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Spring and Autumn Phenology in Sessile Oak (*Quercus petraea*) Near the Eastern Limit of Its Distribution Range

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Abstract: Due to the visible and predictable influence of climate change on species' spatial distributions, the conservation of marginal peripheral populations has become topical in forestry research. This study aimed to assess the spring (budburst, leaf development, and flowering) and autumn (leaf senescence) phenology of sessile oak (*Quercus petraea*), a species widespread across European forests close to its ranges' eastern limit. This study was performed in Romania between spring 2017 and 2020, and it included a transect with three low-altitude populations, a reference population from its inner range, and a sessile oak comparative trial. The temperature was recorded to relate changes to phenophase dynamics. We identified small variations between the reference and peripheral populations associated with climatic conditions. In the peripheral populations, budburst timing had day-of-year (DOY) values <100, suggesting that sessile oak may be more susceptible to late spring frost. Furthermore, we found spring phenophase timing to be more constant than autumn senescence. Moreover, budburst in the sessile oak comparative trial had obvious longitudinal tendencies, with an east to west delay of 0.5–1.4 days per degree. In addition, budburst timing influenced leaf development and flowering, but not the onset of leaf senescence. These findings improve our understanding of the relationship between spring and autumn phenophase dynamics and enhance conservation strategies regarding sessile oak genetic resources.

Keywords: phenology; sessile oak; peripheral populations; comparative trial; provenances; climate change

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1. Introduction

Plant phenology is generally defined as the scientific study of periodic biological events and how they are affected by seasonal climatic and weather conditions [1–6]. The period of phenological events, including budburst, leaf development, flowering, and leaf senescence, are recognised as having increased sensitivity to climate change [7–11].

Monitoring phenophases is relatively simple and, in some cases, long series of data records exist due to many forestry studies being performed to assess or model the phenological variability of forest vegetation [12–18]. Additionally, phenology is considered a key determinant of tree spatial distributions [19]. Consequently, it is frequently used to predict future shifts in species' geographical ranges in response to climate change [20].

There is a rapidly expanding body of evidence indicating that environmental changes are a growing threat to the persistence and sustainability of forests [21], with peripheral populations considered among the ecosystems most vulnerable to these phenomena [22–27]. In this context, peripheral populations play an important role in preserving biodiversity [28] and estimating species evolution [29,30]. Unlike central populations in a species' range, peripheral populations mainly exist in adverse climatic environments [31]. Moreover, they are usually characterised by isolated and small population sizes [32,33], leading to reduced

genetic variation [34] associated with an increased risk of extinction [35–37]. However, peripheral populations, particularly those found at the lower natural range limits, are viewed as better adapted to stressful conditions, and consequently are likely to display valuable adaptations [38–41].

In this study, we focused on sessile oak (*Quercus petraea* [Matt.] Liebl.), a species widespread across European forests that is included in numerous phenological investigations [42–52]. However, the phenology of low-altitude sessile oak populations is not fully known [40,53], particularly for those found near the eastern boundary of the species distribution area. Therefore, it is important to assess both spring and autumn phenology and their relationship with local climate conditions under the expected environmental changes.

In Romania, *Quercus petraea sensu lato* (including *Quercus petraea* (Matt.) Liebl. ssp. *petraea* (Liebl.) Soó, *Quercus petraea*. ssp. *dalechampii* (Ten.) Soó, and *Quercus petraea* ssp. *polycarpa* (Schur) Soó) covers approximately 8.3% of the forested area [54], making it the most widespread native oak species. While the common sessile oak is a hill species with typical mesothermal behaviour [55], there are situations when this species enters the forest–steppe area, forming pure or mixed stands with the other two thermophilic sessile oak trees [56,57]. The climate in these marginal populations differs sharply from the hill area (higher average annual temperatures, lower average annual rainfall, and intense evapotranspiration), leading to numerous consequences for mesophilic species such as sessile oak at the limit of its tolerance range.

While some studies have evaluated sessile oak phenology at its lower altitudes in Romania [58,59], they have focused mainly on a single location. Moreover, sessile oak was a poorly represented taxon among the studied phytocenosis. In this context, the unique characteristics of peripheral populations constantly exposed to climate pressures and soil drought represent an understudied area that requires further consideration. Therefore, this study evaluated the phenological structure of low-altitude sessile oak populations near the eastern limit of the species' general distribution range.

We focused on the following key objectives: (i) assess the onset of budburst and the leaf development dynamics; (ii) analyse the flowering phenology and establish the correspondences or differences from the budburst phenology; (iii) analyse the autumnal leaf senescence; (iv) evaluate the phenological behaviour of sessile oak populations originating from the entire area of the species in Romania and compare it to the areas of the peripheral populations studied. Furthermore, we assessed the intra- and inter-specific phenological structures of low-altitude populations to better understand their adaptive and evolutionary potential under conditions expected to occur due to global climate change. In addition, the data obtained from the comparative analysis of populations will provide a foundation for establishing strategies for the use and conservation of sessile oak genetic resources. Finally, knowledge of the level of intra- and inter-specific phenological variability in sessile oak comparative trials will inform the selection and promotion in plantations of the most suitable provenances to ensure the stability of forest ecosystems.

2. Materials and Methods

2.1. Study Site and Sampling

The phenological research included four populations of sessile oak (Table 1), three of which (SAT, OLT, FUN) are representative for their peripheral/marginal position (at low altitude for sessile oak in the research area, along a north–south transect, respectively, in close proximity to the eastern limit of the general sessile oak distribution). In addition, for the comparative analysis, we chose a reference population from the inner part of the species' range (HEL) and a sessile oak comparative trial (FAN), where 10 provenances from the sessile oak area in Romania were tested (Figure 1, Table 1).

Table 1. Geographic location, sample size, and climate conditions of the sampled sessile oak populations.

Label	Population	No. of Trees	Trees Characteristics			Geographical Position			Climatic Conditions	
			DBH (cm)	Height (m)	Age	Latitude (N)	Longitude (E)	Altitude (m)	Annual Average Temperature (°C)	Annual Rainfall (mm)
FUN	Fundeanu	34	30.3	16.6	88	45°58′	27° 41′	210	9.6	470
OLT	Oltenesti	50	27.6	19.9	73	46°34′	27° 53′	305	9.2	530
SAT	Satu Nou	50	59.6	25.3	107	46°58′	27° 49′	300	9.2	535
HEL	Heltiu	43	34.5	25.0	90	46°14′	26° 55′	490	8.9	544
FAN *	Fantanele	50	18.2	16.1	34	46°39′	26° 43′	260	9.6	590

* Sessile oak comparative trial.

