

GENETIC DIVERSITY PATTERNS IN PHENOLOGICAL TRAITS OF
QUERCUS ROBUR L.

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QUERCUS ROBUR L.**

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ABSTRACT

GENETIC DIVERSITY PATTERNS IN PHENOLOGICAL TRAITS OF *QUERCUS ROBUR* L.

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Oaks are among the most adaptable temperate tree species, which makes them especially valuable in the context of climate change. Phenological traits are major predictors of a tree's response to climate. Hence, this study investigates genetic variation in bud phenology—specifically the timing of bud burst and bud set, as well as growing season length (GSL)—in *Quercus robur* L. (pedunculate oak) seedlings from different populations and mother trees within populations across four Central European countries. To answer the question of how much of the observed variation in bud phenology could be attributed to population-level differences versus among mother trees within populations, phenological data gathered through a common garden experiment was analyzed via nested ANOVA models.

Our findings revealed significant mother tree effects on genetic variation for most phenological traits, while population-level effects were only significant for terminal bud burst timing. Lateral phenological traits showed weak differentiation among popula-

tions, but among mother trees, specifically in bud burst and GSL, considerable variation was detected. Therefore, rather than being shaped by climate or geography, these traits appear to stem from within-population genetic differences. Additionally, the great variability and delayed timing observed in lateral buds may be a consequence of higher phenotypic plasticity in the lateral shoots, which may be contributing to the seedlings' survival in a changing climate.

Keywords: *Quercus robur* L., bud phenology, genetic variation, adaptive traits, climate change



ÖZ

***QUERCUS ROBUR* L. TÜRÜNÜN FENOLOJİK KARAKTERLERİNDE GENETİK ÇEŞİTLİLİK YAPILANMASI**

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Meşeler, en uyumlu ılıman iklim ağaç türlerinden biridir ve bu özellikleri onları iklim değişikliği bağlamında özellikle değerli kılar. Fenolojik özellikler, ağaçların iklimsel koşullara verdiği tepkileri öngörmede başlıca göstergelerdendir. Dolayısıyla bu çalışmada, Orta Avrupa'nın dört farklı ülkesinden ayrı ayrı popülasyonlardan, ve her popülasyon içerisinde farklı ana ağaçlardan gelen *Quercus robur* L. (saplı meşe) fidanlarının tomurcuk fenolojisindeki—özellikle tomurcuk açma ve tutma zamanları ile büyüme sezonu süresindeki (GSL)—genetik varyasyon incelenmektedir. Gözlemlenen varyasyonun ne kadarının popülasyon düzeyindeki farklılıklardan, ne kadarının aynı popülasyon içindeki ana ağaçlar arasındaki farklılıklardan kaynaklandığını anlamak amacıyla, ortak bahçe denemesiyle toplanan fenolojik veriler iç içe ("nested") ANOVA modelleriyle analiz edilmiştir.

Bulgularımız, çoğu fenolojik özellik üzerinde ana ağaçların genetik etkisinin anlamlı olduğunu, buna karşılık popülasyon düzeyindeki farkların yalnızca tepe tomurcuk

patlamasında belirgin olduğunu göstermektedir. Yan sürgünlerin fenolojik özellikleri ise popülasyonlar arasında zayıf bir ayrışma sergilerken, özellikle tomurcuk patlaması ve büyüme dönemi uzunluğu açısından popülasyon içi ana ağaçlar arasında belirgin varyasyon göstermiştir. Bu durum, ilgili özelliklerin bölgesel iklim ya da coğrafi desenlerden çok, popülasyon içindeki genetik farklılıklarla şekillendiğini düşündürmektedir. Yan tomurcukların fenolojisinde gözlenen yüksek değişkenlik ve gecikmeli zamanlama, lateral sürgünlerin daha yüksek fenotipik plastikliğe sahip olmasının bir sonucu olabilir; bu durum da fidanların büyümelerini yerel çevresel koşullara göre daha iyi ayarlayabilmelerine olanak sağlayabilir.

Anahtar Kelimeler: *Quercus robur* L., tomurcuk fenolojisi, genetik çeşitlilik, adaptif özellikler, iklim değişikliği



To the kind people who walk ahead, only to turn back and offer a hand.

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LIST OF ABBREVIATIONS

ABBREVIATIONS

ANOVA	Analysis of Variance
BB	Budburst
BS	Budset
GSL	Growing Season Length
LBB	Lateral Budburst
LBS	Lateral Budset
LGSL	Lateral Growing Season Length
MS	Mean Square
MT	Mother Tree
POP	Population
TBB	Terminal Budburst
TBS	Terminal Budset
TGSL	Terminal Growing Season Length
VC	Variance Component



CHAPTER 1

INTRODUCTION

1.1 The genus *Quercus* & *Quercus robur* L.

Oaks (*Quercus* spp.) are revered tree species that are often regarded as keystone species of temperate forests due to their crucial role in maintaining biodiversity and ecosystem stability [3]. Belonging to the genus *Quercus* within the beech family (*Fagaceae*), these trees and shrubs encompass approximately 450 species, both deciduous and evergreen, distributed throughout the Northern Hemisphere [4]. Characterized by their leaves with lobed edges and often with either toothed or serrate margins, oaks produce nuts known as acorns, which serve as a vital nutritional source for small animals [5, 2]. Beyond providing food through their fruits, these trees foster the habitats of countless organisms [6, 7]. For at least 7000 years, humans have also benefited from their sturdy lumber, as evidenced by the world's oldest wooden structure, a building constructed 7200 years ago from oak wood [8].

The taxonomically diverse genus *Quercus* is traditionally divided into two subgenera: *Quercus* (white oaks) and *Cerris* (Turkey oaks), with further sectional distinctions based on morphological and molecular traits [9]. *Quercus robur* L., commonly known as pedunculate oak or English oak, is a prominent species within section *Quercus* of subgenus *Quercus*. It is one of the most widespread and ecologically significant broadleaf trees in Europe, naturally occurring from the British Isles to the Caucasus, and thriving in a range of habitats including lowland forests, mixed stands, and occasionally pure oak woodlands [3, 2, 6].

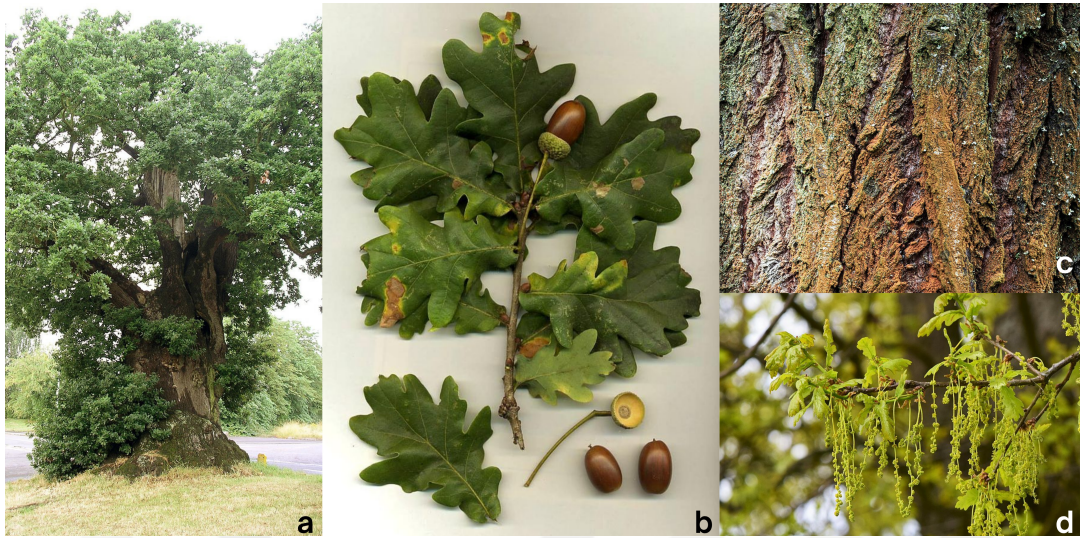


Figure 1.1: Composite image showing key morphological features of *Quercus robur* L.: (a) mature tree form; (b) characteristic lobed leaves and acorns with long stalk; (c) bark texture; (d) male flowers. Images by G-Man, Kurt Stueber, Michael Gäbler, and Krzysztof Ziarnik, used under Creative Commons licenses via Wikimedia Commons.

Q. robur is a large, long-lived deciduous tree that can reach heights of up to 40 meters and live for as long as 800 years [4]. The species is characterized by lobed leaves and long peduncles bearing acorns—traits that aid in its identification. As a monoecious and predominantly allogamous species, it bears both male and female flowers on the same individual but relies heavily on outcrossing, with pollination primarily occurring via wind [10]. This high rate of outcrossing enhances genetic variation within populations, which in turn supports its remarkable ecological plasticity and ability to colonize a wide range of environments across Europe [6]. Moreover, its frequent hybridization with closely related white oaks, particularly *Quercus petraea*, further contributes to this genetic and ecological flexibility [2, 11, 12].

