

# Significant phenological response of forest tree species to climate change in the Western Carpathians

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## Abstract

This study aims to analyse the phenological dynamics of tree species in response to changes in climatic conditions over the last two climate-normal periods (CLINO 1961–1990 and 1991–2020). We focused on the main climax tree species (*Quercus* species, *Fagus sylvatica* L., *Abies alba* Mill., *Picea abies* [L.] Karst., and *Pinus mugo* Turra) dominating eight altitudinal forest vegetation zones (FVZ) and alluvial forests of Western Carpathians and adjacent lowlands in Central Europe. The phenological phases analysed in this study were first leaf (BBCH11) and general leaf colouring (BBCH94) for deciduous species, and the onset of new shoots (BBCH10) for evergreen conifers. The results of partial correlations confirmed that temperature is the main driving factor explaining the shifted onset of phenological phases for the species considered. Furthermore, deciduous species growing in the lower (and warmer) FVZ showed a certain level of drought sensitivity related to the earlier BBCH94. The identified trends in phenology were species-specific and differed between the individual FVZs. The most pronounced shifts toward the earlier BBCH10 and BBCH11 were found in the upper FVZ of the vertical distribution range of species. The presented results will support our understanding of the mechanisms underlying environmental control of tree phenology. This is crucial for predicting how the growing season of trees will be constrained by climate change-induced conditions in individual FVZ.

**Key words:** phenology; trends; temperature; precipitation; climatic water balance

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## 1. Introduction

Phenology has been widely accepted as the biological indicator of climate change impacts on the life cycles' timing of living organisms (Meier et al. 2021; Kubov et al. 2022). The phenological phases of tree species, including leaf unfolding, spring shoots, or leaf colouring, are considerably regulated by weather conditions and the photo-period length (Menzel 2003; Xie et al. 2018). The spring phenology in temperate forests is driven particularly by increasing temperature (Richardson et al. 2018), provided that there is sufficient soil moisture after the winter season with low evapotranspiration losses. Compared to the spring season, the autumn phenology is particularly conditioned by temperature and water supply (Xie et al. 2018; Bigler & Vitasse 2021). The increasing evapotranspiration demand in a warming climate limits the amount of water accessible for ecosystems, leading to the earlier

end of the growing season in some species (Lukasová et al. 2020). However, the drought-induced slowdown in assimilation processes does not necessarily lead to visible signs of earlier leaf colouring (Didion-Gency et al. 2023). In terms of how topography affects phenophases, altitude was found to be an important variable defining the timing of onsets (Hwang et al. 2011; Bucha & Koreň 2017; Chen et al. 2018; Lukasová et al. 2019). Leaf onset in European forests is significantly delayed with an altitudinal gradient from 1 to 3.9 days per 100 meters depending on tree species, type of climate, location and analysed period (Dittmar & Elling 2006; Vitasse et al. 2009; Guyon et al. 2011; Čufar et al. 2012; Lukasová et al. 2019). Variability in the onset of leaf colouring is higher compared to spring phenology, with a weaker correlation with altitude (Čufar et al. 2012; Lukasová et al. 2019), complicating phenological modelling and predictions (Piao et al. 2019).

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Classification of the forest ecosystems in Slovakia is based on the principles of forest geobiocenology elaborated by professor Zlatník in 1948 (Bošela 2010). Considering the effect of altitudinal climate conditions on biocenosis, Zlatník (1960, 1976) designed a unique classification of forest vegetation zones (FVZ, known also as altitudinal vegetation zones). The vegetation zone was characterized as a climax biogeocoenosis dominating an area, which is determined by its vegetation, including the substituting biogeocoenosis modified in relation to the changes in the macroclimate and altitudinal changes in mesoclimate. Using this classification, the area of Western Carpathians and the adjacent Pannonian Basin in Central Europe was divided into 8 FVZs characterised by the dominant climax tree species: *Quercus* species, *Fagus sylvatica* L., *Abies alba* Mill., *Picea abies* [L.] Karst., and *Pinus mugo* Turra. However, the abrupt climate change since the end of the 80s (Reid et al. 2016; Sippel et al. 2020) has considerably changed the climate conditions in this region. Because the contemporary mature forest stands were established prior to the ongoing climate change, forest tree species are shifting the onset of life-cycle events. As a response to climate warming, the spring phenology in Europe advanced within the range from  $-0.2$  to  $-0.6$  days  $\text{yr}^{-1}$  (Chmielewski & Rötzer 2001; Menzel et al. 2001; Menzel et al. 2006; Fu et al. 2014; Chuchma et al. 2016; Meier et al. 2021; Bucha et al. 2023), and autumn phenology generally delayed at the range from  $0.4$  up to  $1.2$  days  $\text{yr}^{-1}$  (Lukasová et al. 2020; Meier et al. 2021). The extent of shifts found in the mentioned studies differed considerably between the tree species, locations and altitudes, and also depended on the length of analysed periods and their timing. Earlier spring development is associated with a higher risk of fruit and forest trees to frost exposure (Vitasse et al. 2018), especially when the probability of occurrence of late spring frosts is high (Škvareninová et al. 2022).

Apart from the rising global temperature, climate change also alters the precipitation regime with significant impacts on forest ecosystems. Over the last decades, forest tree species have encountered different drought stress levels. Drought stress is accompanied by a slowdown in assimilation processes and growth, decreased resistance and earlier termination of growing seasons (Mindáš et al. 1996; Schneider 1997; Camarero et al. 2018; Lukasová et al. 2020; Bigler & Vitasse 2021; Mezei et al. 2022; Bucha et al. 2023), while extreme drought can lead to the death of individual trees or even whole forest stands (Obladen et al. 2021; Frei et al. 2022). There is a risk that climate change might exceed the ability of European forest trees to adapt to upcoming environmental conditions (Petrik et al. 2022), particularly when the rate of global temperature rise is accelerating (Thompson 2010).

In this study, we focused on the phenological response of climax tree species dominating individual FVZs to climate change in the Western Carpathians

and adjacent lowlands. We anticipated that the climate conditions of each FVZ would change significantly since the classification of FVZ by Zlatník (1960, 1976). To assess the impacts of climate change, we calculated mean precipitation amounts, climatic water balance, and air temperature for periods of climate normals (CLINO) 1961–1990 and 1991–2020 for each FVZ. Taking into account the significant effect of seasonal weather fluctuations on tree phenology (Richardson et al. 2013), we hypothesised that there would be shifts in the phenological onset days throughout the period from 1961 to 2020, encompassing both the relatively stable CLINO 1961–1990 and the warming period from 1991 to 2020. Regarding the phenology of individual tree species, we also considered climatic variables that control the timing of the onset of phenophases at each FVZ separately. We used partial correlation to analyse the effect of climate variables, including temperature, precipitation, and climatic water balance on the onset of the first leaf (BBCH11) for deciduous species and new shoots (BBCH10) for evergreen conifers as indicators of the start of the growing season, and general leaf colouring (BBCH94) which indicated the end of the growing season for deciduous species. Our results may help in planning forest management practices, particularly forest establishment for growing forests with high resilience potential against climate change.

## 2. Data and methods

### 2.1. Study region

The study region is located in the forested areas of the Western Carpathians and the northern outcrops of the Pannonian basin at middle latitudes (Central Europe, Slovakia:  $47^{\circ}44'–49^{\circ}37'N$  and  $16^{\circ}50'–22^{\circ}34'E$ ). In terms of the Köppen climate classification, the territory of Slovakia is a continental-climate region with dry winters and warm summers. The climate is characterized by regular alternation of four seasons and variable weather, affected by pressure centres located in the Azores High and Icelandic Low Sea (Mészáros et al. 2022). The local climate is mostly determined by altitude. Based on long-term air temperature measurements, the Danube Lowland is the warmest region, with an average air temperature of  $-1$  to  $-2$  °C in January,  $18$  to  $21$  °C in July, and an annual average of  $9$  to  $11$  °C (SHMI 2015). Precipitation falls mostly during westerly and north-westerly cyclonic situations originating in the Atlantic Ocean, and occasionally also from cyclonic situations from the Mediterranean or the Black Sea (Mészáros et al. 2022). The average annual precipitation totals vary from less than  $500$  mm in the area of the Western Danube Lowland to more than  $2,000$  mm in the High Tatra Mts. (Zbojníčka chata,  $2,130$  mm, SHMI 2015).