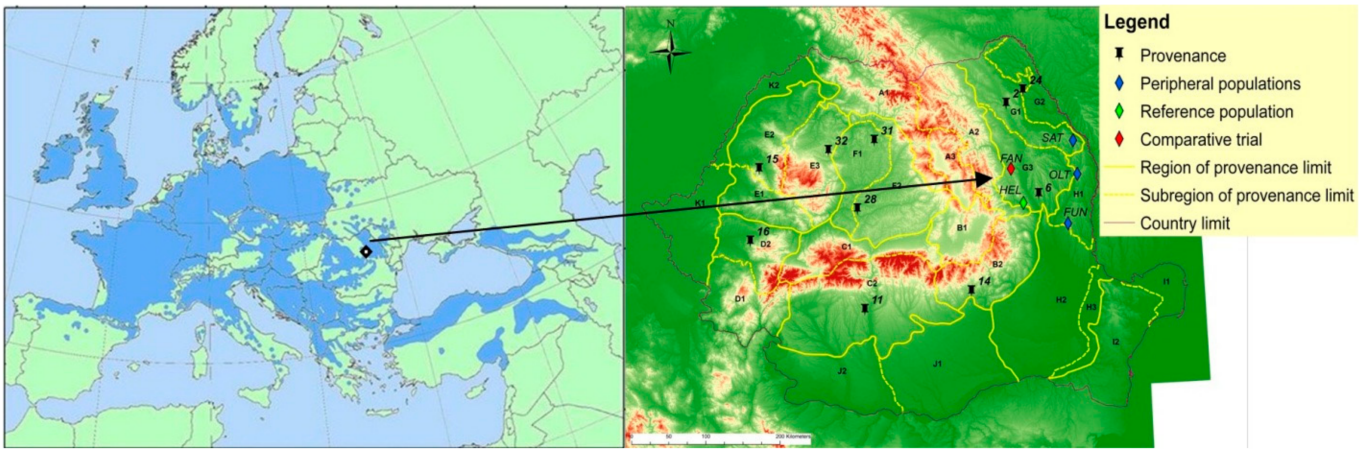


Figure 1. The natural range of sessile oak [60] (**left**), the location of the research area, and the geographic location of the origins according to the ecological subregions (A1 Eastern Carpathians–Weastern range, A2 Eastern Carpathians–Eastern range, A3 Eastern Carpathians: Giurgiu-Ciuc Depression, B1 Curved Carpathians–Brasov Depression, B2 Curved Carpathians-Exterior range, C1 Meridional Carpathians–Northern range, C2 Meridional Carpathians–Southern range, D1 Banat Mountains: Mehedinti-Cerna-Semeniuc, D2 Banat Mountains: Tarcu-Poiana Rusca, E1 Apuseni Mountains-Zarand and Metaliferi Mountains, E2 Western Apuseni Mountains, E3 Eastern Apuseni Mountains, F1 Transylvania Plain, F2 Transylvania Tableland, G1 Suceava Tableland and Siret and Iasi Hills, G2 Jijia Plain, G3 Barlad Tableland and Bacau Hills, H1 Covurlui Tableland, H2 Siret and Baragan Plains, H3 Danube Ponds, I1 Danube Delta, I2 Dobrogea Tableland, J1 Bucharest Plain, J2 Oltenia Plain, K1 Timis and Arad Plains, K2 Crisurile, Carei and Somes Plains) (**right**).

A total of 227 mature individuals were identified and phenologically evaluated in the four selected populations. For the FAN comparative trial, five trees from each of the ten provenances were selected randomly (Table 2).

Table 2. Location and geographical coordinates of the tested provenances in the FAN comparative trial.

Provenance	Ecological Subregion of Provenance		Provenance Location			
	Code *	Name	Forest District Production Unit Amenajistic Unit	Latitude (N)	Longitude (E)	Altitude (m)
2	G150	Suceava Tableland and Siret and Iasi hills	Dolhasca V Dolhasca 20 A	47°07′	26°37′	325
6	G350	Barlad Tableland and Bacau hills	Sascut IV Gaiceana 52A	46°10′	27°05′	300
11	C250	Outer Southern Carpathians	Babeni III Sirineasa 10 A, 26 B	44°55′	24°14′	290
14	B250	Outer Curvature Carpathians	Valeni III Slanic 45 A	45°23′	23°03′	490
15	E250	Western Apuseni Mountains	Beius VII Cerbu 201 C,202 B	46°40′	22°22′	300
16	D250	Banat Mountains: Tarcu Poiana Ruscai	Faget V Vladeana 90 B, 91 B	45°45′	22°05′	410
24	G26C	Jijia Plain	Botosani IV Poienita-Turbuleni 46 B	47°45′	26°40′	130
28	F250	Transylvania Tableland	Blaj II Valea Lunga 19 G	46°12′	23°54′	420
31	F150	Transylvania Plain	Lechinta V Matei 16	47°02′	24°20′	425
32	E350	Eastern Apuseni Mountains	Cluj IX Mara 38	46°45′	23°34′	600

* Subregions of provenance established in Romania [61].

2.2. Phenological Observations

This study was performed between spring 2017 and 2020 to cover the spring phenophases (budburst—BB, leaf development—LD, and flowering—FL) and autumn leaf senescence—LS. The phenological development of all phenophases followed the protocol proposed for oaks as part of the Tree4Future project [62] prepared by E. Chesnoiu (Institutul Național de Cercetare-Dezvoltare în Silvicultură (INCDS) "Marin Drăcea", Bucharest, Romania) and L.E. Pâques (Institut National de la Recherche Agronomique (INRA), Orléans, France), consisting of four different stages for budburst and leaf development (0: > 50% of buds are fully closed (dormant stage); 1: >50% of buds are swollen and the first green leaflets are visible; 2: >50% of buds have grown leaflets without a distinguishable petiole or base shape; 3: >50% of leaves are fully expanded), two stages for flowering (FL; 0: >50% of male inflorescences are formed and green-yellow but have not released pollen; 1: >50% of inflorescence released pollen and are yellow-brown), and three stages for leaf colouring (1: >50% of foliage is still dark green, except the bottom part of leaves, which have begun

to discolour; 2: >50% of leaves change colour to light green with yellow spots; 3: >50% of leaves are yellow).

For the flowering phase, we recorded only the maturation of male inflorescences because the maturation of the male and female flowers is intercorrelated [63], and the flowering phenophase for male flowers is easier to follow than for female flowers [58].