1.2 Distribution of oaks & their significance in a changing climate

Aside from contributing to the survival of many organisms by providing them with the much-needed nutrients and habitat, they also demonstrate remarkable adaptability, thriving in a wide range of climates and soil conditions. In 2023, it was found

that the oak forests in Türkiye make up almost the 30% of the total forest area in the country [13]. Oak species collectively account for 15% of the total timber volume across the United States, and in the eastern states, nearly one-quarter of all growing stock consists of oaks [7]. Throughout Europe, species such as *Quercus robur* and *Q. petraea* seldom form pure stands, but they remain ecologically important components of mixed deciduous forests, particularly in areas where beech is absent or less competitive [2]. Their ability to thrive in varied environments is evident to the high adaptability of oaks.

Especially in these times of escalating climate change, the adaptability and resilience of oaks make them ever more necessary to forest ecosystems. Their deep roots, long lifespans, and tolerance to drought and temperature changes allow them to withstand environmental stresses that are expected to grow in the coming decades [2]. As climate change threatens biodiversity and disrupts ecological balance, oaks continue to provide essential ecosystem services—such as storing carbon, stabilizing soil, and regulating local climates—that help reduce the impacts of extreme weather conditions [7, 14, 15]. Additionally, the genetic diversity within and between populations of oak species offers valuable insights into adaptive traits, making them important subjects in research on climate-resilient forests [6, 4]. Prioritizing the conservation and study of oaks is essential for maintaining the long-term health and sustainability of forested landscapes. Their ecological importance, coupled with their cultural and economic significance, makes oaks an essential subject of study in forest ecosystems.

1.3 Bud burst, bud set & growing season length (GSL)

Phenology is the study of recurring biological events and the factors that influence their timing in relation to both biotic and abiotic conditions, as well as the interactions of these events within or between species [16]. Phenological patterns are considered key indicators of how temperate and boreal ecosystems respond to climate change [17]. Bud burst and bud set are two important phenological events for plants, and the time between these two events gives us the growing season length (GSL) of the plant.



Figure 1.2: Global distribution map of the *Quercus* genus and *Quercus robur* species. The global distribution of the genus was compiled based on data from Wikimedia Commons [1], while the European range of *Q. robur* was redrawn based on Eaton et al. [2].

Bud burst marks the beginning of a plant's growing season. During bud burst, dormant buds that contain and preserve leaves as stem units throughout winter break open when conditions are optimal, which typically coincides with the onset of spring. The most prominent environmental cues that trigger this phenomenon are temperature, photoperiod and winter chilling, although the sensitivity of each plant to each of these cues is affected by their genetic structure. [18, 19] The timing of bud burst is crucial for plant growth and survival, as it should align with optimal conditions for photosynthesis and resource availability. An early bud burst increases the risk of the plant getting exposed to spring frosts, while a late one would cause the growing season of the plant to get shorter.

It has been supported by many studies that the budburst timings of the terminal and lateral shoots differ, due to a concept called the "apical dominance". Apical dominance is described as "the control exerted by the shoot apex over lateral bud outgrowth" and is a form of paradormancy. This control is primarily maintained by the balance between auxin and cytokinin hormones, which are produced in the actively

growing shoot apices and roots, respectively. Auxin suppresses lateral bud outgrowth by moving downward from the apex, while cytokinin promotes bud activation by moving upward from the roots, counteracting auxin's inhibitory effect. The hormonal regulation of apical dominance is commonly explained by the widely accepted model based on the auxin-to-cytokinin ratio. Because of this phenomenon, the lateral bud burst often occurs later than that of the terminal bud [20, 21, 22].

Table 1.1: Descriptions of key terms used in the study

Term	Description in Study Context
Population	A group of trees originating from the same geographical location. In the study, populations represent distinct source environments and serve as the uppermost level of the nested experimental design.
Mother Tree	An individual mature tree within a population from which acorns were collected. Each mother tree represents a unique genetic contributor within its population and their offsprings are treated as their repeated samples.
Family	The group of seedlings derived from a single mother tree. Families represent the lowest genetic unit in the design, and individuals within are treated as repeated samples.
Bud	A meristematic structure on the shoot that develops into a leaf, flower, or another shoot. Within this study, the bud term is used exclusively for shoot buds.
Bud Burst	The phenological event marking the beginning of shoot growth, recorded as the date when a bud swells and gains a greenish hue.
Bud Set	The phenological event marking the cessation of shoot elongation, recorded as the date when the bud is fully formed.
Growing Season Length	The duration of growing season between bud burst and bud set, representing the active shoot elongation period.
Terminal Shoot	The primary axis of shoot growth at the apex of a seedling, representing vertical growth. Terminal buds are located at the shoot tip.
Lateral Shoot	A secondary branch emerging from the main axis, representing horizontal or side growth. Lateral buds form along the sides of the stem.

The bud set signifies the end of the growing season of the plant and the start of the dormancy period that will last through the winter. As the active growth of the plant ceases, the bud starts to form. During the bud set process, dormant buds that will burst in the next spring are formed, to ensure the survival of the plant through the cold, harsh winter days [18]. Accurate regulation of bud set allows the plant to maximize growth potential while minimizing the risk of being subjected to early frost, and for this reason, the timing of this transition phase is crucial for the plant's survival. In indeterminate species, bud set is mostly induced by a photoperiod threshold and low temperatures [23]. On the other hand, in determinate species, as is the case for most oak species, environmental cues are not as important for the initiation of the bud set. The bud set commences in these species once the development of the pre-formed stem units is completed, though the environmental cues may have an effect on the onset and the duration of the process [24, 22]. Since bud set partially coincides with the cessation of growth, variation in growth cessation timing can offer insights into the genetic control of this phenological event. For instance, in a common-garden study, Jensen and Hansen observed that *Q. robur* individuals from the Netherlands and the British Isles ceased growth significantly later than those from northern provenances such as Finland, Norway, and Sweden [3]. This variation in growth cessation timing indicates population-level differences in timing of bud set and highlights the strong genetic control over it.

Growing season length is the total time between the bud burst and the bud set events, within which the growing, as well as the flowering and the pollination of the plant occurs. According to Swiss Agricultural Research findings, the growing season has increased around thirty days since 1900s, possibly due to the climate change [25]. Changes induced to the growing season length through shifts in the timing of bud burst and bud set events can lead to frost or drought damage, and may even prevent the successful maturation of fruits and seeds. Consequently, alterations in seasonal timing could impact productivity and influence species abundance and distribution [19].

While many previous studies have examined population-level responses in bud phenology, they often focus on average bud burst dates and broad geographical comparisons, overlooking the considerable genetic variation that exists within populations — particularly among individual mother trees. This within-population genetic variation has rarely been quantified, despite its relevance for predicting how populations may respond to ongoing climatic shifts. Additionally, most genetic studies have relied on a limited number of genotypes or artificial settings, limiting their ecological relevance [23]. A better understanding of within-population variability and how it compares to between-population variation is crucial for improving phenological models and anticipating forest responses to environmental change [17, 26]. This study addresses these gaps by examining phenological traits of *Q. robur* seedlings grown in a common garden, with a focus on examining variation at both population and mother trees within population levels. By doing so, it provides novel insight into the genetic structure underlying phenology, revealing significant mother tree effects and highlighting the importance of intra-population variation. These findings contribute to current efforts to designate climate-resilient seed sources. Moreover, the study’s emphasis on lateral shoots, which is often overlooked in phenological studies, adds to the inadequate knowledge of their possible role in plant survival and adaptation mechanisms.



CHAPTER 2

OBJECTIVES OF THE STUDY

This study aims to investigate the genetic variation in phenological traits—specifically bud burst, bud set, and growing season length (GSL)—in *Quercus robur* (pedunculate oak). These traits are known to be highly sensitive to climatic conditions and play an essential role in determining how plants respond to environmental changes. Understanding the genetic control of phenological timing is therefore essential for predicting the adaptive potential of a species under changing climate scenarios.

In this study, phenological data from *Q. robur* seedlings raised in a common garden setting from acorns collected from mother trees across multiple European populations were analysed, with a specific focus on quantifying how much of the observed variation in phenological traits could be attributed to differences among populations versus variation among families within populations, represented here by individual mother trees. By breaking down the contributions of population-level and family-level genetic variation to the total variance, this research aims to provide a detailed understanding of both inter- and intra-population genetic structure underlying phenological traits.

Another motivation of this work is the urgent need to identify tree species and seed sources that are well-adapted to future conditions, considering the increasing impact of climate change on forest ecosystems. Oaks, with their high genetic diversity and broad ecological range, offer a promising model for studying such adaptive traits. Understanding how phenological traits are shaped by genetic differences in *Q. robur* can support efforts to manage forests in a changing climate and guide the selection of suitable seed sources for conservation and reforestation.



CHAPTER 3

MATERIALS & METHODS

3.1 Sampling of Populations

All phenological data for this study were collected from the Ankara common garden, which was established in 2022 within the framework of the ACORN Project and regularly visited to monitor *Quercus robur* L. seedlings from diverse genetic backgrounds, despite the study not being directly part of the project. ACORN is a research project that is dedicated to pinpointing seed sources for oak forests that can thrive and adapt effectively in the face of climate change. As part of the project's design, acorns of three different oak species—*Quercus robur*, *Quercus pubescens*, and *Quercus petraea*—were collected from 12 countries spanning two regions: the Eastern Mediterranean and Central Europe. With the start of the project in 2021, from each of these regions, 10 pairs of closely situated populations were identified separately for each of the three oak species. One population of each pair lived in dry soil conditions while the other was situated in moist soil. These acorns were then planted in three different common gardens, located in Ankara, Vienna, and Zurich. These gardens were intended to demonstrate the effects of dry, normal, and moist soil conditions, respectively, on the plastic responses of the oak seedlings that came from different populations [27].