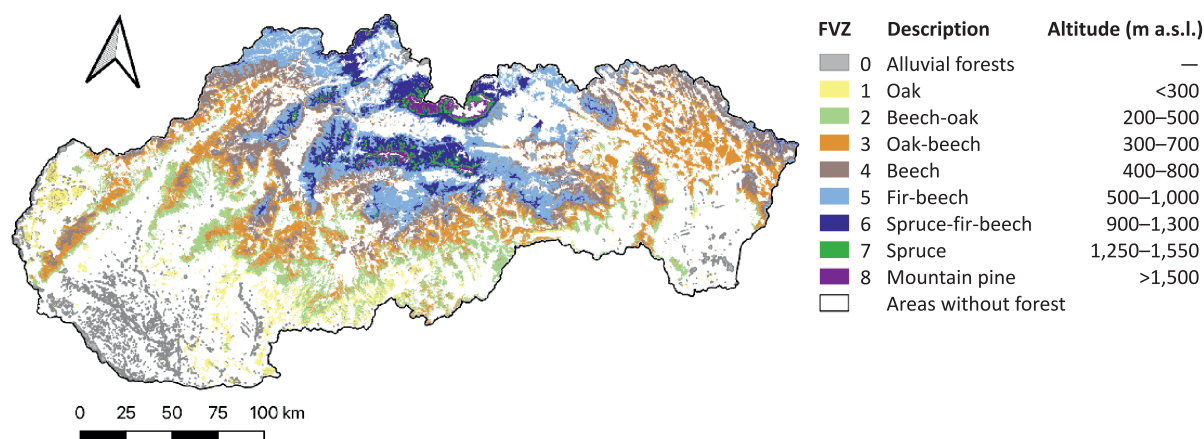


**Fig. 1.** Forest vegetation zones (FVZ) defined in Zlatník (1960, 1976). The altitudinal ranges of FVZ with the climax tree species are listed in the description on the right, where the tree species in the last place is the dominant species of the FVZ.

Tree species analysed in this study have a wide range of natural distribution over Europe and grow from the lowest to the highest altitudes of the studied region – European beech (*Fagus sylvatica* L.), Oak species (*Quercus* sp. – one group containing *Quercus robur* L. and *Quercus petraea* [Matt.] Liebl.), Silver fir (*Abies alba* Mill.), Norway spruce (*Picea abies* [L.] Karst.) and Mountain pine (*Pinus mugo* Turra). The studied tree species match the climax tree species from the classification of forest vegetation zones (FVZ) in Zlatník (1960; 1976). According to this classification, the studied region was divided into 8 altitudinal FVZ and alluvial forests (FVZ 0) within FVZ 1 with high soil water content levels (Fig. 1).

## 2.2. Phenology data

In total, phenological data from 80 stations for *F. sylvatica* L., 66 for *Quercus* sp. [Matt.] Liebl., 38 for *A. alba* Mill., 33 for *P. abies* [L.] Karst., and 3 for *P. mugo* Turra from the Phenological Network of the Slovak Hydrometeorological Institute (SHMI) were considered in this study. Phenological phases at these stations were observed visually employing the methodology described in Braslavská & Kamenský (1996) and assigned to adequate BBCH codes (Meier 2001):

BBCH10 – emergence of new shoots from the apical meristem of coniferous trees;

BBCH11 – first true leaf unfolded in deciduous tree species;

BBCH94 – 50% of leaves coloured in deciduous tree species.

For deciduous tree species, also the growing season length (GSL) as a difference between BBCH11 and BBCH94 was investigated.

We selected only those phenological data series with at least 70% completeness at the same phenological stations in the CLINO 1961–1990 and 1991–2020. After

this elimination, 25 stations for *F. sylvatica* L., 25 for *Quercus* sp. [Matt.] Liebl., 11 for *A. alba* Mill., 15 for *P. abies* [L.] Karst., and 3 for *P. mugo* Turra remained and were further analysed. Phenological stations of individual tree species were classified into FVZ based on the location of the observed group of trees using the description of forest stands from the Forestry Management Plan. The onset days of phenological phases were marked by the day of year (DOY). Then the median of onset days of the phenological phases for each FVZ was calculated for each year.

## 2.3. Climate data and calculations

The climate station data used in this study were obtained from the databases of the SHMI. The temperature and precipitation data from 71 sites that included CLINO 1961–1990 and 1991–2020 were used. The stations were classified into FVZ and the climatic data were averaged over each zone. To assign the meteorological stations to FVZ, we used the FVZ of the phenological station closest to the meteorological station. We examined climate variables such as monthly averages of daily mean air temperature ( $T_a$ ), maximum temperature ( $T_{max}$ ), minimum temperature ( $T_{min}$ ), monthly totals of precipitation ( $P$ ), Standardized Precipitation Index (SPI), and Climatic Water Balance (CWB) of differently long periods before the onset of phenophases as potential driving forces.

SPI was calculated using the application of the National Drought Mitigation Center – UNL – SPI Generator based on the monthly precipitation data from 1961 to 2020. The output time scale was set for monthly, two-monthly, three-monthly, and four-monthly SPI. Monthly averages of daily mean air temperature ( $T$ ) and monthly precipitation totals ( $P$ ) were used to calculate potential evapotranspiration (PET). PET was determined by the Thornthwaite method (Thornthwaite 1948) implemented within the R package ‘SPEI’ Version 1.7

(Vicente-Serrano et al. 2010). The climatic water balance was calculated as the difference between observed precipitation and potential evapotranspiration ( $CWB = P - PET$ ) for individual months.

## 2.4. Statistical analyses

The effect of basic climate variables described in section 2.3 ( $T_a$ ,  $T_{max}$ ,  $T_{min}$ ,  $P$ ,  $SPI$ , and  $CWB$ ) on the onset of spring (BBCH10, BBCH11) and autumn phenophases (BBCH94) were tested using partial correlation. Compared to simple correlation, partial correlation measures the strength and direction of the relationship between two variables after removing the effects of other specified variables. The external effects caused by other variables are held constant. This technique allows the examination of the unique contribution of each variable to the correlation. For instance, in the case of rainy weather in spring, when it is cloudy, the solar radiation is reduced, and surfaces are not heated, it is usually colder so this may significantly affect the tree phenology (Středa et al. 2015). Therefore, when precipitation-based variables ( $P$ ,  $SPI$ ,  $CWB$ ) were correlated with the onset days, the effect of mean temperature was controlled and when temperature-based variables ( $T_{max}$ ,  $T_{min}$ ,  $T_a$ ) were correlated, the effect of precipitation was controlled. The significance level was set to 0.05. Trends in phenology were calculated using a non-parametric Kendall trend test employing Sen's slope as an indicator of the shift. For single tree species and FVZs, we estimated trends of the whole period 1961–2020 and mean onset days for each CLINO separately.

## 3. Results

### 3.1. Changes in climate variables between normal periods

Table 1 presents the annual temperature and precipitation conditions for CLINO 1961–1990 and 1991–2020 calculated from the station data in this study, and those defined in Zlatník (1960, 1976) for individual FVZ.

Regarding the precipitation, CLINO 1991–2020 still fits the established ranges for FVZ defined in Zlatník (1960, 1976), while the temperatures considerably increased above the ranges.

Changes in temperature and precipitation patterns between the CLINOs led to an altered potential evapotranspiration regime, which was reflected in the climatic water balance ( $CWB$ ) throughout the individual months, growing seasons, and years (Fig. 2). During the second CLINO 1991–2020, the temperature increase in the growing seasons was higher compared with the annual means by 0.1–0.3 °C (Fig. 2a).

An increase was observed also in precipitation totals. The link between precipitation and FVZ was apparent, with the upper FVZs experiencing even steeper precipitation gradients. In FVZs 0 to 6, the increase ranged from 18 to 36 mm over the growing season and from 39 to 75 mm over the year. In FVZs 7 and 8, the precipitation increase was 2–3 times higher (Fig. 2b).

Despite the increase in precipitation, the  $CWB$  decreased, particularly during the growing seasons. While the annual  $CWB$  totals were negative only in the FVZs 0 and 1, the sums for the growing season and summer months showed negative values from FVZs 0 to 3 in both CLINO. The most notable change in  $CWB$  was observed in FVZ 3, where the inter-normal difference in  $CWB$  reached -37 mm during the growing season (Fig. 2c).