The phenophases stages were determined at intervals of 2–4 days by examining the entire crown of each individual tree (Table 1), always in the same direction, with 20 × 50 binoculars [64].

A temperature and relative humidity sensor (HOBO Pro v2) were installed at each site to enable the correlation of phenophases stages with climate.

Phenological data were analysed using the STATISTICA v.8.0 statistical software (StatSoft Inc., Tulsa, OK, USA) [65]. Initially, we used the Shapiro–Wilk test to confirm that the phenological variables are normally distributed, given that the studied populations do not have an equal number of trees. Subsequently, because we found them to be non-normally distributed, the Kruskal–Wallis test was used to explore whether significant differences exist between them.

Furthermore, the relationship between variables in each year and the geographic parameters, including the ecophysiological latitude, of each site was assessed using Spearman's rank correlation coefficient (r_s). The ecophysiological latitude (Le) represents the latitude (L) corrected by altitude (A), where a 100 m difference in altitude is equal to one degree of latitude, determined using the formula Le = L + A/100 [66].

3. Results

3.1. Budburst and Leaf Development

The budburst occurrence differed significantly by year ($p < 0.001$, Kruskal–Wallis test) for all populations. Amongst the peripheral populations FUN, OLT, and SAT, sessile oak showed an extremely small difference in the average date for budburst (Table 3). Moreover, there was only a few days difference between them and the reference HEL population, with a maximum average advance of 5 days for the FUN population. Unlike the peripheral populations, HEL showed the lowest inter-annual variability and the smallest range (9 days) for the start of the budburst.

Table 3. Characteristic values of budburst and leaf development phenophases date observed for sessile oak in the analysed populations and FAN comparative trial for the period 2017–2020.

Population	Budburst (DOY)—Stage I					Leaf Development (DOY)—Stage III					BB-LD Dynamic		
	Min	Max	Mean ± SE	Range	SD	Min	Max	Mean ± SE	Range	SD	No. of Days	Average T (°C)	∑ T (°C)
Peripheral populations													
FUN	88	104	96 ± 0.38	16	4.4	101	114	109 ± 0.27	13	3.2	13.2	11.1	230.4
OLT	90	107	98 ± 0.27	17	3.7	104	120	111 ± 0.26	16	3.8	13.2	10.9	217.8
SAT	90	104	98 ± 0.23	14	3.1	106	120	112 ± 0.26	14	3.5	14.0	10.5	217.1
Mean of peripheral populations	89	105	98 ± 0.16	16	3.7	104	118	111 ± 0.16	14	3.5	13.5	10.8	221.8
Reference population													
HEL	97	106	101 ± 0.20	9	2.4	106	120	116 ± 0.25	14	3.3	15.4	10.4	214.5
Comparative trial													
FAN	95	112	103 ± 0.32	17	4.6	109	124	117 ± 0.29	15	3.9	15.4	10.4	236.9

SD—standard deviation; ΣT (°C)—sum of average daily temperatures.

The budburst starts in the peripheral populations before the reference population, except for 2018, when it starts almost at the same time (Figure 2). The later onset of budburst in the peripheral populations in 2018 compared to the other years was associated with lower temperatures between leaf senescence in the previous year and the start of budburst in the current year (data not shown). Consequently, the later start of vegetation growth in

2018 resulted in a shorter time for leaf phenophase (i.e., the number of days from budburst (stage I) until leaves reached the full size (stage III)) in the three peripheral populations. A similar situation was observed with the FAN comparative trial in 2018, where it required 4 days on average for all individuals to budburst, ranging between 7 and 11 days (data not shown).

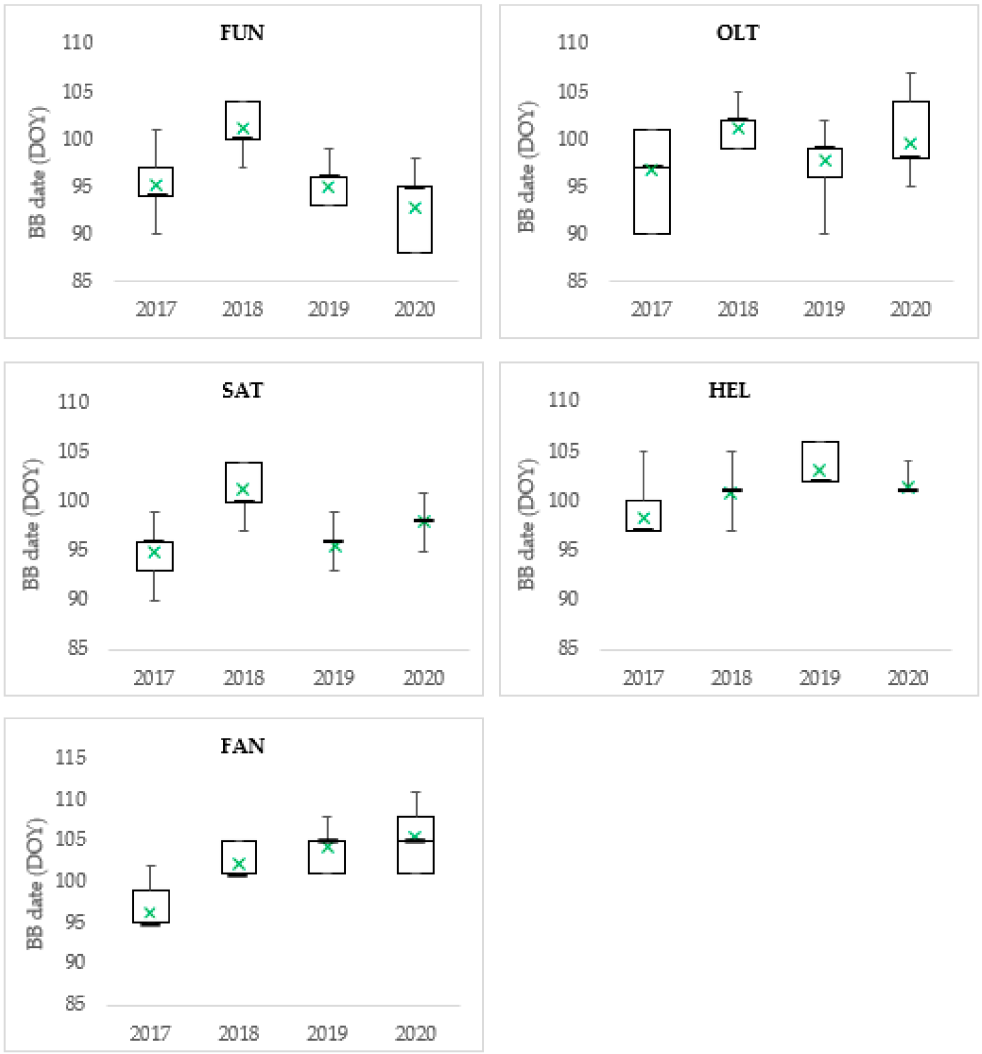


Figure 2. Boxplot diagram of sessile oak budburst phenophase in the studied populations. The bottoms and tops of boxes denote the 25 and 75% quartiles; the bold lines denote the median. The whiskers represent the minimum and the maximum DOY values. The green crosses indicate the mean value across all trees in each population.