The Ankara common garden is located within the National Botanical Garden of Turkey, under the administration of the General Directorate of Agricultural Research and Policies. It consists of three separate nursery beds designated for three oak species: *Quercus robur*, *Q. pubescens*, and *Q. petraea*. These nursery beds were

separated from each other and from the rest of the garden by buffer trees, which were local *Q. robur* seedlings. Among the seedlings grown in the Ankara common garden, leaf bud phenology data were collected for all three species. However, only *Q. robur* was included in the present study. This decision was based on the significantly lower germination rates observed in *Q. pubescens* and the loss of *Q. petraea* acorns due to unsuitable storage conditions, which resulted in reduced and uneven sample sizes that were not suitable for robust statistical analysis. As a result, all phenological observations and evaluations presented here focus exclusively on *Q. robur*, and only the individuals that germinated and survived until April 2023 were included in the analysis, excluding those that failed to germinate or died by then. The final dataset collected for phenological traits in the growing season of 2023 consists of 155 seedlings, representing 8 populations from 4 Central European countries. While the original design of the ACORN project involved ten population pairs per species (each including one dry-site and one moist-site population), the surviving seedlings included in the study came from *Q. robur* populations of unequal number of dry and moist sites. From each population, six mother trees were selected, and six acorns were collected from each mother tree. This yielded a total of 288 *Q. robur* acorns, which were sown in the designated locations in the nursery bed of the Ankara garden in the Spring of 2022 and monitored under uniform conditions for their phenological development for the growing seasons of 2022 and 2023.

Table 3.1: Locations and sampling information for populations used in the study. Each POP ID signifies a plot where a population's acorns were collected, except for 'Garden', which refers to the common garden in Ankara, Türkiye. Coordinates are the mean values across sampled mother trees.

POP ID	Population	Country	Latitude	Longitude	Altitude (m)	Seedlings (n)	Mother Trees (n)
300	Planck am Kamp	Austria	48.555575	15.670348	249.29	24	5
301	Schönberg am Kamp	Austria	48.507603	15.703358	350.42	31	6
302	Diendorf am Walde	Austria	48.515768	15.754649	357.21	14	4
303	Altenhof am Kamp	Austria	48.544203	15.693037	266.00	18	5
377	Locarno	Switzerland	46.165629	8.859032	200.34	21	5
380	Cestas	France	44.782920	-0.697581	50.20	10	4
382	Groane	Italy	45.657659	9.093565	241.43	18	5
383	Bosco Pantano	Italy	40.157375	16.677562	9.63	19	5
Garden	Mixed	Türkiye	39.897935	32.742601	898.73	155	39



Figure 3.1: Locations of all populations acorns have been collected from, and the common garden in Ankara where they have all been sown, denoted by 'Garden'. Image taken from Google Earth.

At the time of the garden's establishment, a soil profile analysis was conducted, and the soil was not fertilized, preserving its natural properties throughout the course of the experiment. After the acorns were first sown in Autumn 2021, the soil surface was covered with hay to protect them from freezing during winter dormancy. Following the germination of seedlings in Spring 2022, routine garden maintenance was carried out three times annually between April and October.

Irrigation was performed once per week from early April to mid-July. Between mid-July and the end of August, watering frequency was increased to twice per week, then reduced again to once per week in September. Irrigation was discontinued upon the arrival of autumn rains and resumed the following April.

3.2 Phenological Traits & Data Collection

The oak seedlings planted in the designated nursery bed within the garden have been observed during their expected bud burst and bud set intervals, which roughly cor-

responds to the months of April–May and August–September, respectively [28, 24]. The bud burst measurements were taken between April 14th and June 1st, and the bud set measurements were taken between August 1st and October 3rd, in the year of 2023, while the seedlings were 2 years old. During observations, the field where the oaks had been planted was visited 3 times a week during spring and 2 times a week during autumn. Each oak was individually checked for burst and formed buds at the corresponding time periods. For each seedling, the bud burst and bud set dates, recorded separately for terminal and lateral shoots, were documented using the Julian date format. Then, each seedling's growing season length was calculated by taking the difference between the latest bud set date and the earliest bud burst date. This calculation was done separately for the terminal and lateral buds.

In cases where the initial terminal bud was lost, the lateral bud closest to the lost terminal bud was registered as the new terminal bud. For seedlings that did not undergo bud burst within the designated observation period but were observed to have formed buds in autumn, the bud burst date was recorded as 152nd Julian day (June 1st) of 2023, which marks the end of the bud burst measurement interval. A similar approach was applied to seedlings whose terminal shoots were still actively growing at the end of the bud set observation period; these were assigned a bud set date of 283rd Julian day (October 10th) of 2023, corresponding to one week after the final measurement date.

The difference in the assigned dates for bud burst and bud set stems from a change in the approach between the spring and autumn measurement periods. During the spring, some terminal buds remained unrecorded in the bud burst dataset. These likely belonged to seedlings whose terminal shoots had died and were not replaced by lateral buds, since substitution was not consistently applied during this period. In contrast, by the time of the autumn measurements, a more consistent method was used: when the terminal bud was found to be dead, it was replaced with the nearest viable lateral bud immediately. Therefore, terminal buds marked as zero in the bud set data typically indicate that the shoot was still actively growing at the time of the final

Table 3.2: Descriptive statistics of each phenological trait

Variable	N	Number of POPs	Number of MTs	Mean	Median	Min	Max
Terminal BB	149	8	39	117.28	114.00	104	142
Terminal BS	147	8	39	252.76	255.00	213	283
Terminal GSL	141	8	39	135.31	134.00	95	172
Lateral BB	145	8	39	128.40	128.00	104	152
Lateral BS	147	8	39	246.33	248.00	213	276
Lateral GSL	141	8	39	117.68	116.00	61	172

field visit, and bud set was assumed to occur one week after the last measurement date.

While this approach introduces a degree of uncertainty in the exact timing of phenological events, it allowed the inclusion of seedlings that had formed new leading shoots after terminal bud damage, thereby ensuring a more complete representation of the surviving individuals in the dataset.

3.3 Data Analysis

The data for bud burst, bud set, and growing season length were evaluated for normality. Although some deviation was observed, the sample sizes were sufficiently large to meet the assumptions of ANOVA, as the test is robust to minor violations of normality. A nested ANOVA approach was used to analyse the sources of variation in terminal and lateral bud phenologies—including bud burst and bud set timings, as well as growing season lengths (GSLs). These tests were followed by Tukey’s HSD post-hoc comparisons when significant differences were detected between populations. Variance component analyses were conducted for each phenological trait, and the contributions of different populations and of individual mother trees within those populations were reported separately, alongside the nested ANOVA results. All analyses were conducted using data from 8 populations and 39 mother trees, although the number of individuals varied slightly due to missing values. Boxplots were generated for each phenological trait, displaying terminal and lateral bud data side by

side to make comparison easier. To identify potential patterns between phenological traits that might suggest coordination within them, Pearson's correlation test was applied, given the approximate normality of the dataset. For better visualization of terminal and lateral shoot GSLs, two separate density graphs were created to depict the normalized number of individuals within the active growth period. Different populations were distinguished using variations in line colour and style. This approach allowed general trends in terminal and lateral bud phenology to be observed more clearly, while also highlighting differences between populations. All calculations and visualization were carried out in the Python environment using the packages pandas, NumPy, SciPy, statsmodels, Matplotlib and seaborn [29, 30, 31, 32, 33, 34, 35].

CHAPTER 4

RESULTS

4.1 Comparing the bud phenology of different populations

4.1.1 The variation patterns in the terminal bud phenology across different mother trees and populations

The descriptive statistics of 8 populations for each phenological trait are presented in Table 4.1. A nested ANOVA was conducted to evaluate variation in terminal bud burst timings, and its results can be seen in Table 4.2 along with the nested ANOVA results and variance components of other phenological traits. Significant differences were found at both the population level ($F = 2.33$, $p = 0.044$) and among mother trees within populations ($F = 1.94$, $p = 0.004$), with residual variation accounting for the majority (72.25%) of the total variance (Table A.1). Population and mother tree-level effects on genetic variation contributed 10.02% and 17.73% to the total variance in terminal bud burst timings, respectively. Tukey's HSD test revealed significant differences in mean terminal BB values involving population 383, which had consistently earlier bud burst compared to the populations 300, 301, 302, 377, 380, and 382 ($p < 0.05$) (Table A.3). This difference in the terminal bud burst timing of seedlings that came from the population 383 can also be seen in the box plot given in the Figure 4.1.