### 3.2. Trends in phenology and correlations between phenophases and climate variables

#### *Quercus* species

**Spring phenology.** Results of partial correlations showed that, except for alluvial forests in FVZ 0, the temperature increase in winter and spring months significantly advanced the BBCH11 of *Quercus* sp. (Table 2). In FVZ 0, BBCH11 correlated significantly only with the maximum temperature in April, the increase of which led to an earlier onset. Precipitation-based parameters considerably affected the timing of BBCH11 only in FVZ 4. Here, the partial correlation revealed that the lower precipitation

**Table 1.** Mean annual temperatures ( $T$ ) and precipitation totals ( $P$ ) defined in Zlatník (1960, 1976) and those calculated over the normal periods 1961–1990 and 1991–2020 for each FVZ.

| FVZ | Zlatník (1976) |             | 1961–1990 |          | 1991–2020 |          |
|-----|----------------|-------------|-----------|----------|-----------|----------|
|     | $T$ (°C)       | $P$ (mm)    | $T$ (°C)  | $P$ (mm) | $T$ (°C)  | $P$ (mm) |
| 0   | —              | —           | 9.0       | 568      | 10.3      | 606      |
| 1   | > 8.5          | < 600       | 9.1       | 575      | 10.2      | 617      |
| 2   | 6.0–8.5        | 600–700     | 8.8       | 640      | 9.7       | 696      |
| 3   | 5.5–7.5        | 700–800     | 7.5       | 746      | 8.8       | 792      |
| 4   | 5.0–7.0        | 800–900     | 6.8       | 754      | 7.5       | 825      |
| 5   | 4.5–6.5        | 900–1,050   | 6.0       | 786      | 6.9       | 827      |
| 6   | 3.5–5.0        | 1,000–1,300 | 4.6       | 1,012    | 5.8       | 1,087    |
| 7   | 2.0–4.0        | 1,100–1,600 | 3.8       | 1,094    | 4.3       | 1,251    |
| 8   | < 2.5          | > 1,500     | 0.3       | 1,159    | 1.3       | 1,325    |

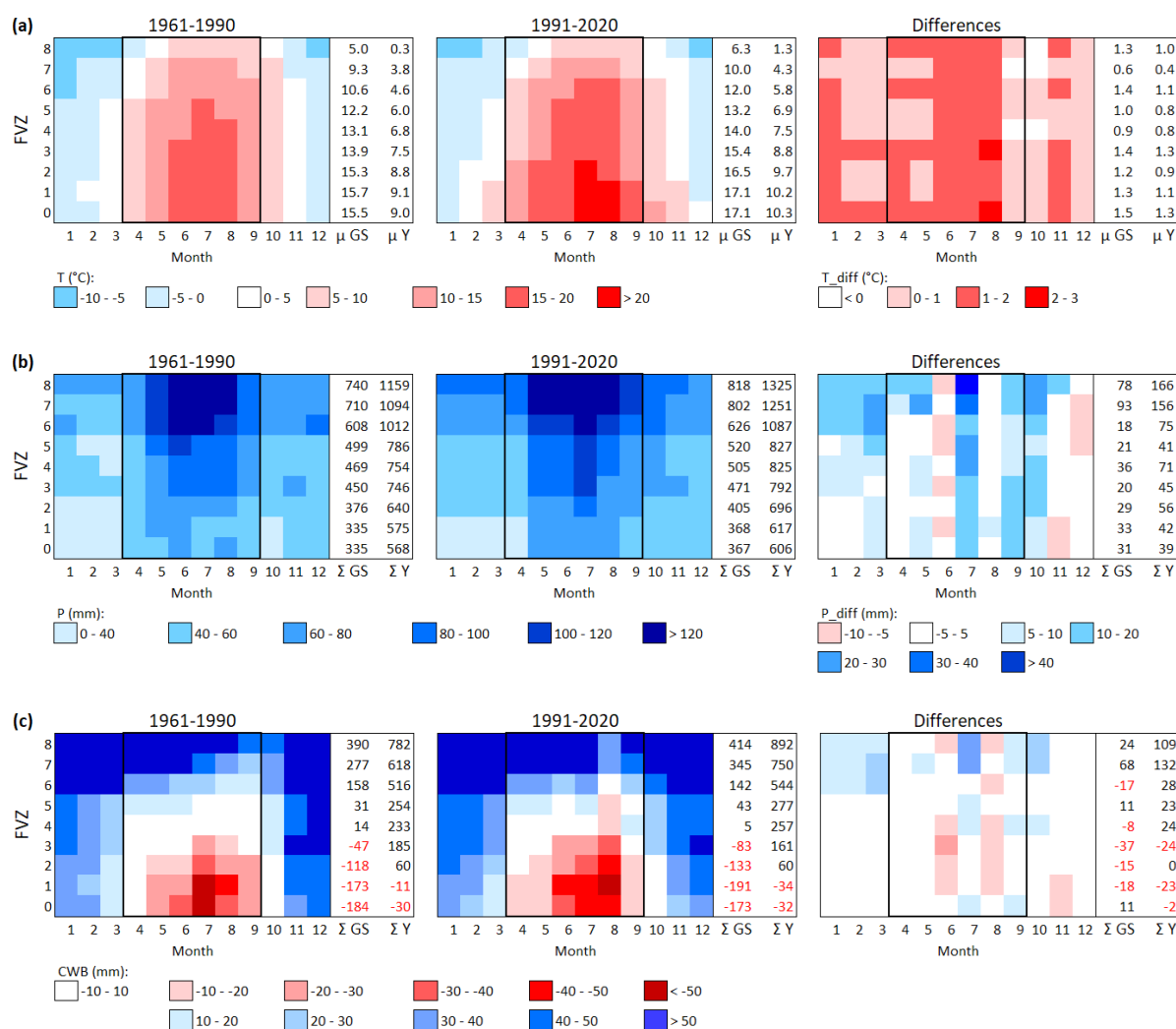


**Fig. 2.** Heat matrix of (a) temperature – T, (b) precipitation – P and (c) climatic water balance – CWB for each forest vegetation zone (FVZ) in normal periods 1961–1990 and 1991–2020 calculated for individual months (1–12), years (Y) and the growing seasons (GS). The growing season is framed in bold lines. In Figure (c), GS and Y data in red font indicate negative CWB and those in black font indicate positive CWB.

in May delayed the onset, while sufficient precipitation advanced it. According to Fig. 2, CWB in May in FVZ 4 was balanced over both recent CLINOs, therefore, we expect further advancement in BBCH11 with increasing temperatures rather than a delay in the upcoming decades. Significant shifts to an earlier onset of BBCH11 between 1961 and 2020, indicated by the Mann-Kendall trend, occurred in FVZ 2 and 4, specifically by  $\sim 0.17$  and  $\sim 0.20$  days  $\text{yr}^{-1}$ , respectively (Fig. 3) that can be explained by the increase in temperature variables, as indicated by the partial correlation results. On the contrary, in FVZ 1, which spreads out in lowlands mainly in the southern and western parts of Slovakia, the trend indicated a significant shift to the later onset by  $\sim 0.15$  days  $\text{yr}^{-1}$  over the 60 years.

**Autumn phenology.** The onset of BBCH94 in *Quercus* sp. was significantly affected by both temperature and precipitation-based variables (Table 2). Warming in

the summer season, particularly in September, delayed the onset in FVZs 0 to 3. However, in FVZs 0, 1, and 2 the lack of precipitation and low CWB significantly correlated with earlier BBCH94. These lower FVZs were described as zones where drought intensifies mainly during the summer months (Fig. 2c), which may affect the growing season length of *Quercus* sp. in upcoming decades. The trend in BBCH94 was significant only in FVZ 0 in alluvial forests (Fig. 3) with a slope of  $\sim 0.50$  days  $\text{yr}^{-1}$ . Since there were no performed phenological observations during CLINO 1961–1990, this trend was derived only over the shorter period 1991–2020. Shifts in BBCH11 and BBCH94 bounding the growing season led to changes in the extent of the growing season lengths (GSL). In CLINO 1961–1990, the longest growing season, lasting 173 days, occurred in FVZ 1 (Fig. 3). However, the close-to-significant trend with  $p=0.07$  indicated shortening by  $\sim 0.13$  days  $\text{yr}^{-1}$  over 1961–2020 in this FVZ. On the other side, in 1991–2020, the longest mean

**Table 2.** Pearson's partial correlation analyses between phenological phases BBCH11 and BBCH94 of *Quercus* sp. and climate variables: P (Precipitation), SPI (Standardized Precipitation Index), CWB (Climatic Water Balance), and T (Temperature) of individual months and periods in individual FVZ (Forest Vegetation Zones). A significant ( $p < 0.05$ ) correlation is marked with \*. Positive correlations are set in blue; those negatives are set in pink.