In the FAN comparative trial, the budburst date range was the largest at 17 days, the earliest budburst dates recorded in 2017 (DOY 95) and the latest in 2020 (DOY 112; Figure 2).

The number of days required for leaves to complete expansion (from stage I to stage III) was between 13 to 16 days on average across all populations, with the process at its fastest in the peripheral populations.

There were extremely small differences in the thermal sum (sum of daily average temperatures) between 1 January and budburst across peripheral populations, decreasing from the southern to the northern regions of the transect (Table 4). In the HEL population, the thermal sum was slightly higher than in the peripheral populations (11.3% for SAT,

3.6% for OLT, and 1.8% for FUN) over this period and about 4.3% smaller than the FAN comparative trial.

Table 4. Average daily temperature summed from 1 January to budburst (A) and from LS in the previous year until BB in the current year (B).

Population / ∑ T (°C) ± SD	FUN	OLT	SAT	HEL	FAN
(A) 1 January-BB DOY	191.5 ± 5.5	188.0 ± 5.6	173.0 ± 5.6	195.1 ± 5.5	203.8 ± 5.6
(B) LS DOY-BB DOY	438.4 ± 5.0	445.3 ± 5.3	447.0 ± 5.1	500.2 ± 4.7	500.8 ± 5.0

SD—standard deviation; ΣT (°C)—sum of average daily temperatures.

Conversely, the thermal sum between leaf senescence in the previous year and budburst in the current year increased from the most southerly peripheral population to the most northerly. However, the differences were very small. The thermal sums of the HEL and FAN populations were similar and higher than those of the peripheral populations. Additionally, from the standard deviation values, it can be mentioned that all populations' interannual variability shows similar patterns of variation over the recorded period (Table 4).

The local provenances 2 Dolhasca, 6 Sascut, and 24 Botosani—all within the G region (The Moldavian Plateau) where the comparative trial was conducted—were among the fastest to reach budburst dynamic stage I in all studied years. Moreover, the budburst onset for the local provenances occurred at about the same time as the HEL population, located in the G region, except in spring 2017. The same was true for the SAT population, also located in the G region, for the first two years of the study. However, the local provenances had a later budburst in the last two years of the study. While the differences in the average budburst date across provenances are not considerable, the slowest onset of budburst was found for the provenances 32 Cluj and 15 Beius, both in the E region (Apuseni Mountains).

Furthermore, a significant positive correlation was found between the budburst and provenance altitude in the data of the FAN comparative trial for all four years of the study (Table 5). Moreover, the budburst was significantly and indirectly correlated with the longitude of the sites, reflecting the positive correlation between site longitude and the rate of leafing. Therefore, our sessile oak data indicate a delay in budburst from east to west of 0.5 to 1.4 days for each degree of longitude. However, no significant correlations were observed between the budburst date and ecophysiological latitude (Table 5).

Table 5. Spearman's rank correlation coefficients and their significance levels between phenophases and the geographical gradients of the origins.

Phenophase	Year of Observation	Altitude (m)	Latitude (N)	Ecophysiological Latitude	Longitude (E)
Budburst	2017	0.310 * 0.012	−0.104 0.481	0.251 0.079	−0.379 * 0.022
	2018	0.322 * 0.022	−0.254 0.075	0.179 0.213	−0.322 * 0.020
	2019	0.300 * 0.034	−0.049 0.736	0.210 0.142	−0.493 *** <0.001
	2020	0.386 ** 0.006	−0.239 0.095	0.253 0.077	−0.581 *** <0.001

Table 5. *Cont.*

Phenophase	Year of Observation	Altitude (m)	Latitude (N)	Ecophysiological Latitude	Longitude (E)
Flowering	2017	0.276 0.067	0.027 0.860	0.223 0.141	−0.334 * 0.025
	2018	0.204 0.155	−0.463 *** <0.001	0.046 0.751	−0.419 ** 0.002
	2019	0.283 * 0.046	−0.304 * 0.032	0.183 0.234	−0.574 *** <0.001
	2020	0.132 0.363	−0.349 * 0.013	−0.038 0.795	−0.322 * 0.022
Senescence	2017	−0.391 ** 0.005	−0.256 0.073	−0.457 ** 0.001	0.331 * 0.019
	2018	−0.034 0.814	−0.260 0.068	−0.262 0.054	0.262 0.066
	2019	−0.184 0.202	−0.277 0.051	−0.243 0.090	0.089 0.538

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Both budburst and leaf development had small standard deviation values, suggesting low interannual variability. Across populations, the greatest variation was found in the comparative trial and the lowest was found in the reference population.

3.2. Flowering

During the flowering phenophase in spring 2017, a wide geographic area, including all studied populations, experienced a period of thermal stress. Following a period with mean air temperatures above 10 °C, the air temperature decreased and persisted for several days (DOY 109–115). The sudden drop in temperature was accompanied by heavy snow, catching the flowers in the full maturation process, and minimum temperatures dropped below 0 °C at night. Across sites, minimum temperatures ranged from −2.0 °C to −0.9 °C.

Therefore, individuals with visible flower injuries were observed in all populations. The reference population was the worst affected, with only 53.5% of the individuals having completed the flowering process. In the peripheral populations, the percentage of individuals that suffered from the low temperatures was smaller, 24.0% in SAT, 12.0% in OLT, and 11.8% in FUN. In the FAN comparative trial, there were injuries only to individuals in provenances 11 Babeni, 14 Valeni, and 24 Botosani, the latter having the largest proportion of injured trees. Nevertheless, the flowering phenophase overlapped with the leaf-development phenophase for all populations, except for the FUN population, where the lowest average DOY values were recorded (Table 6).

Pollen release started after 11–14 days after the budburst and lasted 7–10 days on average, depending on the population. Consistent with the other two spring phenophases, the flowering phenophase shows a similar pattern of standard deviation.