Table 4.1: Trait summary statistics per population (with sample sizes)

POP ID	Descriptive Statistics	Terminal BB	Terminal BS	Terminal GSL	Lateral BB	Lateral BS	Lateral GSL
300 (n = 22)	Mean \pm SD	119.45 \pm 8.27	243.55 \pm 14.42	124.09 \pm 14.07	129.55 \pm 14.36	240.68 \pm 14.57	111.14 \pm 20.42
	Min – Max	107 – 142	213 – 262	95 – 148	111 – 152	213 – 269	61 – 151
301 (n = 29)	Mean \pm SD	114.00 \pm 5.55	252.59 \pm 14.28	138.59 \pm 13.59	123.86 \pm 14.24	243.41 \pm 15.12	119.55 \pm 20.55
	Min – Max	104 – 131	220 – 276	113 – 165	107 – 152	220 – 276	68 – 162
302 (n = 14)	Mean \pm SD	119.79 \pm 8.81	253.50 \pm 17.19	133.71 \pm 18.39	132.14 \pm 12.91	248.00 \pm 11.32	115.86 \pm 12.45
	Min – Max	107 – 135	220 – 276	96 – 158	114 – 152	220 – 262	96 – 141
303 (n = 16)	Mean \pm SD	115.94 \pm 9.03	262.00 \pm 14.23	146.06 \pm 19.23	130.12 \pm 15.41	244.50 \pm 9.90	114.38 \pm 21.41
	Min – Max	104 – 142	241 – 283	113 – 169	104 – 152	220 – 262	71 – 158
377 (n = 19)	Mean \pm SD	118.42 \pm 6.38	251.32 \pm 19.57	132.89 \pm 21.36	129.63 \pm 14.89	246.16 \pm 18.79	116.53 \pm 25.82
	Min – Max	111 – 131	213 – 276	95 – 165	111 – 152	220 – 276	78 – 162
380 (n = 9)	Mean \pm SD	123.78 \pm 8.26	249.56 \pm 13.90	125.78 \pm 14.79	127.56 \pm 12.36	247.22 \pm 16.95	119.67 \pm 14.66
	Min – Max	114 – 135	227 – 269	99 – 144	114 – 152	220 – 276	103 – 148
382 (n = 15)	Mean \pm SD	120.87 \pm 8.44	255.00 \pm 9.90	134.13 \pm 16.01	135.07 \pm 13.07	248.93 \pm 14.22	113.87 \pm 20.10
	Min – Max	107 – 135	241 – 276	113 – 165	114 – 152	227 – 276	85 – 152
383 (n = 17)	Mean \pm SD	110.76 \pm 9.13	255.00 \pm 18.52	144.24 \pm 21.03	122.59 \pm 17.69	253.76 \pm 15.89	131.18 \pm 20.38
	Min – Max	104 – 135	213 – 276	106 – 172	104 – 152	220 – 276	106 – 172

Table 4.2: Nested ANOVA summary table for all traits (* $p < .05$, ** $p < .01$, *** $p < .001$)

Traits	Populations		Mother Trees within Populations		Error	
	MS (df = 7)	% Var	MS (df = 38)	% Var	MS (df)	% Var
TBB	265.57*	10.02	113.81**	17.73	58.74 (110)	72.25
TBS	196.39	0.00	314.62	8.36	234.10 (108)	91.64
TGSL	665.65	2.96	483.73*	16.00	282.26 (102)	81.04
LBB	220.84	0.00	311.58*	16.58	179.20 (106)	83.42
LBS	364.63	2.33	267.80	7.40	204.61 (108)	90.28
LGSL	795.96	1.35	691.55**	22.76	331.78 (102)	75.89

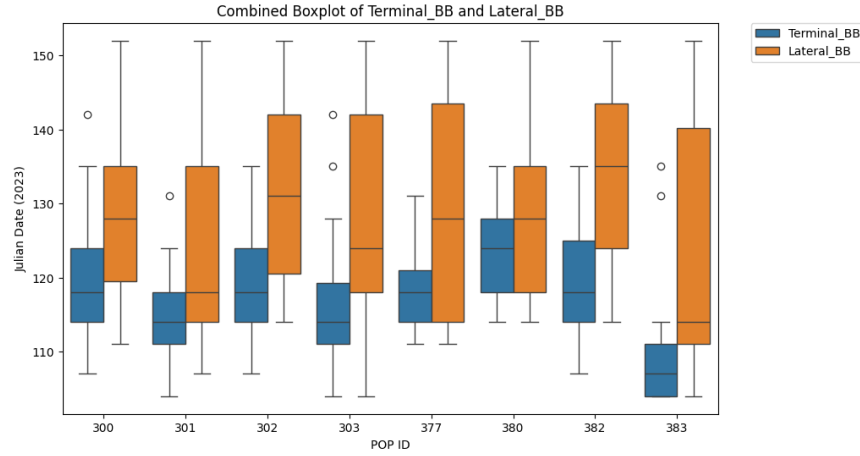


Figure 4.1: Combined box plot of terminal and lateral bud burst dates according to the POP ID of the population they came from

Similar to the terminal bud burst analysis, a nested ANOVA approach was used to assess variation in terminal bud set timings. No significant differences were found at the population level ($F = 0.62$, $p = 0.733$), and differences among mother trees within populations were also not statistically significant ($F = 1.34$, $p = 0.121$) (Table A.4). The majority of the variance was explained by residual variation (91.64%), with mother tree and population effects accounting for 8.36% and 0%, respectively (Table 4.2). The box plot in Figure 4.2 also shows no striking differences between bud set timings of populations (both for the terminal and lateral shoots), consistent with the non-significant population-level variation found in the nested ANOVA.

Another nested ANOVA was conducted to assess variation in the GSL of terminal buds. While the population effect was not statistically significant ($F = 1.38$, $p = 0.244$), significant variation was detected among mother trees within populations ($F = 1.71$, $p = 0.017$) (Table A.6). The majority of the total variance (81.04%) was attributed to residual effects, while populations and mother trees within populations accounted for 2.96% and 16.00%, respectively (Table 4.2). Figure 4.3 presents the distribution of GSL across populations for both terminal and lateral shoots, demonstrating negligible variation among populations for this phenological trait, in line with the statistical findings.

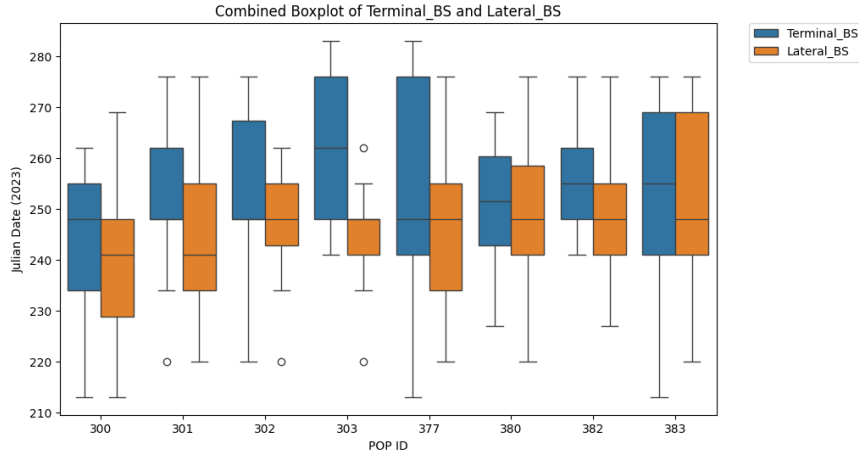


Figure 4.2: Combined box plot of terminal and lateral bud set dates according to the POP ID of the population they came from

4.1.2 The variation patterns in the lateral bud phenology across different mother trees and populations

A nested ANOVA was conducted to examine variation in lateral bud burst timings. The population effect was not statistically significant ($F = 0.71$, $p = 0.665$), while mother trees within populations showed significant variation ($F = 1.74$, $p = 0.014$) (Table A.8). The majority of the variance was attributed to residual effects (83.42%), with 16.58% explained by mother tree differences and none by population (Table 4.2). Although the box plot in Figure 4.1 shows considerable variation among populations for terminal bud burst timings, no similarly pronounced visual differences are observed for lateral bud burst, in agreement with the nested ANOVA results.

Nested ANOVA used to assess variation in lateral bud set timings did not show any significant differences at the population level ($F = 1.36$, $p = 0.250$), nor among mother trees within populations ($F = 1.31$, $p = 0.143$) (Table A.10). According to the variance component estimates, the majority of the variation (90.28%) was attributable to residual error, while the mother tree and population effects explained 7.40% and 2.33% of the variance, respectively (Table 4.2).

