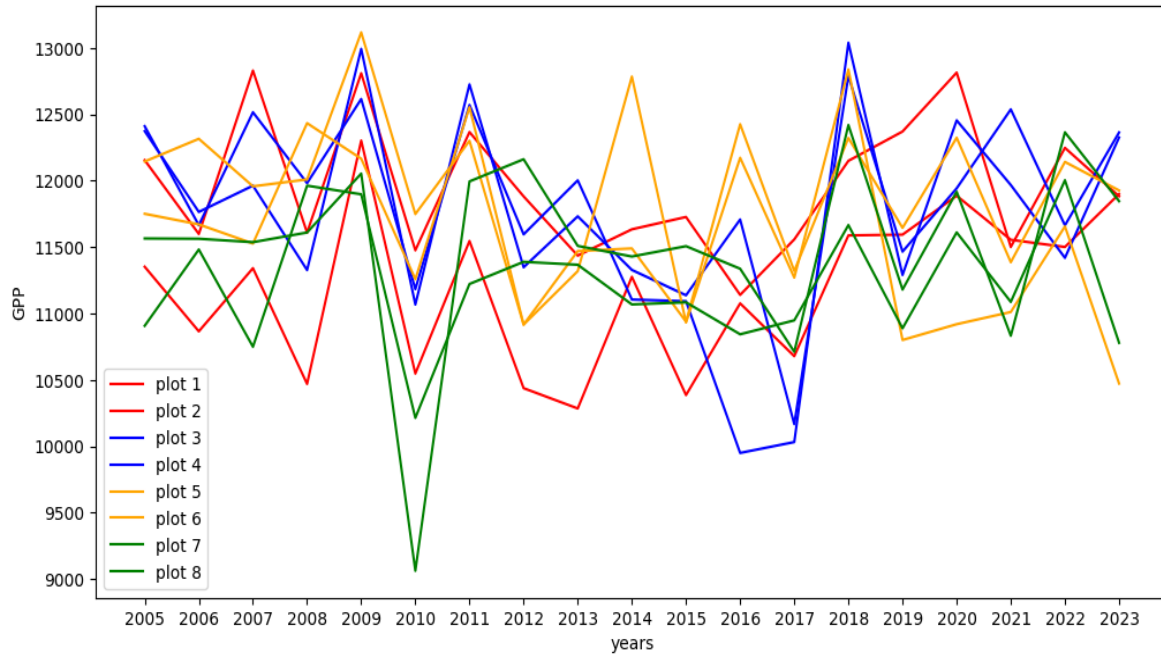


Fig. 2. Temporal GPP distribution

We tested a wide range of models: Light Gradient Boosting Machine (LGBM), Extreme Gradient Boosting (XGBOOST, `xgb_limitdepth`), CatBoost, Random Forest (RF), and ExtraTrees, each with an extensive set of internal parameters (He et al. 2021).

Results

The LGBM model showed the best results. Model accuracy, evaluated using the R^2 score, was tested yearly through cross-validation and with various training and test year sets. Cross-validation accuracy ranges from 0.78 to 0.85, while regression accuracy on training sets from one year and test sets from another ranges from 0.63 to 0.77.

The accuracy of models trained solely on numerical features (climatic, topographic, coordinates) varies from 0.45 to 0.52.

We assess the contribution of different features, with the size class contributing the most significantly (see Fig. 3). We also analyze the spatial and temporal variability in feature importance.