The average daily recorded temperatures of the OLT, SAT, and HEL populations were highly similar. The FUN population, located at the southernmost point in terms of altitude and latitude, had the highest temperature, leading to faster flowering compared to the other populations.

Within our comparative trial area, flowering time was positively correlated with latitudinal and longitudinal gradients (Table 5), except in 2017, when it was only correlated with longitude. Moreover, flowering time and altitude were significantly positively correlated in 2019 ($p < 0.05$, Spearman's rank correlation test), but not in the other years. However, we observed no significant correlation between flowering time and ecophysiological latitude.

Table 6. Representative flowering phenophase dates for sessile oak observed in the studied populations and the FAN comparative trial.

Population	Flowering (DOY)					Temperature °C		
	Min	Max	Mean ± SE	Range	SD	Average	∑T > 5 °C	No. of Days [a]
Peripheral populations								
FUN	101	114	109 ± 0.31	13	3.7	12.4	80.0	7.0
OLT	104	117	110 ± 0.22	13	3.1	11.8	96.6	8.3
SAT	106	120	111 ± 0.23	14	3.4	11.4	94.3	8,5
Mean of peripheral populations	104	117	110 ± 0.15	13	3.4	11.9	90.3	7.9
Reference population								
HEL	106	120	113 ± 0.28	14	3.1	11.1	90.5	8.0
Comparative trial								
FAN	109	124	117 ± 0.24	15	3.4	10.1	107.9	9.5

[a] The difference between DOY BB and DOY flowering; SD—standard deviation; ΣT (°C)—sum of average daily temperatures.

3.3. Leaf Senescence

Differences in the onset of leaf senescence across years were also statistically significant ($p < 0.01$, Kruskal–Wallis test). Sessile oak showed greater inter-individual variation in the date of leaf senescence (DOY 281–313, 32 days) than in budburst (DOY 88–112, 24 days) across the five populations (Tables 3 and 7). The average date of leaf senescence varied by less than one week among the peripheral populations, which differed from the reference population by almost three weeks (Table 7). However, there were only small differences in the leaf senescence duration among populations, ranging between 23 and 26 days.

Table 7. Representative values of leaves senescence and bioactive season date observed for sessile oak in the studied populations and the FAN comparative trial.

Population	SS (DOY)				Bioactive Season			SD
	Min	Max	Mean ± SE	Range	No. of Days [a]	Climate Conditions		
						Average T (°C)	∑ T (°C)	
Peripheral populations								
FUN	287	313	301 ± 0.65	26	225	17.8	3806.7	6.5
OLT	287	310	297 ± 0.40	23	220	17.5	3576.3	4.9
SAT	287	310	296 ± 0.48	23	220	17.4	3500.4	5.8
Mean of peripheral populations	287	311	298 ± 0.29	24	222	17.6	3627.8	5.7
Reference population								
HEL	281	307	282 ± 0.66	26	210	17.1	3271.2	7.5
Comparative trial								
FAN	281	307	293 ± 0.47	26	212	17.2	3347.1	5.7

[a] The difference between DOY BB and DOY leaves senescence; ΣT (°C)—sum of average daily temperatures; SD—standard deviation.

For the year 2018, which had a later budburst start date, the peripheral populations had an earlier onset of autumn leaf senescence (Figure 3).

During the first two seasons, the peripheral populations had later leaf colouring compared to the HEL population by more than 14 days in 2017 and almost a week in 2018, but occurred at about the same time in 2019, with a delay of 4 days for the FUN population and only 1 day for OLT and SAT.

Compared to the HEL population, the comparative trial also had a similar inter-individual variation range but a later average leaf senescence date (Tables 3 and 7).

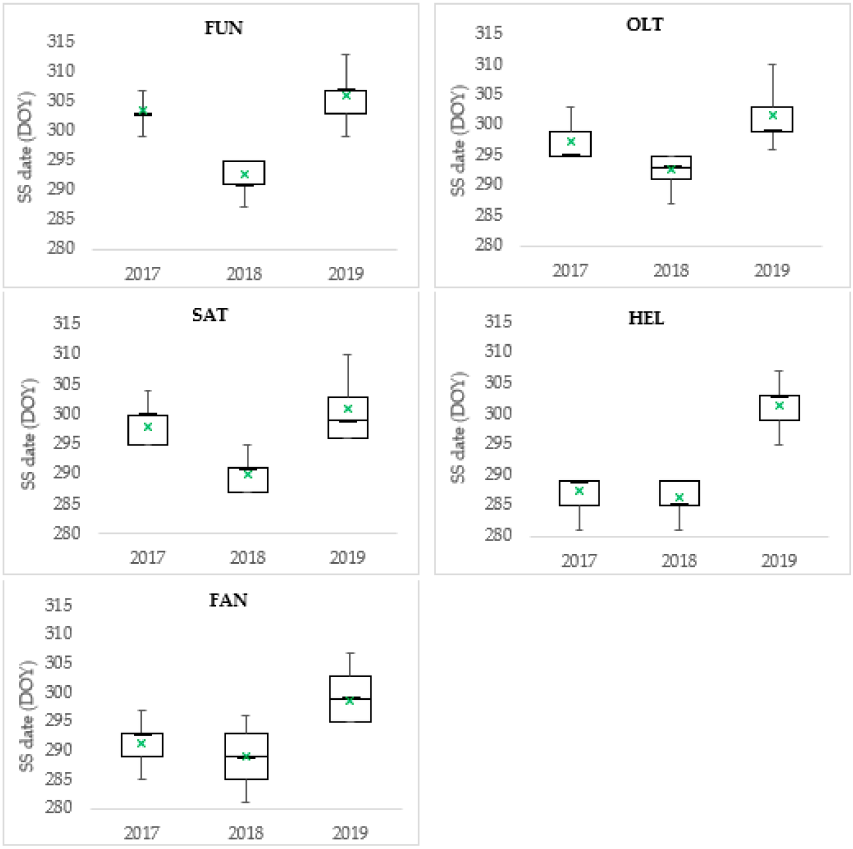


Figure 3. Boxplot diagram of sessile oak senescence phenophase in the studied populations. The bottoms and tops of boxes denote the 25 and 75% quartiles; the bold lines denote the median. The whiskers represent the minimum and the maximum DOY values. The green crosses indicate the mean value across all trees in each population.

In contrast with budburst, leaf senescence was significantly correlated with the geographical gradients of the origins only in 2017. Specifically, leaf senescence had weak negative correlations with altitude and longitude and a moderately positive correlation with the ecophysiological latitude (Table 5).