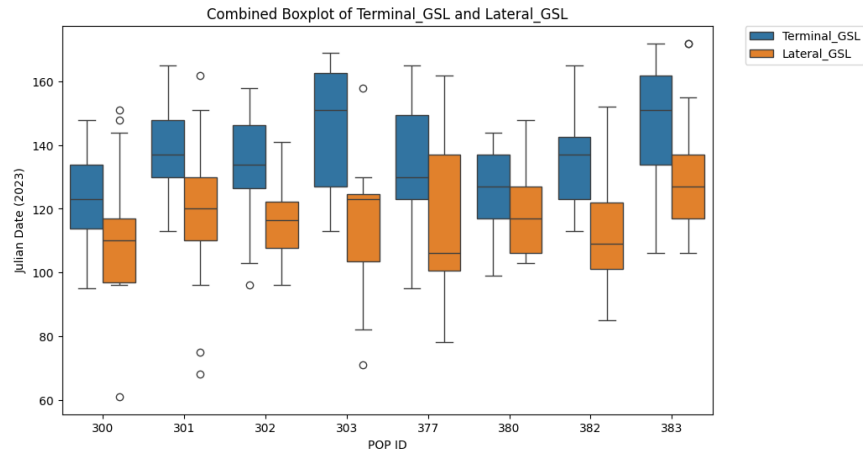


Figure 4.3: Combined box plot of terminal and lateral growing season lengths according to the POP ID of the population they came from

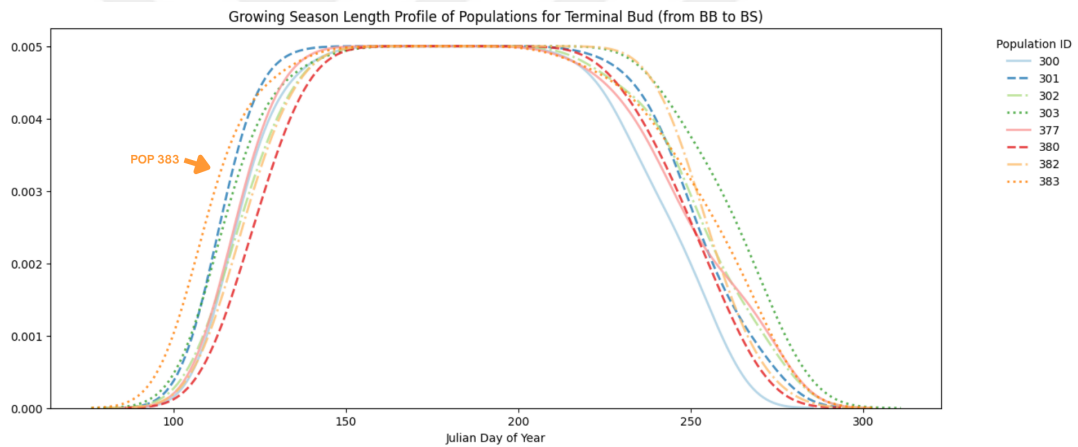


Figure 4.4: The growing season profile of populations for terminal shoots of seedlings in active growth phase, from BB to BS

Another nested ANOVA was performed to examine variation in lateral GSL. The population effect was not statistically significant ($F = 1.15$, $p = 0.353$), but variation among mother trees within populations was significant ($F = 2.08$, $p = 0.002$) (Table A.12). Variance component analysis indicated that most of the variation was attributed to residual effects (75.89%), while mother tree differences contributed 22.76% and population-level differences accounted for only 1.35% of the total variance (Table 4.2).

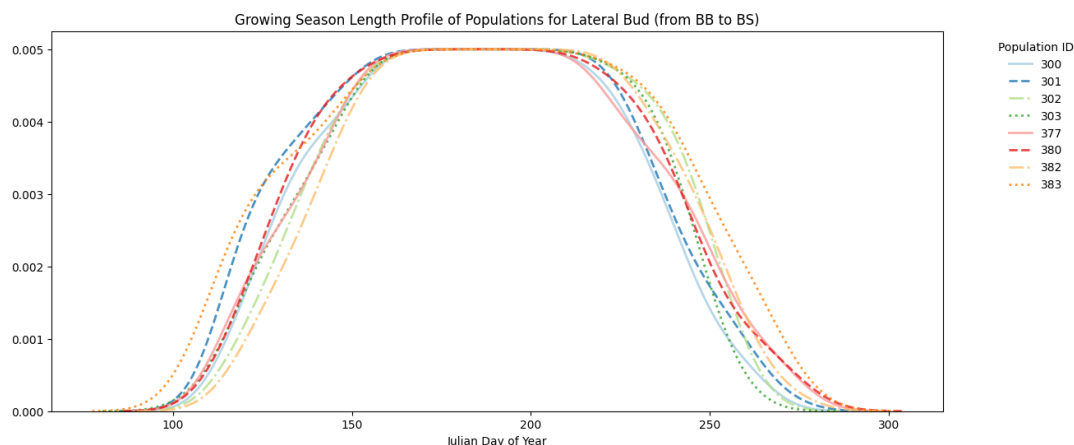


Figure 4.5: The growing season profile of populations for lateral shoots of seedlings in active growth phase, from BB to BS

4.2 Comparison of the terminal and lateral bud phenologies, & correlations within phenological traits

The density plots presented in Figures 4.4 and 4.5 illustrate the temporal distribution of seedlings in the active growth phase, displaying the growing season profile of terminal (Figure 4.4) and lateral (Figure 4.5) shoots, respectively – from bud burst to bud set between April and October. For each plot, populations are distinguished by different line styles and colours, allowing for visual comparison. The y-axis reflects the proportion of seedlings in active growth at each time point, rather than absolute counts, as values were normalized to enable clearer comparison between populations regardless of sample size differences. These plots effectively highlight the timing and duration of growth activity across populations, providing insight into both inter-population differences and seasonal growth dynamics in terminal and lateral shoots.

Pearson's correlation coefficients between bud burst and bud set timings, as well as growing season lengths (GSLs), for both terminal and lateral shoots are presented in Figure 4.6. The table includes pairwise correlation values among all six phenological traits: terminal bud burst, lateral bud burst, terminal bud set, lateral bud set, terminal GSL, and lateral GSL. Terminal bud burst showed a moderate positive correlation with lateral bud burst ($r = 0.388$, $p < 0.001$), and moderate negative correlations with

terminal GSL ($r = -0.492$, $p < 0.001$) and lateral GSL ($r = -0.295$, $p < 0.001$). Terminal bud set was strongly positively correlated with terminal GSL ($r = 0.888$, $p < 0.001$), and weakly positively correlated with lateral bud set ($r = 0.183$, $p = 0.026$). Lateral bud burst was negatively correlated with terminal GSL ($r = -0.206$, $p = 0.014$) and strongly negatively correlated with lateral GSL ($r = -0.689$, $p < 0.001$). A strong positive correlation was also observed between lateral bud set and lateral GSL ($r = 0.702$, $p < 0.001$). (Table B.1)

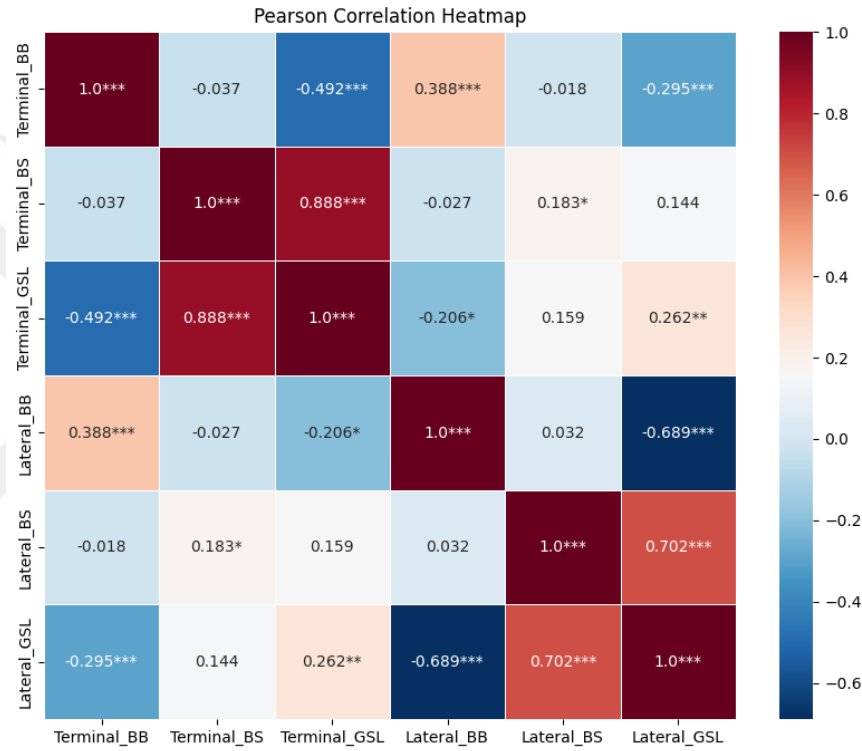


Figure 4.6: Heatmap of Pearson correlation coefficient matrix, their significance level annotated by asterisks (* $p < .05$, ** $p < .01$, *** $p < .001$)



CHAPTER 5

DISCUSSION

5.1 Analysis of terminal bud phenology

5.1.1 Bud burst timings of terminal shoots

When the differences in the terminal bud burst timings of oak seedlings that came from 8 different populations are examined, it is seen that a single population numbered 383 displays a very distinct pattern compared to other populations. This population is within the Bosco Pantano forest, located directly on the Mediterranean coast of Southern Italy. Although there is another population, numbered 380 (Cestas, France), that is located close to the coast of Atlantic Ocean, POP 383 is the only one with a direct coastline on the sea. Earlier bud burst timings observed in seedlings from POP 383 could be reflecting adaptation to a milder maritime climate, where spring temperatures rise earlier and frost risk is lower. Coastal environments often buffer against extreme cold, potentially selecting for genotypes with earlier growth onset. Comparing coastal vs. inland phenological responses in other oak studies may help confirm whether this trend is consistent across species and regions [36]. The unusually early terminal bud burst observed in POP 383 may also be attributed to its geographic position, as it is located at the lowest latitude, and thus the southernmost point among all sampled populations. This pattern aligns with findings from other studies reporting earlier bud burst in southern or lower-latitude provenances [28, 37]. However, further research is needed, as our study was not specifically designed to test latitudinal trends and included populations from a relatively narrow latitudinal range.