| FVZ    | 0    |    |    |     |     | 1   |    |    |     |     | 2   |    |    |     |     | 3   |    |    |     |     | 4   |    |    |     |     |   |
|--------|------|----|----|-----|-----|-----|----|----|-----|-----|-----|----|----|-----|-----|-----|----|----|-----|-----|-----|----|----|-----|-----|---|
| BBCH11 | P    | ns | ns | ns  | ns  | ns  | ns | ns | ns  | ns  | ns  | ns | ns | ns  | ns  | ns  | ns | ns | ns  | ns  | ns  | ns | *  |     |     |   |
|        | SPI  | ns | ns | ns  | ns  | ns  | ns | ns | ns  | ns  | ns  | ns | ns | ns  | ns  | ns  | ns | ns | ns  | ns  | ns  | ns | *  |     |     |   |
|        | CWB  | ns | ns | ns  | ns  | ns  | ns | ns | ns  | ns  | ns  | ns | ns | ns  | ns  | ns  | ns | ns | ns  | ns  | ns  | ns | ns |     |     |   |
|        | Tmax | ns | ns | ns  | ns  | *   | *  | *  | *   | *   | *   | *  | *  | *   | *   | *   | *  | *  | *   | *   | *   | *  | *  |     |     |   |
|        | Tmin | ns | ns | ns  | ns  | ns  | ns | ns | *   | *   | *   | *  | *  | *   | *   | *   | *  | *  | *   | *   | *   | *  | *  |     |     |   |
|        | Ta   | ns | ns | ns  | ns  | ns  | *  | ns | *   | *   | *   | *  | ns | *   | *   | *   | *  | *  | *   | *   | *   | ns | *  | *   |     |   |
| Period | 1–4  | 1  | 2  | 3   | 4   | 1–4 | 1  | 2  | 3   | 4   | 1–4 | 1  | 2  | 3   | 4   | 1–4 | 1  | 2  | 3   | 4   | 1–4 | 1  | 2  | 3   | 4   | 5 |
| BBCH94 | P    | ns | ns | ns  | *   | ns  | ns | *  | *   | *   | ns  | ns | *  | *   | *   | ns  | ns | ns | ns  | ns  | ns  | ns | ns | ns  | ns  |   |
|        | SPI  | ns | ns | ns  | ns  | ns  | ns | ns | *   | *   | *   | ns | ns | *   | *   | *   | ns | ns | ns  | ns  | ns  | ns | ns | ns  | ns  |   |
|        | CWB  | ns | ns | ns  | *   | ns  | ns | *  | *   | *   | ns  | ns | *  | *   | *   | ns  | ns | ns | ns  | ns  | ns  | ns | ns | ns  | ns  |   |
|        | Tmax | *  | ns | ns  | *   | ns  | ns | ns | ns  | ns  | ns  | ns | *  | *   | *   | ns  | ns | *  | ns  | ns  | ns  | ns | ns | ns  | ns  |   |
|        | Tmin | *  | ns | *   | *   | ns  | ns | *  | ns  | ns  | ns  | ns | *  | *   | *   | ns  | ns | *  | ns  | ns  | ns  | ns | ns | ns  | ns  |   |
|        | Ta   | *  | ns | *   | *   | ns  | ns | *  | ns  | ns  | ns  | ns | *  | *   | *   | ns  | ns | *  | ns  | ns  | ns  | ns | ns | ns  | ns  |   |
| Period | 7    | 8  | 9  | 7–9 | 8–9 | 7   | 8  | 9  | 7–9 | 8–9 | 7   | 8  | 9  | 7–9 | 8–9 | 7   | 8  | 9  | 7–9 | 8–9 | 7   | 8  | 9  | 7–9 | 8–9 |   |

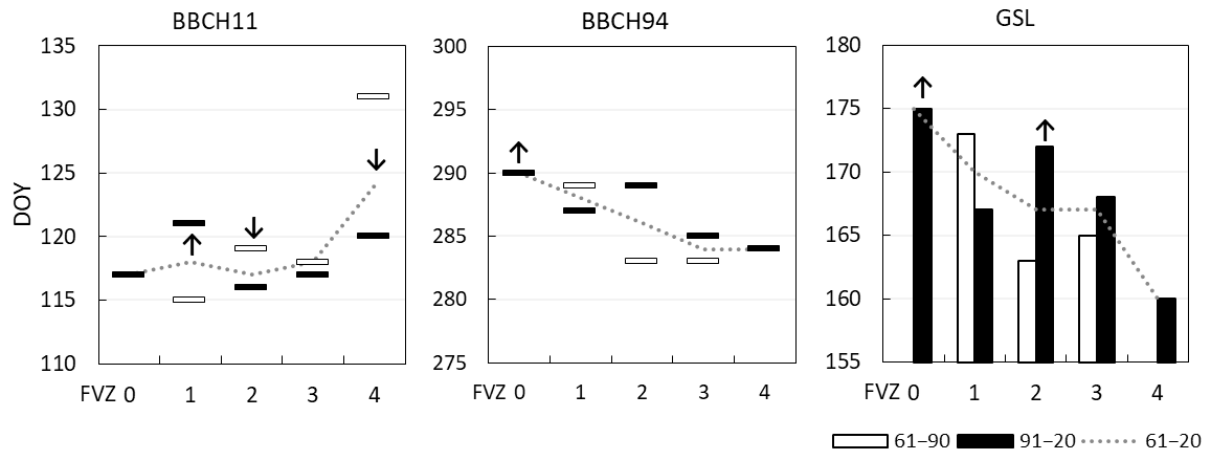


**Fig. 3.** Mean onset of BBCH11, BBCH94, and GSL (growing season length) of *Quercus* species in individual FVZ in the normal periods 1961–1990, 1991–2020, and over the whole period 1961–2020 are shown in graphs. The black arrows indicate the directions of Sen's slopes only of significant Mann-Kendall trends over the whole period of observations.

GSL occurred in FVZ 0, lasting 175 days, and in FVZ 2, lasting 172 days, where growing seasons significantly extended by  $\sim 0.83$  over the last 30 years and by  $\sim 0.29$  days  $\text{yr}^{-1}$  over 60 years, respectively.

#### *Fagus sylvatica* L.

**Spring phenology.** Partial correlations revealed that rising temperatures in the months preceding BBCH11 of beech were the main driving factors advancing its onset across FVZs (Table 3). The inhibiting effect of lower precipitation to BBCH11 was observed only in FVZ 0. On the contrary, in FVZ 6, at higher altitudes with sufficient precipitation, the significant correlation with SPI indicated delayed onset when precipitation increased above normal. In lower FVZs 0 to 4, the trends indicated non-significant changes in the onset of BBCH11. The differences in BBCH11 between the normal periods were less than 4 days in single FVZs, and the mean onset days in CLINO 1991–2020 occurred within one week between DOY 109 and 115 (Fig. 4). Conversely, in FVZs 5 and 6, the shifts to earlier BBCH11 were significant, indicating an earlier onset by  $\sim 0.18$  days  $\text{yr}^{-1}$  over 60 years in FVZ 5

and  $\sim 0.25$  days  $\text{yr}^{-1}$  over 30 years in FVZ 6 (only CLINO 1991–2020).

**Autumn phenology.** Higher temperatures and sufficient precipitation during the summer were the main preconditions for the later onset of BBCH94 in *F. sylvatica* L. (Table 3). However, partial correlations between P, SPI, and CWB in FVZs 2 and 3 and BBCH94 indicated a significantly earlier onset when these variables were lower than usual. Despite this commencing negative effect of drought mainly at lower FVZs, the trend of BBCH94 in warming climates was significantly delayed during the studied period 1961–2020 in these FVZs. The significant prolongations of growing seasons found in alluvial forests in FVZ 0 by  $\sim 1.54$  days  $\text{yr}^{-1}$  (only CLINO 1991–2020) and in FVZ 3 by  $\sim 0.17$  days  $\text{yr}^{-1}$  were caused mainly by significant trends in later BBCH94 by  $\sim 1.21$  and  $\sim 0.17$  days  $\text{yr}^{-1}$  respectively (Fig. 4). In FVZ 5, the mean growing season length remained almost unchanged between CLINOs (shifting from 150 to 149), despite the earlier onset of BBCH11, since BBCH94 also started significantly earlier by  $\sim 0.14$  days  $\text{yr}^{-1}$ .

**Table 3.** Pearson's partial correlation analyses between phenological phase BBCH11 and BBCH94 of *Fagus sylvatica* L. and climate variables: P (Precipitation), SPI (Standardized Precipitation Index), CWB (Climatic Water Balance) and T (Temperature) of individual months and periods in individual FVZ (Forest Vegetation Zones). A significant ( $p < 0.05$ ) correlation is marked with \*. Positive correlations are highlighted in blue and the negative in pink.