Overall, the variation of leaf senescence from one year to the next was small in the comparative trial. However, there were changes at the level of provenance, particularly in 32 Cluj, which had the earliest leaf autumn colouring for each of the three consecutive years.

In addition, the standard deviation values showed that senescence has smaller interannual variability than budburst (Table 7). The coefficients of variation were smaller for the peripheral populations compared to the reference one at the population level, indicating a greater consistency in leaf senescence.

The recorded temperatures during the bioactive season were higher in the peripheral populations, with only slight differences between them. The onset of senescence occurred earlier (DOY 281) and finished faster (DOY 307) in the HEL reference population than in the FAN comparative trial because these populations are located in the sub-Carpathian area, resulting in a shorter bioactive season in these areas.

3.4. Correlations

The budburst across the studied years was significantly positively correlated with medium-to-low correlation coefficients (Table 8). Significant correlations were also found with leaf development phenophase across the studied years, but only in half of the areas

studied. Flowering was also significantly correlated across the studied years, but with low to medium correlation coefficients.

Table 8. Spring and autumn phenophase correlations based on the phenological records.

Phenophase	Population	Years of Observation											
		2017–2018		2018–2019		2019–2020		2017–2019		2017–2020		2018–2020	
		r_s	*p*	r_s	*p*	r_s	*p*	r_s	*p*	r_s	*p*	r_s	*p*
BB	FUN	0.347 *	0.044	0.343 *	0.047	0.440 **	0.009	0.433 *	0.011	0.656 ***	<0.001	0.402 *	0.018
	OLT	0.585 ***	<0.001	0.304 *	0.043	0.471 ***	<0.001	0.487 *	0.014	0.487 ***	<0.001	0.416 **	0.002
	SAT	0.417 **	0.003	0.397 **	0.005	0.340 *	0.018	0.586 ***	<0.001	0.348 *	0.015	0.596 ***	<0.001
	HEL	0.474 **	0.002	0.321 *	0.038	0.375 *	0.015	0.341 *	0.027	0.495 ***	<0.001	0.310 *	0.045
	FAN	0.533 ***	<0.001	0.370 **	0.008	0.438 **	0.001	0.301 *	0.033	0.479 ***	<0.001	0.448 **	0.001
LD	FUN	0.063	>0.05	0.165	>0.05	0.403 *	0.018	0.252	0.150	0.450 **	0.008	0.165	>0.05
	OLT	0.175	>0.05	0.149	>0.05	0.237	>0.05	0.214	>0.05	0.197	>0.05	0.063	>0.05
	SAT	0.355 *	0.013	0.580 ***	<0.001	0.394 **	0.006	0.329 *	0.022	0.173	>0.05	0.361 *	0.012
	HEL	0.235	>0.05	0.174	>0.05	0.305 *	0.049	0.400 **	0.009	0.375 *	0.014	0.225	>0.05
	FAN	0.442 **	0.001	0.347 *	0.013	0.308 *	0.030	0.354 *	0.012	0.273	>0.05	0.399 **	0.004
FL	FUN	0.358 *	0.037	0.340 *	0.049	0.539 **	0.001	0.523 **	0.001	0.527 **	0.001	0.361 *	0.036
	OLT	0.372 *	0.012	0.428 **	0.002	0.395 **	0.005	0.320 *	0.034	0.375 *	0.012	0.417 **	0.003
	SAT	0.353 *	0.035	0.331 *	0.022	0.389 **	0.006	0.347 *	0.038	0.372 *	0.026	0.421 **	0.003
	HEL	0.417 *	0.048	0.488 **	0.001	0.405 **	0.008	0.425 *	0.043	0.401	>0.05	0.479 **	0.001
	FAN	0.317 *	0.034	0.560 ***	<0.001	0.388 **	0.005	0.314 *	0.036	0.300 *	0.045	0.327 *	0.020
SS	FUN	0.110	>0.05	0.171	>0.05	-	-	0.266	>0.05	-	-	-	-
	OLT	0.282 *	0.047	0.170	>0.05	-	-	0.180	>0.05	-	-	-	-
	SAT	0.396 **	0.005	0.208	>0.05	-	-	0.172	>0.05	-	-	-	-
	HEL	0.448 **	0.003	0.015	>0.05	-	-	0.091	>0.05	-	-	-	-
	FAN	0.632 ***	<0.001	0.412 **	0.003	-	-	0.562 ***	<0.001	-	-	-	-

r_s—Spearman rank coefficient; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Statistically significant correlations were found with leaf senescence in the FAN comparative trial. Moreover, significant correlations with leaf senescence were also detected for the OLT, SAT, and HEL populations in 2017 and 2018.

Sessile oak showed significant correlations between the spring phenophases across years, particularly budburst with leaf development and flowering (Table 9). However, significant correlations were not frequent between budburst and leaf senescence (Table 9), suggesting that the onset of budburst does not influence the start of senescence.

Table 9. Correlations between phenophases based on the recorded phenological years.

Phenophase	Population	Years of Observation							
		2017		2018		2019		2020	
		r_s	*p*	r_s	*p*	r_s	*p*	r_s	*p*
BB-LD	FUN	0.605 ***	<0.001	0.551 **	<0.001	0.348 *	0.044	0.740 ***	<0.001
	OLT	0.363 **	0.009	0.293 *	0.039	0.327 *	0.020	0.488 ***	<0.001
	SAT	0.292 *	0.044	0.371 **	0.009	0.333 *	0.021	0.427 **	0.002
	HEL	0.319 *	0.039	0.361 *	0.019	0.376 *	0.014	0.332 *	0.031
	FAN	0.066 **	0.008	0.557 ***	<0.001	0.463 ***	<0.001	0.567 ***	<0.001
BB-FL	FUN	0.562 **	0.001	0.348 *	0.044	0.618 ***	<0.001	0.648 ***	<0.001
	OLT	0.344 *	0.022	0.403 **	0.004	0.723 ***	<0.001	0.702 ***	<0.001
	SAT	0.328 *	0.044	0.291 *	0.045	0.399 **	0.005	0.336 *	0.020
	HEL	0.423 *	0.045	0.329 *	0.033	0.327 *	0.034	0.485 **	0.001
	FAN	0.441 **	0.002	0.503 ***	<0.001	0.446 **	0.001	0.743 ***	<0.001

Table 9. *Cont.*

Phenophase	Population	Years of Observation							
		2017		2018		2019		2020	
		r_s	*p*	r_s	*p*	r_s	*p*	r_s	*p*
BB-SS	FUN	0.528 **	0.001	0.188	>0.05	0.231	>0.05	-	-
	OLT	0.282 *	0.047	0.180	>0.05	0.170	0.238	-	-
	SAT	0.130	>0.05	0.224	>0.05	0.319 *	0.027	-	-
	HEL	0.001	>0.05	0.380 *	0.013	0.243	>0.05	-	-
	FAN	−0.220	>0.05	−0.078	>0.05	−0.187	>0.05	-	-

r_s—Spearman rank coefficient; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Finally, no significant correlation between budburst and previous year senescence was observed for most of the populations (Table 10).