5.1.2 Bud set timings of terminal shoots

While many studies have demonstrated strong genetic control over bud phenology traits like bud burst and bud set, often linked to climatic adaptation along environmental gradients, we could not detect any significant differences in the terminal bud set timings neither among seedlings from different populations nor from different mothers within populations through the nested ANOVA analysis [3, 38, 19, 23, 12]. This contrast with the general consensus could be explained by the overriding influence of the environmental conditions in the Ankara common garden since the site has experienced a long period of high day temperatures late in the growing season of 2023, accompanied by drought stress. This may have induced an early and uniform bud set across all seedlings, regardless of genetic origin. In such conditions, trees may prioritize survival by ending the growing season early, reducing the number of actively growing shoots and going through bud set sooner [14, 21, 6]. This environmental uniformity could have masked any underlying genetic variation in bud set timings, similar to findings in studies where harsh conditions led to a convergence in phenological traits [3, 24]. Therefore, although genetic differentiation may exist, the climatic conditions at the trial site may have limited its expression in this particular season.

5.1.3 The GSL of terminal shoots

The population effect was not significant for GSL of terminal buds, but significant variation was detected among the mother trees within populations, revealed by the nested ANOVA for this trait. The observed variance between mother trees implies some genetic or inherited environmental control over growing season length, and shows great intra-population diversity.

5.2 Analysis of lateral bud phenology

5.2.1 Bud burst timings of lateral shoots

The bud burst timings of lateral shoots do not show significant difference between seedlings coming from different populations, however those coming from different mother trees within the same population show significant variation in this trait. From these results on the lateral budburst timings, we can deduce that lateral budburst timings exhibit substantial genetic differentiation at the family level within populations. This suggests that even in the absence of population-level effects, local genetic variability among mother trees plays an important role in shaping this trait. Such variation could arise from adaptive differentiation to fine-scale environmental gradients or differences in the genetic makeup of the mother trees and epigenetic effects.

5.2.2 Bud set timings of lateral shoots

None of the nested ANOVA values for lateral bud set timings were significant either, as it was the case in the bud set timings of terminal shoots. The lack of differentiation among populations and families within populations likely stems from the same overriding environmental factors discussed earlier. The high stress conditions in the Ankara common garden during the growing season of 2023 may have triggered a uniform stress response, prompting early and synchronized lateral bud set across all seedlings. As with terminal bud set, these conditions could have masked potential genetic variation, leading to homogeneity in lateral bud phenology.

5.2.3 The GSL of lateral shoots

Nested ANOVA done for the lateral bud GSL has shown no significant population effect for this trait, while the variation among mother trees were highly significant, contributing 22.76% of the total variance. As it was for the lateral bud burst timings, it can be said that the intra-population variance for the lateral bud GSL is higher than

the inter-population variance for the same trait. This could mean that the control of growing season length of lateral shoots is more strongly influenced by genetic differences within populations than by broader geographic origins. The consistently high intra-population variance across multiple populations, supports the idea that lateral GSL is a heritable trait at the family level, likely shaped by local selection pressures or mother tree effects.

5.3 Comparing terminal and lateral bud phenologies

When Figure 4.1 is examined, it can be seen that the bud burst dates—especially those of the terminal buds—have a right-skewed distribution. This could be interpreted as the bud burst period having started earlier than anticipated, causing the data to appear skewed. Many studies have shown that recent warming trends have advanced the timing of spring events, including bud burst dates [39, 26, 18, 17]. This general advancement in timing could very well explain the non-normal distribution observed in bud burst.

Another pattern that can be seen from Figure 4.1 is that, in almost every population, terminal bud burst occurred earlier than lateral bud burst, which is a general pattern reinforced by apical dominance [20]. The bud burst period for the terminal buds also appears to be shorter and more concentrated, while the lateral bud burst dates are more spread out. This supports the idea that lateral buds in oak trees demonstrate greater phenotypic plasticity in bud burst timing compared to terminal buds. This is likely due to the influence of apical dominance and deeper dormancy in lateral buds, leading to delayed and more variable bud burst. However, there aren't many studies focused specifically on lateral bud phenology, and further investigation is needed. Given that lateral buds may allow for more flexible responses to environmental variability, understanding their dynamics is crucial for forest management and predicting tree responses to climate change.

The bud set dates of lateral shoots generally seemed to be earlier than the bud set of terminal shoots, as can be seen in the Figure 4.2. An interesting pattern illustrated

in Figure 4.3 was that the GSL of lateral shoots was much shorter than the terminal ones, which aligns with the later bud burst and earlier bud set dates observed. This pattern may reflect a more conservative growth strategy in the lateral shoots, possibly enhancing the plant's chances of survival if the terminal bud is damaged or lost.

Bud set dates showed less consistent patterns when compared with the bud burst dates. While bud burst timings of terminal and lateral shoots were moderately correlated, bud burst and bud set timings within the same shoot type were weakly or not correlated at all (Figure 4.6). This suggests that the onset of the growing season does not strongly predict the timing of growth cessation, and that these two phases may be influenced by distinct genetic or environmental factors. As expected, since growing season length (GSL) was calculated as the difference between bud set and bud burst dates, it showed strong correlations with both. GSL of terminal shoots was positively associated with the bud set of terminal shoots and negatively with terminal bud burst, and a similar trend was observed for lateral shoots.



CHAPTER 6

CONCLUSION

This study investigated the patterns of genetic variation in phenological traits—bud burst, bud set, and growing season length (GSL)—of both terminal and lateral shoots in *Quercus robur* seedlings, grown in a common garden environment in Ankara, and originating from eight different European populations. Nested ANOVA results revealed several key patterns regarding the extent and structure of this variation.

The bud burst timings of terminal shoots exhibited some population-level differentiation, with one population (383, Bosco Pantano, Italy) displaying markedly earlier bud burst. This may reflect local adaptation to coastal conditions or relatively low latitude. However, no strong population-level differentiation was observed for the other phenological traits. In contrast, substantial intra-population variation—particularly among different mother trees—was found in both bud burst and GSL for terminal and lateral shoots. These findings suggest that while broad geographic origin contributed little to phenological variation, genetic differences among families within populations played a significant role, likely shaped by fine-scale environmental conditions or mother tree effects.

When comparing terminal and lateral shoot phenologies, terminal buds generally burst earlier and exhibited more synchronized timing than lateral buds. Lateral bud traits were more variable overall, and the lateral shoot GSL was significantly shorter than that of the terminal shoots. These observations are consistent with the influence of apical dominance and deeper dormancy in lateral buds, supporting the view that lateral shoot phenology is more plastic and responsive to environmental variation. The shorter and more variable GSL of lateral shoots, along with the absence of corre-

lations between bud burst and bud set within shoot types, suggests that the onset and cessation of growth may be shaped by distinct genetic and environmental drivers.

Bud set in both terminal and lateral shoots was not significantly influenced by either population or mother tree effects. This suggests weak or absent genetic control over bud set timing in one-year-old *Quercus robur* seedlings.

In summary, this study demonstrates that substantial genetic variation in phenological traits exists at the family level within populations, indicating that local genetic diversity may provide adaptive potential under changing climate conditions. These findings also highlight the importance of considering for both terminal and lateral shoot dynamics in phenological studies, as lateral shoots may represent more flexible growth strategies under variable conditions. Furthermore, assessing the phenological traits of individual mother trees may allow researchers to make more informed decisions when choosing climate-resilient seed sources, given that mother tree effects appeared to have a greater influence than population-level differences in the seedlings studied.