| FVZ    | 0    |    |    |     |     | 2   |    |    |     |     | 3   |    |    |     |     | 4   |    |    |     |     | 5   |    |    |     |     | 6  |     |    |     |     |    |   |
|--------|------|----|----|-----|-----|-----|----|----|-----|-----|-----|----|----|-----|-----|-----|----|----|-----|-----|-----|----|----|-----|-----|----|-----|----|-----|-----|----|---|
| BBCH11 | P    | *  | ns | ns  | ns  | ns  | ns | ns | ns  | ns  | ns  | ns | ns | ns  | ns  | ns  | ns | ns | ns  | ns  | ns  | ns | ns | ns  | ns  | ns | ns  | ns | ns  | ns  |    |   |
|        | SPI  | ns | ns | ns  | ns  | ns  | ns | ns | ns  | ns  | ns  | ns | ns | ns  | ns  | ns  | ns | ns | ns  | ns  | ns  | ns | ns | ns  | ns  | ns | *   | ns | ns  | ns  |    |   |
|        | CWB  | ns | ns | ns  | ns  | ns  | ns | ns | ns  | ns  | ns  | ns | ns | ns  | ns  | ns  | ns | ns | ns  | ns  | ns  | ns | ns | ns  | ns  | ns | ns  | ns | ns  | ns  |    |   |
|        | Tmax | *  | ns | ns  | ns  | *   | *  | *  | *   | *   | ns  | *  | *  | *   | *   | *   | *  | *  | *   | *   | *   | *  | *  | *   | *   | *  | *   | *  | *   | *   |    |   |
|        | Tmin | *  | ns | ns  | ns  | *   | *  | *  | *   | *   | ns  | *  | *  | *   | *   | *   | *  | *  | *   | *   | *   | *  | *  | *   | *   | *  | *   | *  | *   | *   |    |   |
|        | Ta   | *  | ns | ns  | ns  | *   | *  | ns | *   | *   | *   | *  | ns | *   | *   | *   | *  | *  | *   | *   | *   | *  | *  | *   | *   | *  | *   | *  | *   | *   |    |   |
| Period | 1–4  | 1  | 2  | 3   | 4   | 1–4 | 1  | 2  | 3   | 4   | 1–4 | 1  | 2  | 3   | 4   | 1–4 | 1  | 2  | 3   | 4   | 1–4 | 1  | 2  | 3   | 4   | 5  | 1–4 | 1  | 2   | 3   | 4  | 5 |
| BBCH94 | P    | ns | ns | ns  | ns  | ns  | *  | ns | ns  | ns  | ns  | ns | ns | *   | *   | *   | *  | ns | ns  | ns  | ns  | ns | ns | ns  | ns  | ns | ns  | ns | ns  | ns  | ns |   |
|        | SPI  | ns | ns | ns  | ns  | ns  | *  | ns | ns  | ns  | ns  | ns | ns | *   | *   | *   | *  | ns | ns  | ns  | ns  | ns | ns | ns  | ns  | ns | ns  | ns | ns  | ns  | ns |   |
|        | CWB  | ns | ns | ns  | ns  | ns  | *  | ns | ns  | ns  | ns  | ns | ns | *   | *   | *   | *  | ns | ns  | ns  | ns  | ns | ns | ns  | ns  | ns | ns  | ns | ns  | ns  | ns |   |
|        | Tmax | ns | ns | ns  | ns  | ns  | ns | ns | *   | *   | *   | ns | *  | ns  | ns  | *   | ns | ns | ns  | *   | ns  | ns | ns | ns  | ns  | ns | ns  | ns | ns  | ns  | ns |   |
|        | Tmin | ns | ns | ns  | ns  | *   | ns | ns | *   | *   | *   | *  | *  | *   | *   | *   | *  | *  | *   | *   | *   | *  | *  | *   | *   | *  | *   | *  | *   | *   |    |   |
|        | Ta   | ns | ns | ns  | ns  | ns  | ns | ns | *   | *   | *   | *  | *  | *   | *   | *   | *  | *  | *   | *   | *   | *  | *  | *   | *   | *  | *   | *  | *   | *   |    |   |
| Period | 7    | 8  | 9  | 7–9 | 8–9 | 7   | 8  | 9  | 7–9 | 8–9 | 7   | 8  | 9  | 7–9 | 8–9 | 7   | 8  | 9  | 7–9 | 8–9 | 7   | 8  | 9  | 7–9 | 8–9 | 7  | 8   | 9  | 7–9 | 8–9 |    |   |

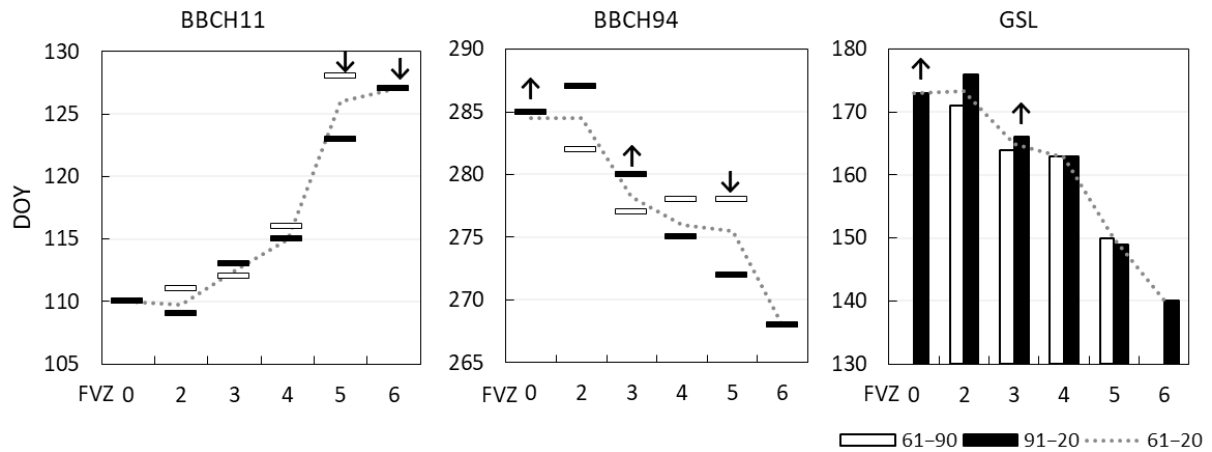


**Fig. 4.** Mean onset of BBCH11 (a) and BBCH94 (b) of *Fagus sylvatica* L. in individual FVZ in the normal periods 1961–1990, 1991–2020 and over the whole period 1961–2020 are shown in graphs. The black arrows indicate the directions of Sen's slopes of significant Mann-Kendall trends over the whole period of observations.

#### *Abies alba* Mill.

In the lower FVZs 0 to 2, the results of partial correlation indicated non-significant correlations between BBCH10 and climate variables (Table 4). Since there was no data

available from these FVZs in CLINO 1961–1990, it was not possible to compare the mean onset days to those from CLINO 1991–2020. The trends were non-significant over the last 30 years as well. On the contrary, in FVZs 3

**Table 4.** Pearson's partial correlation analyses between phenological phase BBCH10 of *Abies alba* Mill. and climate variables: P (Precipitation), SPI (Standardized Precipitation Index), CWB (Climatic Water Balance) and T (Temperature) of individual months and periods in individual FVZ (Forest Vegetation Zones). A significant ( $p < 0.05$ ) correlation is marked with \*. Positive correlations are set in blue; the negatives in pink.

| FVZ    | 0    |    |    |    |    |    | 1   |    |    |    |    |    | 2   |    |    |    |    |    | 3   |    |    |    |    |   |
|--------|------|----|----|----|----|----|-----|----|----|----|----|----|-----|----|----|----|----|----|-----|----|----|----|----|---|
| BBCH10 | P    | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns |   |
|        | SPI  | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns | ns |    |   |
|        | CWB  | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns | ns |    |   |
|        | Tmax | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns | ns |    |   |
|        | Tmin | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns | ns |    |   |
|        | Ta   | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns | ns |    |   |
| Period | 1-4  | 1  | 2  | 3  | 4  | 5  | 1-4 | 1  | 2  | 3  | 4  | 5  | 1-4 | 1  | 2  | 3  | 4  | 5  | 1-4 | 1  | 2  | 3  | 4  | 5 |
| FZV    | 4    |    |    |    |    |    | 5   |    |    |    |    |    | 6   |    |    |    |    |    |     |    |    |    |    |   |
| BBCH10 | P    | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns |   |
|        | SPI  | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns |   |
|        | CWB  | ns | ns | ns | *  | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns |   |
|        | Tmax | *  | *  | ns | *  | *  | *   | *  | *  | ns | ns | *  | *   | *  | *  | *  | *  | *  | *   | *  | *  | *  | *  |   |
|        | Tmin | *  | ns | ns | *  | *  | *   | *  | *  | ns | ns | *  | *   | *  | *  | *  | *  | *  | *   | *  | *  | *  |    |   |
|        | Ta   | *  | *  | ns | *  | *  | *   | *  | *  | ns | ns | *  | *   | *  | *  | *  | *  | *  | *   | *  | *  | *  |    |   |
| Period | 1-4  | 1  | 2  | 3  | 4  | 5  | 1-4 | 1  | 2  | 3  | 4  | 5  | 1-4 | 1  | 2  | 3  | 4  | 5  |     |    |    |    |    |   |