Table 10. Correlations between budburst and previous year senescence based on the recorded phenological years.

Phenophase	Population	Years of Observation					
		2017–2018		2018–2019		2019–2020	
		r_s	*p*	r_s	*p*	r_s	*p*
Previous year SS-BB	FUN	0.256	>0.05	0.202	>0.05	0.32	>0.05
	OLT	0.045	>0.05	0.079	>0.05	0.114	>0.05
	SAT	0.238	>0.05	0.319 *	0.027	0.017	>0.05
	HEL	0.009	>0.05	0.414 **	0.006	0.069	>0.05
	FAN	−0.085	>0.05	−0.229	>0.05	−0.239	>0.05

r_s—Spearman rank coefficient; * $p < 0.05$, ** $p < 0.01$

4. Discussion

4.1. Budburst Phenology

Despite the sum of the average daily temperatures between 1 January and the date of budburst decreasing in the peripheral populations from the south of the transect to the north, small phenological differences were observed between populations. This finding can be explained by thermal differences not significantly influencing populations located along the ~120 km latitudinal transect. The average budburst date in the peripheral sessile oak populations (DOY 98, 8 April) was similar to that reported by Tomescu [67] in the Dobrina forest in Romania (DOY 99, 9 April), located at 200 m altitude near our OLT population. However, the duration of the time series observations and the locations were not the same and, therefore, these comparisons should be treated with caution. Still, the results show that similar budburst dates 70 years ago and nowadays could be encountered. More recent phenological observations carried out in the Fundeanu forest [58,68] showed an identical average value for sessile oak budburst (Apostol unpublished data) to our data. Our observations made at the same location (FUN population) showed a two-day advance in the average budburst (DOY 96, 6 April). This very small difference in average budburst for sessile oak at the same location could be because only a smaller number of sessile oak trees were monitored in previous studies.

Moreover, compared to extra-Carpathian sessile oak phenological studies, the average budburst in our peripheral populations occurred almost two weeks earlier than the average budburst indicated for sessile oak in the OPTIMix experimental plots in France (DOY 111; [69]) and 3 to 6 days later than the average budburst obtained for sessile oak in low-elevation populations (<387 m above sea level) in the Gave Valley, France (DOY 92–95; [70]).

However, this difference is only illustrative because both previous studies considered different evaluation scales for leaf unfolding. These differences highlight the adaptive phenological features of sessile oak populations located near the eastern limit of the species' general area.

We observed that the average budburst in the reference HEL population was very close to that of the peripheral populations (+2 days), and the range of budburst variation was almost twice as small as the peripheral populations. However, most individuals completed phenophase close to the average date, suggesting a greater reduction in behavioural diversity in the reference population for budburst. For instance, de Sauvage et al. [71] studied nine populations of sessile oak along an altitudinal gradient in the central Pyrenees in France and found smaller phenological variability for populations situated at higher elevations.

Numerous studies performed in comparative trials of sessile oak [42–44] have shown that the budburst phenology varies with latitude, with southern leafing earlier than northern populations. However, these findings contrast with those of Jensen [72], who found in comparative trials of sessile oak and pedunculate oak that northern provenances budded earlier than southern provenances. However, some studies have also reported similar clinal variations along altitudinal gradients [46,47].

In the FAN comparative trial, it was observed that the adaptive variation of the sessile oak provenances followed a longitudinal and altitudinal rather than latitudinal tendency (Table 5), with the lower eastern altitudes leafing earlier, indicating that less heating is required to trigger this phenophase than in higher western altitudes.

Unlike latitude, the influence of longitude in plant phenology is more obscure because it does not affect day length [73]. The effect of longitude on budburst can be considered a possible mechanism for adapting to local conditions associated with the need to avoid exposing leaves to late frosts, a behaviour observed in beech [74]. However, we found a clear east–west tendency at the time of budburst for the studied provenances.

4.2. Flowering Phenology

The abnormal spring event in 2017, where temperatures dropped sharply below 0 °C after a period with average air temperatures over 10 °C, coincided with a period of pollen release that partially compromised the flowering phenophase. It is important to note that several studies define this type of event as frost [46,75–77]. Unlike vegetative structures, the reproductive structures are reported to be more sensitive to frost [78], supported by the absence of damage to the leaves.

The effects of spring frost on temperate oak species phenology have been well documented. They are associated with the early timing of flowering, potentially resulting in reproductive failure [79], since there is a high probability that the pollen release process will occur during adverse meteorological conditions. Therefore, the unfavourable climatic conditions in 2017 during pollen release likely harmed the flowering process, interrupting microsporogenesis and the elongation of the catkins, leading to their death [80].

The reference HEL population had the highest proportion of frost-injured individuals among the studied populations because its average flowering DOY was closer to the average frost date. The differences between populations in the damage intensity can be attributed to the stage of development at the time of frost exposure [42,81].

It should also be noted that in the long-term phenological study conducted by Chesnoiu [68] in the Fundeanu forest, sudden drops in temperature in 2009 (minimum temperature −1 °C) and 2015 (minimum temperature −3 °C) were recorded at the time of flowering (23 April), partially affecting tree inflorescence. Therefore, our observations confirm those previously reported in this forest.

In the FAN comparative trial, flower injuries were also associated with the developmental stage at the time of frost exposure. Consequently, the three provenances (11 Babeni, 14 Valeni, and 24 Botosani) that had trees in a more advanced flowering stage suffered flower damage in 2017, potentially explaining the increased frost sensitivity. However,

these results should be treated with caution, since there was only one episode of spring frost during this study, and further studies are required to confirm this observation.

In addition, there were geographic patterns with latitude and longitude and, to a lesser extent, altitude in flowering time in the FAN comparative trial (Table 5). The flowering date was negatively correlated with latitude and longitude, indicating that flowering occurs earlier in northern and eastern provenances than in southern and western provenances. There was also a significant positive correlation between flowering date and altitude only in 2019, suggesting lower-altitude provenances tend to release pollen earlier than higher altitude provenances.