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Appendix A

NESTED ANOVA AND TUKEY'S HSD TEST RESULTS FOR EACH PHENOLOGICAL TRAIT



Table A.1: Nested ANOVA Table for Terminal BB

Source	Sum Sq	df	Mean Sq	F	PR(>F)
Pop ID	1858.97	7.00	265.57	2.33	0.044
Mother Tree(Pop ID)	4324.73	38.00	113.81	1.94	0.004
Error	6460.98	110.00	58.74	NaN	NaN
Corrected Total	12644.69	155.00	NaN	NaN	NaN

Table A.2: Type 1 Estimates of Variance Components with Percentage Contributions for Terminal BB

Variance Component	Estimate	% of Total Variance
Var(Pop ID)	8.15	10.02
Var(Mother Tree(Pop ID))	14.41	17.73
Var(Error)	58.74	72.25

Table A.3: Tukey HSD Post-hoc Test Results for Terminal BB and Pop ID

group1	group2	meandiff	p-adj	lower	upper	reject
300	301	-6.17	0.088	-12.79	0.46	False
300	302	-0.38	1.000	-8.52	7.75	False
300	303	-3.28	0.883	-10.82	4.26	False
300	377	-1.75	0.996	-9.17	5.68	False
300	380	3.61	0.938	-5.84	13.07	False
300	382	0.27	1.000	-7.54	8.08	False
300	383	-9.75	0.002	-17.17	-2.32	True
301	302	5.79	0.316	-2.04	13.62	False
301	303	2.89	0.921	-4.32	10.10	False
301	377	4.42	0.541	-2.67	11.51	False
301	380	9.78	0.029	0.58	18.97	True
301	382	6.44	0.149	-1.05	13.93	False
301	383	-3.58	0.777	-10.67	3.51	False
302	303	-2.90	0.968	-11.52	5.72	False
302	377	-1.36	1.000	-9.88	7.16	False
302	380	3.99	0.934	-6.34	14.33	False
302	382	0.65	1.000	-8.20	9.50	False
302	383	-9.36	0.020	-17.88	-0.84	True
303	377	1.53	0.999	-6.42	9.49	False
303	380	6.89	0.391	-2.99	16.76	False
303	382	3.55	0.892	-4.76	11.86	False
303	383	-6.47	0.204	-14.42	1.49	False
377	380	5.36	0.698	-4.43	15.15	False
377	382	2.02	0.995	-6.19	10.22	False
377	383	-8.00	0.042	-15.85	-0.15	True
380	382	-3.34	0.971	-13.42	6.74	False
380	383	-13.36	0.001	-23.15	-3.57	True
382	383	-10.02	0.006	-18.22	-1.81	True

Table A.4: Nested ANOVA Table for Terminal BS

Source	Sum Sq	df	Mean Sq	F	PR(>F)
Pop ID	1374.70	7.00	196.39	0.62	0.733
Mother Tree (Pop ID)	11955.48	38.00	314.62	1.34	0.121
Error	25283.18	108.00	234.10	NaN	NaN
Corrected Total	38613.37	153.00	NaN	NaN	NaN

Table A.5: Type 1 Estimates of Variance Components with Percentage Contributions for Terminal BS

Variance Component	Estimate	% of Total Variance
Var(Pop)	0.00	0.00
Var(Mother Tree (Pop))	21.36	8.36
Var(Error)	234.10	91.64

Table A.6: Nested ANOVA Table for Terminal GSL

Source	Sum Sq	df	Mean Sq	F	PR(>F)
Pop ID	4659.55	7.00	665.65	1.38	0.244
Mother Tree (Pop ID)	18381.70	38.00	483.73	1.71	0.017
Error	28790.57	102.00	282.26	NaN	NaN
Corrected Total	51831.82	147.00	NaN	NaN	NaN

Table A.7: Type 1 Estimates of Variance Components with Percentage Contributions for Terminal GSL

Variance Component	Estimate	% of Total Variance
Var(Pop)	10.32	2.96
Var(Mother Tree (Pop))	55.73	16.00
Var(Error)	282.26	81.04

Table A.8: Nested ANOVA Table for Lateral BB

Source	Sum Sq	df	Mean Sq	F	PR(>F)
Pop ID	1545.86	7.00	220.84	0.71	0.665
Mother Tree(Pop ID)	11839.98	38.00	311.58	1.74	0.014
Error	18994.82	106.00	179.20	NaN	NaN
Corrected Total	32380.66	151.00	NaN	NaN	NaN

Table A.9: Type 1 Estimates of Variance Components with Percentage Contributions for Lateral BB

Variance Component	Estimate	% of Total Variance
Var(Pop)	0.00	0.00
Var(Mother Tree(Pop))	35.61	16.58
Var(Error)	179.20	83.42

Table A.10: Nested ANOVA Table for Lateral BS

Source	Sum Sq	df	Mean Sq	F	PR(>F)
Pop ID	2552.42	7.00	364.63	1.36	0.250
Mother Tree(Pop ID)	10176.48	38.00	267.80	1.31	0.143
Error	22098.18	108.00	204.61	NaN	NaN
Corrected Total	34827.09	153.00	NaN	NaN	NaN

Table A.11: Type 1 Estimates of Variance Components with Percentage Contributions for Lateral BS

Variance Component	Estimate	% of Total Variance
Var(Pop)	5.27	2.33
Var(Mother Tree(Pop))	16.76	7.40
Var(Error)	204.61	90.28

Table A.12: Nested ANOVA Table for Lateral GSL

Source	Sum Sq	df	Mean Sq	F	PR(>F)
Pop ID	5571.70	7.00	795.96	1.15	0.353
Mother Tree(Pop ID)	26278.75	38.00	691.55	2.08	0.002
Error	33841.88	102.00	331.78	NaN	NaN
Corrected Total	65692.34	147.00	NaN	NaN	NaN

Table A.13: Type 1 Estimates of Variance Components with Percentage Contributions for Lateral GSL

Variance Component	Estimate	% of Total Variance
Var(Pop)	5.92	1.35
Var(Mother Tree(Pop))	99.51	22.76
Var(Error)	331.78	75.89

Appendix B

PEARSON CORRELATION P-VALUES

Table B.1: P-values of Pearson correlation coefficients among phenological traits

	Terminal BB	Terminal BS	Terminal GSL	Lateral BB	Lateral BS	Lateral GSL
Terminal BB						
Terminal BS	0.664					
Terminal GSL	5.58×10^{-10}	9.93×10^{-49}				
Lateral BB	1.47×10^{-6}	0.756	0.014			
Lateral BS	0.836	0.026	0.060	0.709		
Lateral GSL	0.001	0.087	0.002	3.41×10^{-21}	2.91×10^{-22}	



Appendix C

DESCRIPTIVE STATISTICS OF PHENOLOGICAL TRAITS FOR DIFFERENT POPULATIONS AND FAMILIES OF DIFFERENT MOTHER TREES



Table C.1: Descriptive statistics for Terminal BB values for each Pop ID

Pop ID	N	Number of Mother Trees	Mean	Median	Minimum	Maximum
300	24	5	120.17	118	107	142
301	30	6	114.00	114	104	131
302	14	4	119.79	118	107	135
303	18	5	116.89	114	104	142
377	19	5	118.42	118	111	131
380	9	4	123.78	124	114	135
382	16	5	120.44	118	107	135
383	19	5	110.42	107	104	135

Table C.2: Descriptive statistics for Terminal BB values for each Mother Tree

Mother Tree	N	Mean	Median	Minimum	Maximum
30002	6	123.83	124	107	135
30003	6	122.17	119	111	142
30004	5	115.60	114	114	118
30005	4	115.25	116	111	118
30006	3	123.00	124	121	124
30101	5	118.40	118	111	131
30102	6	111.33	111	104	121
30103	6	117.17	118	111	124
30104	4	111.75	111	107	118
30105	6	111.33	111	107	114
30106	3	114.00	114	114	114
30201	4	114.25	114	111	118
30202	5	118.20	114	107	135
30203	4	126.25	126	118	135
30205	1	124.00	124	124	124
30301	3	120.00	114	111	135
30302	2	116.00	116	111	121
30303	3	120.00	114	104	142
30304	5	112.20	111	111	114
30306	5	118.20	114	111	128
37701	2	119.50	119	111	128
37702	4	116.00	116	114	118
37704	4	123.50	122	118	131
37705	5	113.00	111	111	118
37706	4	122.00	119	118	131
38001	1	124.00	124	124	124
38002	2	131.50	131	128	135
38004	4	120.25	116	114	135
38005	2	123.00	123	118	128
38201	2	124.50	124	114	135
38203	1	107.00	107	107	107
38204	5	121.20	118	118	128
38205	4	121.00	121	111	131
38206	4	120.25	116	114	135
38301	4	112.50	107	104	131
38302	3	108.33	107	107	111
38303	5	108.80	111	104	114
38304	4	104.75	104	104	107
38305	3	120.00	114	111	135

Table C.3: Descriptive statistics for Terminal BS values for each Pop ID

Pop ID	N	Number of Mother Trees	Mean	Median	Minimum	Maximum
300	22	5	243.55	248	213	262
301	30	6	252.67	248	220	276
302	14	4	253.50	248	220	276
303	16	5	262.00	262	241	283
377	21	5	252.00	248	213	283
380	10	4	250.10	251	227	269
382	17	5	255.82	255	241	276
383	17	5	255.00	255	213	276