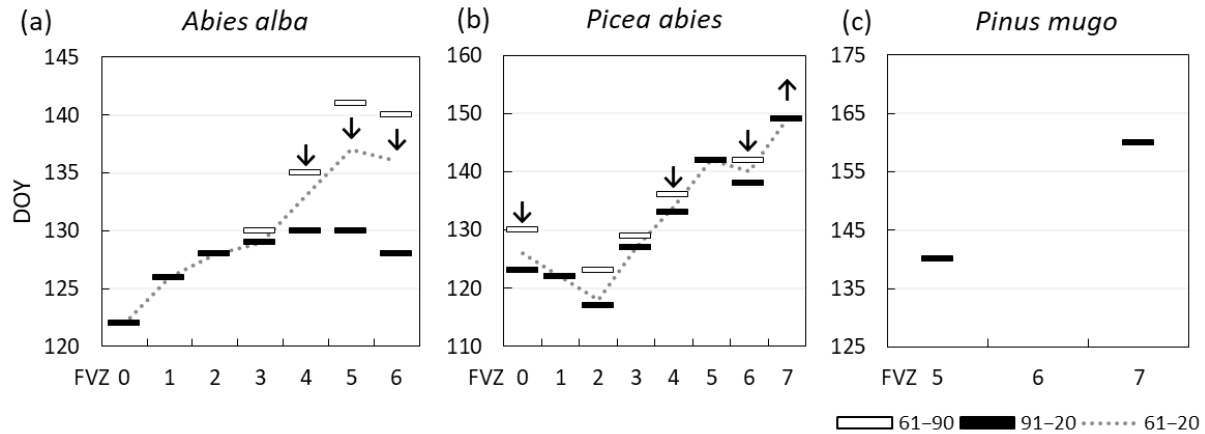


**Fig. 5.** Mean onset of BBCH10 for (a) *Abies alba* Mill., (b) *Picea abies* [L.] Karst. and (c) *Pinus mugo* Turra in individual FVZ in the normal periods 1961–1990, 1991–2020 and over the whole period 1961–2020 are shown in graphs. The black arrows indicate the directions of Sen's slopes of significant Mann-Kendall trends over the whole period of observations.

to 6, a significant correlation occurred between increasing temperatures and the earlier BBCH10 (Table 4). In these upper FVZs, the trends indicated significant shifts to earlier BBCH10 (Fig. 5a) by  $\sim 0.05$ ,  $\sim 0.15$ , and  $\sim 0.20$  days  $\text{yr}^{-1}$  in FVZs 4, 5, and 6, respectively. These advances of mean BBCH10 decreased the altitude-related temporal variability in onsets between individual FVZs causing BBCH10 to start within 4 days in FVZs from 1 to 6. The effect of precipitation-based variables was found only in FVZ 4 where lower CWB in March led to the later onset and vice versa.

#### *Picea abies* [L.] Karst.

In FVZs 0 to 6, the results of partial correlations (Table 5) showed a significant effect of higher temperature-based variables in the months preceding BBCH10 on earlier onset. The Mann-Kendall trends indicated a significant shift to an earlier onset in FVZ 0, 4, and 6 (Fig. 5b) by  $\sim 0.23$ ,  $\sim 0.13$ , and  $\sim 0.18$  days  $\text{yr}^{-1}$ , respectively, and close to significant in FVZ 2 by  $\sim 0.16$  days  $\text{yr}^{-1}$  ( $p = 0.06$ ) and FVZ 3 by  $\sim 0.09$  days  $\text{yr}^{-1}$  ( $p = 0.10$ ). In FVZ 1 and 5, we did not have comparable station data in CLINO 1961–1990.

In FVZs 4 and 6, the correlation with precipitation-based variables (P, CWB, SPI, Table 5) identified the earlier onset of BBCH10 when these variables were higher. Figures 2b and 2c show balanced or increased P and CWB between CLINO 1961–1990 and 1991–2020 in these FVZs, therefore, the limiting effect of precipitation-based variables for earlier BBCH10 is not expected. With the warming climate, a contradictory trend was found in FVZ 7 (Fig. 5b) indicating a delay of BBCH10 by  $\sim 0.34$  days  $\text{yr}^{-1}$  over CLINO 1991–2020. In FVZ 7, BBCH10 significantly correlated only with minimum temperatures in February and the winter-spring season (months 1–4) indicating the delayed onsets with increasing minimum temperatures (Table 5). These unusual reactions of spruce in FVZ 7 to temperature may relate to the overall fitness and vitality of spruce forests in FVZ 7 of the studied region.

#### *Pinus mugo* Turra

The sufficiently long datasets of *Pinus mugo* Turra phenological observations (at least 70% of data during a 30-year long normal period) were available only in CLINO

**Table 5.** Pearson's partial correlation analyses between phenological phase BBCH10 of *Picea abies* [L.] Karst. and climate variables: P (Precipitation), SPI (Standardized Precipitation Index), CWB (Climatic Water Balance) and T (Temperature) of individual months and periods in individual FVZ (Forest Vegetation Zones). A significant ( $p < 0.05$ ) correlation is marked with \*. Positive correlations are set in blue, the negative in pink.

| FVZ    | 0    |    |    |    |    | 1  |     |    |    |    | 2  |    |     |    |    | 3  |    |    |     |    |    |    |    |    |
|--------|------|----|----|----|----|----|-----|----|----|----|----|----|-----|----|----|----|----|----|-----|----|----|----|----|----|
| BBCH10 | P    | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns |    |    |    |
|        | SPI  | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns |    |    |    |
|        | CWB  | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns |    |    |    |
|        | Tmax | *  | *  | *  | *  | *  | *   | *  | *  | *  | ns | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns |    |    |    |
|        | Tmin | *  | *  |    | ns | ns | *   | *  | *  | *  |    | ns | ns  | ns | ns | *  | ns | ns | ns  | ns | ns |    |    |    |
|        | Ta   | *  | *  | *  |    | ns | *   | *  | *  | *  | *  | ns | ns  | ns | ns | *  | ns | ns | ns  | ns | ns |    |    |    |
| Period | 1–4  | 1  | 2  | 3  | 4  | 5  | 1–4 | 1  | 2  | 3  | 4  | 5  | 1–4 | 1  | 2  | 3  | 4  | 5  | 1–4 | 1  | 2  | 3  | 4  | 5  |
| FZV    | 4    |    |    |    |    | 5  |     |    |    |    | 6  |    |     |    |    | 7  |    |    |     |    |    |    |    |    |
| BBCH10 | P    | ns | ns | ns | *  | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns | *  | ns | ns | ns  | ns | ns | ns | ns | ns |
|        | SPI  | ns | ns | ns | *  | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns | *  | ns | ns | ns  | ns | ns | ns | ns | ns |
|        | CWB  | ns | ns | ns | *  | ns | ns  | ns | ns | ns | ns | ns | ns  | ns | ns | *  | ns | ns | ns  | ns | ns | ns | ns | ns |
|        | Tmax | *  | ns | ns | *  | *  | *   | *  | *  | *  | *  | *  | *   | ns | *  | *  | *  | *  | *   | *  | *  | *  | *  | *  |
|        | Tmin | *  | ns | ns | ns | *  | *   | *  | *  | *  | *  | *  | *   | *  | *  | *  | *  | *  | *   | *  | *  | *  | *  | *  |
|        | Ta   | *  | ns | ns | *  | *  | *   | *  | *  | *  | *  | *  | *   | *  | *  | *  | *  | *  | *   | *  | *  | *  | *  | *  |
| Period | 1–4  | 1  | 2  | 3  | 4  | 5  | 1–4 | 1  | 2  | 3  | 4  | 5  | 1–4 | 1  | 2  | 3  | 4  | 5  | 1–4 | 1  | 2  | 3  | 4  | 5  |

1991–2020 in two FVZs. The difference in mean onset of BBCH10 between the FVZs was 20 days, from DOY 140 in FVZ 5 to DOY 160 in FVZ 7 (Fig. 5c). The trends in BBCH10 were not significant and opposite, pointing to a delayed onset in FVZ 5 by  $\sim 0.10$  days  $\text{yr}^{-1}$  but an advanced onset in FVZ 7 by  $\sim 0.30$  days  $\text{yr}^{-1}$ . The results of partial correlations indicated that only temperature-based climate variables significantly affected the onset of BBCH10. While the higher the mean and maximum temperatures in May, the earlier the onset (Table 6), but the warmer the February, the delay in BBCH10 was observed.