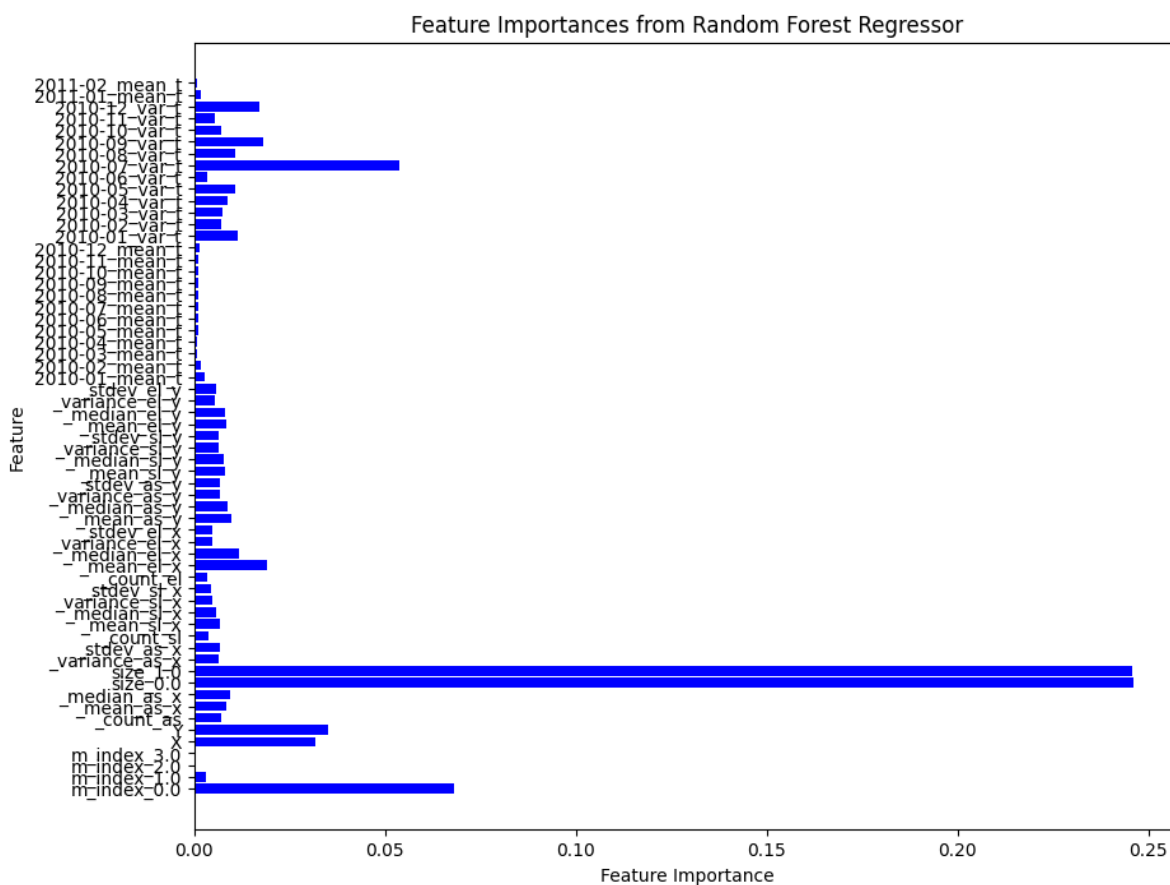


Fig.3. *Feature importance of different variables*

Conclusions

Our model can be used both for direct predictions of GPP values and for analyzing the factors influencing its formation. We have observed significant spatial and temporal variability. This variability is largely consistent with the tree ring observations conducted by J. Kaspar. Specifically, a relatively greater dependence on precipitation is characteristic of the northern and southeastern slopes of the Carpathians. In contrast, the role of temperature is significant for the southeastern slopes but not for the northern ones.

We also analyze the physical nature of the two size classes. The higher GPP tends to be in the foothills facing the open plains (Pannonian and Wallachian) (see Fig.4).

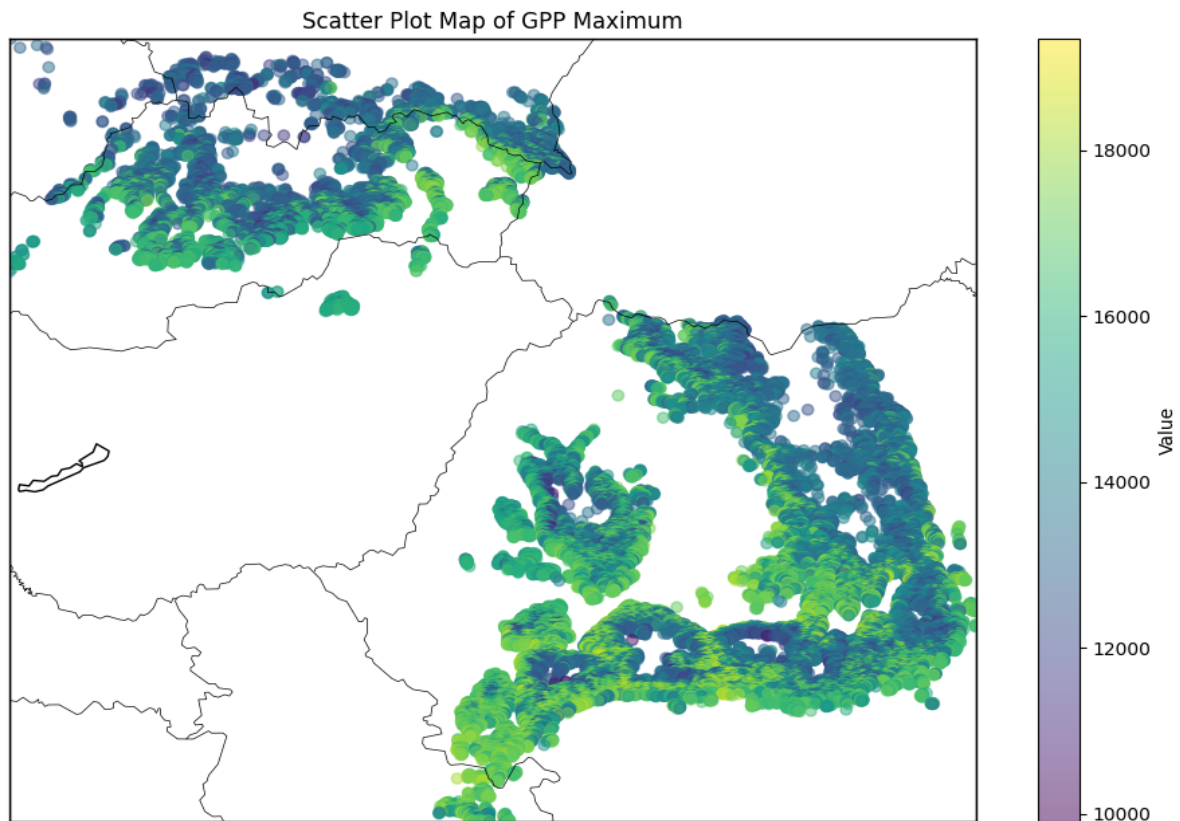


Fig.4. Maximum GPP distribution

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