Table C.4: Descriptive statistics for Terminal BS values for each Mother Tree

Mother Tree	N	Mean	Median	Minimum	Maximum
30002	5	245.20	248	227	262
30003	5	239.60	234	227	262
30004	5	243.80	248	227	262
30005	4	241.00	244	213	262
30006	3	250.33	255	241	255
30101	6	250.33	248	248	255
30102	6	257.33	258	234	276
30103	6	258.50	258	234	276
30104	4	244.50	244	241	248
30105	6	252.67	255	220	276
30106	2	244.50	244	234	255
30201	4	258.50	255	248	276
30202	5	249.40	248	220	276
30203	4	260.25	258	248	276
30205	1	227.00	227	227	227
30301	2	251.50	251	241	262
30302	2	244.50	244	241	248
30303	2	265.50	265	262	269
30304	5	270.40	276	262	276
30306	5	263.40	269	241	283
37701	2	258.50	258	241	276
37702	4	242.75	241	213	276
37704	4	235.75	234	227	248
37705	6	265.50	269	241	283
37706	5	253.60	248	234	276
38001	2	248.00	248	241	255
38002	2	237.50	237	227	248
38004	4	251.50	255	234	262
38005	2	262.00	262	255	269
38201	1	248.00	248	248	248
38203	2	265.50	265	262	269
38204	6	252.67	251	241	262
38205	4	258.50	258	241	276
38206	4	255.00	255	248	262
38301	4	253.25	255	227	276
38302	3	241.00	241	213	269
38303	3	266.67	269	255	276
38304	4	249.75	248	241	262
38305	3	266.67	269	255	276

Table C.5: Descriptive statistics for Terminal GSL values for each Pop ID

Pop ID	N	Number of Mother Trees	Mean	Median	Minimum	Maximum
300	22	5	124.090	123	95	148
301	29	6	138.586	137	113	165
302	14	4	133.714	134	96	158
303	16	5	146.062	151	113	169
377	19	5	132.894	130	95	165
380	9	4	125.777	127	99	144
382	15	5	134.133	137	113	165
383	17	5	144.235	151	106	172

Table C.6: Descriptive statistics for Terminal GSL values for each Mother Tree

Mother Tree	N	Mean	Median	Minimum	Maximum
30002	5	122.20	120	106	141
30003	5	118.60	120	103	134
30004	5	128.20	130	113	148
30005	4	125.75	130	95	148
30006	3	127.33	131	117	134
30101	5	131.00	134	117	137
30102	6	146.00	144	130	162
30103	6	141.33	144	120	158
30104	4	132.75	132	130	137
30105	6	141.33	142	113	165
30106	2	130.50	130	120	141
30201	4	144.25	142	134	158
30202	5	131.20	137	96	148
30203	4	134.00	129	120	158
30205	1	103.00	103	103	103
30301	2	139.00	139	127	151
30302	2	128.50	128	127	130
30303	2	142.50	142	120	165
30304	5	158.20	162	148	165
30306	5	145.20	158	113	169
37701	2	139.00	139	130	148
37702	4	126.75	125	95	162
37704	4	112.25	113	96	127
37705	5	149.00	151	130	165
37706	4	136.50	132	123	158
38001	1	117.00	117	117	117
38002	2	106.00	106	99	113
38004	4	131.25	130	120	144
38005	2	139.00	139	137	141
38201	1	113.00	113	113	113
38203	1	162.00	162	162	162
38204	5	129.60	124	120	144
38205	4	137.50	131	123	165
38206	4	134.75	141	113	144
38301	4	140.75	140	110	172
38302	3	132.67	134	106	158
38303	3	157.00	162	144	165
38304	4	145.00	144	137	155
38305	3	146.67	155	120	165

Table C.7: Descriptive statistics for Lateral BB values for each Pop ID

Pop ID	N	Number of Mother Trees	Mean	Median	Minimum	Maximum
300	23	5	129.48	128	111	152
301	30	6	124.47	118	107	152
302	14	4	132.14	131	114	152
303	17	5	129.41	124	104	152
377	19	5	129.63	128	111	152
380	9	4	127.56	128	114	152
382	15	5	135.07	135	114	152
383	18	5	123.28	114	104	152

Table C.8: Descriptive statistics for Lateral BB values for each Mother Tree

Mother Tree	N	Mean	Median	Minimum	Maximum
30002	6	134.67	129	121	152
30003	5	130.60	131	111	152
30004	5	119.60	118	114	128
30005	4	122.75	122	111	135
30006	3	142.67	152	124	152
30101	5	121.20	118	114	135
30102	6	114.83	112	111	128
30103	6	131.50	131	114	152
30104	4	112.50	112	107	118
30105	6	126.83	124	111	152
30106	3	146.33	145	142	152
30201	4	126.25	124	114	142
30202	5	139.00	142	114	152
30203	4	130.50	131	118	142
30205	1	128.00	128	128	128
30301	2	124.50	124	114	135
30302	2	122.50	122	114	131
30303	3	121.33	118	104	142
30304	5	130.80	124	118	149
30306	5	137.60	142	118	152
37701	2	145.00	145	145	145
37702	4	135.00	142	114	142
37704	4	139.25	138	128	152
37705	5	113.60	114	111	118
37706	4	127.00	124	114	145
38001	1	135.00	135	135	135
38002	2	141.50	141	131	152
38004	4	121.00	117	114	135
38005	2	123.00	123	118	128
38201	1	135.00	135	135	135
38203	1	135.00	135	135	135
38204	5	148.00	152	142	152
38205	4	124.50	121	114	142
38206	4	129.50	127	118	145
38301	4	122.00	121	104	142
38302	3	121.33	111	111	142
38303	4	126.25	124	104	152
38304	4	118.75	111	104	149
38305	3	129.00	121	114	152

Table C.9: Descriptive statistics for Lateral BS values for each Pop ID

Pop ID	N	Number of Mother Trees	Mean	Median	Minimum	Maximum
300	22	5	240.68	241	213	269
301	30	6	243.80	241	220	276
302	14	4	248.00	248	220	262
303	16	5	244.50	248	220	262
377	21	5	247.00	248	220	276
380	10	4	248.70	248	220	276
382	17	5	248.82	248	227	276
383	17	5	253.76	248	220	276

Table C.10: Descriptive statistics for Lateral BS values for each Mother Tree

Mother Tree	N	Mean	Median	Minimum	Maximum
30002	5	234.00	234	213	248
30003	5	242.40	241	220	269
30004	5	242.40	234	227	262
30005	4	241.00	237	227	262
30006	3	245.67	248	241	248
30101	6	248.00	251	227	262
30102	6	246.83	241	234	262
30103	6	238.67	234	220	262
30104	4	235.75	234	227	248
30105	6	250.33	248	227	276
30106	2	234.00	234	227	241
30201	4	241.00	244	220	255
30202	5	250.80	248	241	262
30203	4	251.50	251	241	262
30205	1	248.00	248	248	248
30301	2	244.50	244	241	248
30302	2	248.00	248	241	255
30303	2	255.00	255	248	262
30304	5	238.20	241	220	248
30306	5	245.20	248	234	255
37701	2	251.50	251	248	255
37702	4	241.00	244	220	255
37704	4	244.50	241	227	269
37705	6	264.33	265	248	276
37706	5	231.20	220	220	248
38001	2	255.00	255	248	262
38002	2	251.50	251	234	269
38004	4	237.50	241	220	248
38005	2	262.00	262	248	276
38201	1	255.00	255	255	255
38203	2	244.50	244	234	255
38204	6	246.83	248	227	262
38205	4	262.00	262	248	276
38206	4	239.25	237	227	255
38301	4	249.75	248	234	269
38302	3	252.67	248	241	269
38303	3	266.67	262	262	276
38304	4	251.50	255	220	276
38305	3	250.33	241	241	269

Table C.11: Descriptive statistics for Lateral GSL values for each Pop ID

Pop ID	N	Number of Mother Trees	Mean	Median	Minimum	Maximum
300	22	5	111.14	110	61	151
301	29	6	119.55	120	68	162
302	14	4	115.86	116	96	141
303	16	5	114.38	123	71	158
377	19	5	116.53	106	78	162
380	9	4	119.67	117	103	148
382	15	5	113.87	109	85	152
383	17	5	131.18	127	106	172

Table C.12: Descriptive statistics for Lateral GSL values for each Mother Tree

Mother Tree	N	Mean	Median	Minimum	Maximum
30002	5	98.00	106	61	117
30003	5	111.80	110	96	130
30004	5	122.80	113	99	148
30005	4	118.25	113	96	151
30006	3	103.00	96	96	117
30101	5	125.40	130	106	148
30102	6	132.00	130	113	151
30103	6	107.17	113	68	123
30104	4	123.25	123	116	130
30105	6	123.50	116	99	162
30106	2	85.50	85	75	96.
30201	4	114.75	114	106	124
30202	5	111.80	106	96	141
30203	4	121.00	120	113	131
30205	1	120.00	120	120	120
30301	2	120.00	120	113	127
30302	2	125.50	125	124	127
30303	2	132.00	132	106	158
30304	5	107.40	123	71	130
30306	5	107.60	113	82	124
37701	2	106.50	106	103	110
37702	4	106.00	102	78	141
37704	4	105.25	108	85	120
37705	5	151.20	158	137	162
37706	4	100.00	102	89	106
38001	1	113.00	113	113	113
38002	2	110.00	110	103	117
38004	4	116.50	116	106	127
38005	2	139.00	139	130	148
38201	1	120.00	120	120	120
38203	1	99.00	99	99	99
38204	5	100.00	103	85	110
38205	4	137.50	146	106	152
38206	4	109.75	109	96	124
38301	4	127.75	125	106	155
38302	3	131.33	130	127	137
38303	3	143.33	148	110	172
38304	4	132.75	125	109	172
38305	3	121.33	120	117	127