**Table 6.** Pearson's partial correlation analyses between the phenological phase BBCH10 of *Pinus mugo* Turra and the climate variables: P (Precipitation), SPI (Standardized Precipitation Index), CWB (Climatic Water Balance) and T (Temperature) of the individual months and periods within the individual FVZ (Forest Vegetation Zones). A significant ( $p < 0.05$ ) correlation is marked with \*. Positive correlations are set in blue, the negative in pink.

| FVZ    |      | 5  |    |    |    |    | 7   |    |    |    |    |    |
|--------|------|----|----|----|----|----|-----|----|----|----|----|----|
| BBCH10 | P    | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns | ns |
|        | SPI  | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns | ns |
|        | CWB  | ns | ns | ns | ns | ns | ns  | ns | ns | ns | ns | ns |
|        | Tmax | ns | ns | *  | ns | ns | *   | ns | ns | *  | ns | *  |
|        | Tmin | ns | ns | *  | ns | ns | *   | ns | ns | *  | ns | *  |
|        | Ta   | ns | ns | *  | ns | ns | *   | ns | ns | *  | ns | *  |
| Period | 1–4  | 1  | 2  | 3  | 4  | 5  | 1–4 | 1  | 2  | 3  | 4  | 5  |

### 3.3. Comparison of species phenology between forest vegetation zones

**FVZ 0 and 1.** Zlatník (1976) did not distinguish the alluvial forests from the basic classification of FVZs. Still, our results indicate that the mean growing season of *Quercus* sp. approached 180 days defined for FVZ 1 (Table 7) only in FVZ 0. On the contrary, the significant negative trend in the GSL of *Quercus* sp. in FVZ 1 due to both, later BBCH11 and earlier BBCH94, shortened the GSL to a mean length of 167 days. Regarding *F. sylvatica* L., all phenological stations from FVZ 1 were situated in alluvial forests (FVZ 0). Although the GSL of this species in FVZ 0 is not the longest of all, according to the trend analysis it has significantly delayed over CLINO

1990–2020. The trend to earlier BBCH10 was observed also in *P. abies* [L.] Karst. in FVZ 0, where it started a day later than in FVZ 1. As for *A. alba* Mill., we observed an earlier onset of BBCH10 in FVZ 0 than in FVZ 1, but both trends were not significant over the last CLINO.

**FVZ 2.** The GSL of *Quercus* sp. increased from 163 to 172 days between CLINOs and spanned into the range of 165–180 days defined in Zlatník (1976). The trend toward GSL extension in FVZ 2 was significant and related to the earlier BBCH11. The mean onset of spring phenophases in CLINO 1990–2020 for both, *Quercus* sp. and *Picea abies* [L.] Karst., was by DOY 116. *Fagus sylvatica* L. started leafing one week earlier and reached the longest GSL (176 days), which occurred in the ranges stated in Zlatník (1976, Table 7). Spring phenophases did not significantly shift and started the latest in *A. alba* Mill. (DOY 127 in CLINO 1990–2020).

**FVZ 3.** In both, *Quercus* sp. and *F. sylvatica* L., the GSL slightly exceeded the range of 150–165 days defined in Zlatník (1976). While trends in *Quercus* sp. were not significant, the GSL significantly extended in *F. sylvatica* L., which was related to later BBCH94. The onset of spring phenology was the earliest in *F. sylvatica* L. (DOY 113), followed by *Quercus* sp. (DOY 116), while the conifers were considerably delayed (DOY 128 and 129 for *P. abies* [L.] Karst. and *A. alba* Mill., respectively).

**FVZ 4.** In CLINO 1991–2020, the GSL was slightly longer in *F. sylvatica* L. (164 days) than in *Quercus* sp. (160 days), and still close to the upper limit of the range stated in Zlatník (1976, Table 7). While the phenophases delimiting the growing season in *F. sylvatica* L. did not change in a warming climate, *Quercus* sp. significantly advanced BBCH11 from DOY 131 to 120 between CLINOs. Similarly significant shifts in spring phenophases were observed in spruce and fir stations in FVZ 4.

**FVZ 5.** GSL in *F. sylvatica* L. exceeded the range stated in Zlatník (1976, Table 7) by 20 days but did not significantly change between CLINOs. *A. alba* Mill. utilized climate warming and started BBCH10 significantly earlier (DOY 130), which is 11 days earlier than *P. abies*

**Table 7.** Comparison of growing season lengths in days defined for each forest vegetation zone (FVZ) in Zlatník (1960, 1976) and those calculated over the normal periods 1961–1990 and 1991–2020 for *Quercus* sp. and *Fagus sylvatica* L.

| Species | not specified  | <i>Quercus</i> sp. |           | <i>Fagus sylvatica</i> L. |           |
|---------|----------------|--------------------|-----------|---------------------------|-----------|
| FVZ     | Zlatník (1976) | 1961–1990          | 1991–2020 | 1961–1990                 | 1991–2020 |
| 0       | —              | no data            | 175       | no data                   | 173       |
| 1       | 180            | 173                | 167       | —                         | —         |
| 2       | 165–180        | 163                | 172       | 171                       | 176       |
| 3       | 150–165        | 165                | 168       | 164                       | 166       |
| 4       | 130–160        | no data            | 160       | 163                       | 163       |
| 5       | 110–130        | —                  | —         | 150                       | 149       |
| 6       | 90–120         | —                  | —         | no data                   | 140       |
| 7       | 70–100         | —                  | —         | —                         | —         |
| 8       | < 60           | —                  | —         | —                         | —         |

[L.] Karst. and *P. mugo* Turra but still 7 days later than *F. sylvatica* L.

**FVZ 6.** GSL of *F. sylvatica* L. took 140 days in CLINO 1990–2020 and exceeded the range stated in Zlatník (1976, Table 7) by 20 days. *Fagus sylvatica* L., as well as *A. alba* Mill. and *P. abies* [L.] Karst., shifted their spring phenophases to earlier dates in a warming climate. In CLINO 1990–2020, *F. sylvatica* L. and *A. alba* Mill. started equally on average on DOY 128, and *P. abies* [L.] Karst. started 10 days later.

**FVZ 7.** Only two of all analysed species were observed in FVZ 7 – *P. abies* [L.] Karst. and *P. mugo* Turra. While *P. mugo* Turra slightly advanced BBCH10 in CLINO 1990–2020 (non-significant trend), *P. abies* [L.] Karst. significantly shifted the onset to later dates.

#### 4. Discussion

Climate data presented in Table 1 and Fig. 2 showed that the precipitation conditions still fit the established ranges for FVZs defined in Zlatník (1960, 1976), while the temperatures considerably increased above the ranges. During the second CLINO 1991–2020, we observed the increase of both, the annual air temperature and precipitation totals, but the climatic water balance (CWB) indicated increasing drought, particularly during the growing seasons. In Central Europe, heat and drought events occur more frequently than before recent climate change (Trnka et al. 2016; Lukasová et al. 2021a). As was indicated by Allen et al. (2015) or Středová et al. (2020), the negative effect of abiotic stressors like drought, high temperatures etc. leading to forest damage is considerably stronger when these occur at the same time or when a given area is affected by more of them in a short time. Based on modelled climate trajectories, Hlásny et al. (2014) suggested a change in species composition towards a higher share of drought-tolerant species as well as the use of drought-resistant provenances identified as paramount actions in forest adaptation in the region of Western Carpathians and adjacent lowlands.

In *Quercus* sp., the increased temperature in the winter and spring months significantly advanced the BBCH11 leading to shifts to an earlier onset of BBCH11 in FVZ 2 and 4 (Fig. 3). However, in FVZ 1, which spreads out in lowlands mainly in the south and west of Slovakia, significant shift to a later onset despite the positive effect of increasing temperature was revealed. We assume, that this trend in delayed BBCH11 by  $\sim 0.15$  days  $\text{yr}^{-1}$  could relate to low soil water content, which was however not evaluated in this study but should be further examined. This trend was found by taking advantage of the long-term observations at stands below 300 m of altitude and by distinguishing the alluvial forests (FVZ 0) from FVZ 1.

Therefore, our results differ from studies that analysed recent shorter periods (Bucha et al. 2023) or did not consider altitudinal differences (Kolářová et al. 2014). Compared to BBCH11, BBCH94 was significantly affected by both temperature and precipitation-based variables. While warming in months preceding BBCH94 delayed the onset in FVZs 0 to 3, the low precipitation and CWB advanced it in FVZs 0, 1, and 2. In these lower FVZs, the drought intensifies mainly during the summer months (Fig. 2c) and despite the xerothermic structure of the leaf and the root system, which can deal with different levels of soil water content (Škvareninová et al. 2017; Čehulić et al. 2019; Ciceu et al. 2020), *Q. robur* L. and *Q. petraea* [Matt.] Liebl. showed a certain level of drought sensitivity. From this group of *Quercus* sp., *Q. petraea* [Matt.] Liebl. is more tolerant to drought than *Q. robur* L. because of its more developed deep taproots (Eaton et al. 2016). The drought-related earlier colouring occurred particularly in lower FVZs, where the *Q. robur* L. prevails. Despite the effect of drought on the earlier onset of BBCH10, the trend to later BBCH94 was significant in FVZ 0 (Fig. 3) and this phenophase started later also in FVZs 2 and 4 in CLINO 1991–2020. The extension of GSL by  $\sim 0.83$  over 30 years in FVZ 0 is similar to that published in Kolářová et al. (2014), which indicated prolongation by  $0.90$  days  $\text{yr}^{-1}$  (31.6 days over 35 years). The lengthening of the growing period in response to climate warming, however, does not necessarily lead to higher productivity, as might be expected (de Sauvage et al. 2022), since the growth of these *Quercus* sp. is also strongly influenced by precipitation and CWB (Bose et al. 2021).