In sessile oak, the role of geographic gradients in flowering onset has not been studied as extensively as budburst. For example, [82] found an association between the start of the oak pollen season and latitude, where southern populations flowered earlier than northern populations. In addition, [83] studied four *Quercus* species in the US, observing that latitude, longitude, and elevation were more likely to influence DOY flowering in western (*Quercus agrifolia* Née and *Quercus lobata* Née) than in eastern and central (*Quercus alba* L. and *Quercus rubra* L.) species.

In the four consecutive years studied, no meaningful differences in flowering period length (7–10 days) were observed among sites. This interval falls within limits observed in previous studies in mixed oak stands that reported a flowering period of 6 [58] to 12 days [59,68].

4.3. Leaf Senescence

The average leaf senescence date observed in the peripheral populations (DOY 298) is later than the average senescence DOY values reported in previous studies performed over half a century ago at the national level in sessile oak forest stands. For example, Tomescu [67] reported a DOY of 289 for sessile oak in the Dobrina forest, and Tomescu [84] reported a DOY of 273 for sessile oak in the Poieni forest located 360 m from our RAD population, suggesting a delay in leaf senescence of 1.7–4.6 days per decade. As mentioned previously, these differences should be treated with caution, since the phenological observation protocol is not the same, and the influence of inter-observer variability is very high [85]. Similarly, we observed a small delay in the average date of leaf senescence in the reference HEL population (DOY 282) and the FAN comparative trial (DOY 293) compared with nearby sites such as the Bradatel forest (DOY 273) and Casa cu Nuci forest (DOY 289; [84]). However, the average leaf senescence date for the peripheral populations was very close to that obtained by Chesnoiu [68] in the Fundeanu forest (DOY 299). Moreover, the differences in the leaf colouring average DOY in the peripheral populations were small compared to some European studies on autumn senescence in sessile oak that reported DOY of 299 [86] and 303 [45].

Numerous studies have indicated that leaf senescence will be progressively delayed over time under future climate-change scenarios [15,45,87–92]. In a prospective analysis, Delpierre et al. [86] proposed a pattern for sessile and pedunculate oak using data provided by the RENECOFOR network in France from 1997 to 2006. They predicted a trend toward a delay in leaf colouring of 1.7 days per decade for the period 1951–2099. In sessile oak in France, the simulations performed by Vitasse et al. [45] showed a delay in senescence of 1.4 days per decade. Moreover, the models explored by Nölte et al. [92] for sessile oak in Southwest Germany predicted a delay of 6–11 days per decade for the period 2070–2100 compared to 1985–2015. In contrast, it was shown that, due to global warming, the budburst phenology of oaks starts earlier by 1–3 days·°C^{-1} [93,94] up to 5–7 days·°C^{-1} [95,96].

These changes in the occurrence of phenological phases are also reflected in the length of the vegetation season [87,96–98], as can be seen in comparisons between our results and those reported previously for bioactive season lengths. Based on observations between 1956–1965, Tomescu [85] found that the vegetation period in sessile oak lasted, on average, 180 days regardless of geographical gradients (200 days at 100 m altitude and 160 at 650 m).

Therefore, we can observe a lengthening of the growing season by ca. 40 days over the last few decades. Indeed, many studies based on phenological observations highlight an obvious extension in growing season length [99,100], with positive effects on forest productivity [101,102]. However, this pattern was not evident in sessile oak [71].

The difference in the length of the growing season between the peripheral populations, the reference population, and the comparative trial is apparently associated with the sum of the average daily temperatures recorded during the vegetation season. This association was expected, as the reference HEL population and FAN comparative trial are located in premontane areas.

The magnitude of the spring phenophases' interannual variability (expressed by standard deviation) is higher than for leaf senescence.

While leaf senescence showed small variations across years for the FAN comparative trial, some differences were observed between provenances. For instance, the provenance 32 Cluj showed late budburst and early senescence across the three autumn seasons studied, likely reflecting its marginal location within the experimental trial.

Similar to budburst, leaf colouring variation in sessile oak with latitude has been reported [43,103]. Senescence is triggered earlier in high-latitude populations than in low-latitude populations due to variations in photoperiod length [104]. However, Vitasse et al. [105] found that the gradient variation of senescence with altitude is more likely to be caused by temperature than by photoperiod, a fact explained by the proximity between the sampled populations, leading to no variation in photoperiod between sites.

4.4. Correlations

In agreement with previous studies [49,106,107], the budburst timing was repeatable from year to year. However, the magnitude of repetition ($r_s < 0.6$) was medium to low, suggesting that not all sampled trees start to budburst at the same time in different years [63]. Nevertheless, microenvironmental variation can help explain the individual consistency between years in budburst development [94].

Similarly, the repeatable order of flowering in consecutive springs was observed despite inter-year differences in the time of pollen release. However, the low-to-medium Spearman's correlation coefficients we obtained indicate that only a small proportion of the sampled trees maintain their order when pollen is released, consistent with the observations of Craciunesc [59] and Chesnoiu [68].

Furthermore, we obtained positive correlations of budburst with leaf development and flowering. Therefore, the timing of budburst is a good indicator for the onset of leaf development and flowering. While this is consistent with some earlier studies [21,108], it is not with others [48,109].

In comparison, the timing of budburst and leaf senescence were correlated, albeit to a lesser extent, indicating that budburst is a poor indicator for the onset of leaf senescence. This finding is consistent with some earlier phenological studies [49,110], but not others [95,111]. Finally, no relationship was observed between budburst and previous year senescence, contradicting an earlier finding with sessile oak [110].

5. Conclusions

This study considered three peripheral sessile oak populations, a reference population from its inner range, and a comparative trial, and obtained results that contribute to the phenological understanding of the sessile oak. While variations in DOY were small among studied sites, they were sufficient to be associated with climatic conditions. In the peripheral populations, the specific climatic conditions resulted in budburst occurring before DOY 100. Consequently, sessile oak might be affected more often by late spring frost in the future.

We found that budburst and flowering dates were repeatable from year to year, consistent with the view that these phenophases are under genetic control. Interestingly, our results also showed that budburst in the FAN comparative trial followed longitudinal and altitudinal tendencies, likely reflecting the shared variation of environmental variables,

such as average annual temperature, the severity of the winter season, and other seasonal climatic variations among the origins of the seeds, rather than the influence of longitudinal differences themselves. Moreover, we found that the timing of the budburst influences the leaf development and flowering phenophases, but not necessarily the leaf senescence.

These data can serve as the foundation for establishing strategies for using and conserving sessile oak genetic resources and predicting future phenological changes under the threat of climate and environmental change.

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