*Fagus sylvatica* L. and *Picea abies* [L.] Karst. are expected to lose great parts of their potential distribution range and be substituted by warm-adapted species (Thurm et al. 2018). In our study, earlier spring phenology in *Fagus sylvatica* L. significantly correlated with rising temperatures in the months preceding BBCH11. However, in the warming climate, the trends were non-significant in lower FVZs from 0 to 4, but significant in those higher. In FVZs 5 and 6, BBCH11 shifted to earlier dates by  $\sim 0.18$  and  $\sim 0.25$  days  $\text{yr}^{-1}$  respectively. These long-term trends are close to those published in Čufar et al. (2012), pointing to the advance by more than 1.5 days  $\text{decade}^{-1}$  ( $0.15$  days  $\text{yr}^{-1}$ ) for altitudes  $\sim 1,000$  m. In FVZ 6, at higher altitudes with sufficient precipitation, the significant correlation with SPI indicated delayed onset when precipitation increased above normal which may relate to the sensitivity of *F. sylvatica* L. to waterlogging. Geßler et al. (2007) concluded that waterlogged soils due to higher-than-average precipitation during the spring could negatively impact nutrient uptake and growth of beech. This negative effect of above-standard precipitation on BBCH11 in FVZ 6 will be further investigated. Compared to BBCH11, the later onset of BBCH94 in *F. sylvatica* L. (Table 3) depended on increased temperatures and sufficient precipitation. The earlier onsets were caused by lower P, SPI, and CWB during summer

in FVZs 2 and 3, which confirm that European beech autumn phenology at mid-to-high altitudes currently profits from climate warming, while it is susceptible to drought at lower altitudes and xeric climates (Mátyás et al. 2010; Lukášová et al. 2020). Our results follow the previously indicated premature leaf colouring caused by severe summer droughts (Bréda et al. 2006; Estrella & Menzel 2006) that was confirmed by widespread leaf discolouration and premature leaf shedding induced by the extreme summer droughts in 2015 and 2018 in European beech forests (Schuldt et al. 2020; Bigler & Vitasse 2021; Rukh et al. 2023). Despite the effect of drought, significant trends in delayed BBCH94 (Fig. 4) by  $\sim 1.21$  and  $\sim 0.17$  days  $\text{yr}^{-1}$  occurred in FVZs 0 and 3, respectively. On the contrary, in FVZ 5 the BBCH94 significantly shifted to an earlier onset by  $\sim 0.14$  days  $\text{yr}^{-1}$ . The results from the Swiss Alps pointed to similar patterns in leaf senescence in *F. sylvatica* L. At sites above 560 m a.s.l., beech experienced an advancement of leaf colouring with rates of  $1.35$  days  $\text{decade}^{-1}$  ( $0.14$  days  $\text{yr}^{-1}$ ), while at low elevations (at 200 m a.s.l.) it was delayed by  $0.55$  days  $\text{decade}^{-1}$  ( $0.06$  days  $\text{yr}^{-1}$ , Meier et al. 2021). Besides phenology, summer droughts also limit the growth of *F. sylvatica* L. at low elevations, especially in southern Europe (Filippo et al. 2007; Hartl-Meier et al. 2014), but decreased annual gross primary production due to water stress in mid-summer was reported from stands in central Europe (Dolschak et al. 2019), and also from the northern limits (Harvey et al. 2020).

As for *Picea abies* in FVZ 0 to 6, BBCH11 started earlier with increasing temperature-based variables, which confirms the importance of temperatures in spruce spring phenology indicated in previous studies (Svystun et al. 2021). A significant shift to an earlier onset was observed in FVZs 0, 4, and 6 (Fig. 5b), but close to significant trends occurred also in FVZs 2 and 3. The earlier onset of the vegetative phenophases on spruce between 155 and 860 m a.s.l. was reported also by Hájková et al. (2012) based on phenological data from the Czech Hydrometeorological Institute. However, despite the advancement in the start of growing seasons, the current climatic conditions in the Central European region are not suitable for growing Norway spruce at lower and middle elevations since severe drought at these altitudes has a substantial negative impact on the annual stem radial increment (Krejza et al. 2021). In addition, with the warming climate, a contradictory trend was found in *P. abies* [L.] Karst. in FVZ 7 (Fig. 5b) indicating a significant delay of BBCH10. In FVZ 7, increasing minimum temperatures in February and the winter-spring season (months 1–4) significantly correlated with the later onset of BBCH10 (Table 5). Phenological stations in FVZ 7, which were included in this study, are located in the High Tatra Mountains – Dolný Smokovec (1,400 m a.s.l.) and Štrbské pleso (1,340 m a.s.l.). In High Tatra Mts., the vitality of *P. abies* [L.] Karst. started to decline after the windstorm in 2004 (Šustek et al. 2017) when the forests

became destabilized and exposed to the spruce bark beetle infestation, climate extremes, and fires (Bartík et al. 2014; Mezei et al. 2017; Vaneková et al. 2020; Lukášová et al. 2021a; Hláška et al. 2022). Therefore, this negative trend in BBCH10 may relate to the decreased vitality and adverse environmental conditions in spruce forests in the highest altitudes.

*Abies alba* Mill. significantly shifted to earlier BBCH10 (Fig. 5a) in FVZs 4, 5, and 6, respectively. These shifts were related to the significant effect of increasing temperature, which was observed only in these upper FVZs. The effect of precipitation-based variables was found only in FVZ 4, where lower CWB led to later onset and vice versa. The adaptation of *A. alba* Mill. to increasing summer drought is coupled with slow growth (Csilléry et al. 2020), nevertheless, it exhibits wider growth rings than *P. abies* [L.] Karst.. Furthermore, *A. alba* Mill. shows the overall highest resistance to drought, particularly at higher altitudes (Vitali et al. 2017), and high resilience potential in the modelled future climate (Mátyás et al. 2021), but in climatic marginal sites, warming and water deficit could attenuate its growth (Mihai et al. 2021).

In *Pinus mugo* Turra only temperature-based climate variables significantly affected the onset of BBCH10 when the higher temperatures in May led to earlier onset (Table 6), while higher temperatures in February delayed BBCH10. In FVZs 5 and 7, the mean temperature in February ranges between  $-5$  and  $0$  °C (Fig. 2a) but the higher temperatures may occur during warmer winters or when freezing temperatures are interrupted by winter warm spells. Lukášová et al. (2021b) studied the effect of winter-to-spring climate variables on the greenness of *P. mugo* Turra thickets. They concluded that while warmer winter seasons correlated with the increase in greenness, the winter warm spells led to its decrease. During winters when frozen soil blocks water uptake for several months, the low water potentials in combination with freeze-thaw events expose *P. mugo* Turra to increased temperature stress and impair recovery processes (Mayr et al. 2019). The onset of new sprouts may therefore be affected by the physiological condition after the winter. Compared to temperature, the precipitation-based variables did not affect the onset of BBCH10. The *P. mugo* Turra phenological stations were located in FVZs with sufficient precipitation (above 800 mm per year, Table 1, Fig. 2b) and highly positive CWB (Fig. 2c), therefore, the effect of temperature and photosynthetic active radiation is more pronounced compared to other climate variables (Lukášová et al. 2022).

## 5. Conclusions

Phenological patterns of climax tree species growing in forest vegetation zones of Western Carpathian forests were examined in the context of the change in climatic

conditions during two recent climate-normal periods (1961–1990 and 1991–2020). The trend analyses indicate that the greatest shifts to earlier spring phenophases were found in FVZ 0 and the upper FVZs of the vertical distribution ranges of species, where the onsets during CLINO 1961–1990 were considerably delayed. The only exception were spruce stands in FVZ 7, where the trend indicated a shift to later BBCH10.

The phenological responses to climate variables were species-specific and differed between individual FVZs. Results of partial correlations indicate that temperature was the main factor controlling the onset of phenological phases for the considered species. However, with reduced precipitation and adverse climatic water balance during the summer period, the onset of BBCH94 started significantly earlier in FVZs 0 to 2 in *Quercus* species and FVZs 2 and 3 in the case of *Fagus sylvatica* L. The differences in the climatic water balance between CLINOs point to an increase in summer drought over the last 30 years particularly in FVZ 1 (oak), 2 (beech-oak) and 3 (oak-beech); therefore, we consider summer droughts to be significant limiting factor for the length of the growing season in oak (FVZs 1 and 2) and beech forests (FVZs 2 and 3) in the Western Carpathian region.

An interesting avenue for future research remains the analysis of potential changes under various climate-change scenarios using regional climate models in combination with the presented results. The recommendations for forest management coming from this study are to focus on the provenience research, e.g.: i) to support the establishment of the provenience trials with provenances originating from drier regions in FVZs, where the effect of drought was the most pronounced; ii) to implement the results of provenance trials in forest management practice and national legislation.

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