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Genetic variability of European beech in provenance trials in Romania

SUMMARY

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CONTENTS

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The results from four years of study are presented in this doctoral thesis, which was conducted with the support of the National Institute for Research and Development in Forestry "Marin Dracea" at the Brasov Station, under the guidance of the Interdisciplinary Doctoral School at Transilvania University of Brasov. The research aimed to assess the adaptive potential of beech by conducting multidirectional analyses in provenance trials in Romania, focusing on the behaviour of international provenances under local conditions. All the work was supported by numerous specialists' colleagues and my family, without whom this study wouldn't have been possible. Thus, in what follows, I would like to affirm my gratitude for their involvement in my professional progress.

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ABBREVIATIONS

F. sylvatica – *Fagus sylvatica*;

F. orientalis – *Fagus orientalis*;

a.s.l – above sea level;

EQ – Ellenberg Quotient index;

SDM – Species Distribution Model;

URF – Universal Response Function;

G - genotype;

M – environment;

ΔEQ – Ecological transfer distance;

C – Carbunari trial;

S – Sacele trial;

A – Alesd trial;

F – Fantanele trial;

Sr – survival;

Db – breast height diameter;

Ht – total height;

Fk – forking;

Ct – stem quality;

N – reference level;

CR – analysed trait;

SV – variation source;

GD – degree of freedom;

MP – mean square;

F – F value test;

P – statistical significance value;

MD – general mean;

AS – standard deviation;

ES – standard error;

CV – variation coefficient;

H – the value of the differences between the distributions of the groups;

XS – the value of the differences between observed and expected values;

KS – Kolmogorov-Smirnov test.

V%– variance;

χ^2 - Chi-square test;

R – the result of the regression equation;

site_Tmax_sm and prov_Tmax_sm – maximal summer temperature from the testing site and provenance origin;

site_PPT_sp and prov_PPT_sp – spring precipitations from the testing site and provenance origin;

site_AHM and prov_AHM – Annual Heat-Moisture Index from the testing site and provenance origin;

prov_PPT_01 – precipitation from January at the provenance origin;

OOB - Out-Of-Bag;

Hn – normalised height;

He – estimated height;

RCP – Representative Concentration Pathway;

GLMM – Generalised Linear Mixed Models;

GDD – Growing degree days;

SDD – Senescence degree days;

DOY – day of the year;

GAM – General additive model;

MRW – mean ring width;

MLA – mean lumen area;

MVA – mean vessel area;

TRW – tree ring width.

r – the value of the correlation between climatic and anatomical parameters;

CD – cell density;

Dh – hydraulic diameter;

Ks – hydraulic conductance;

MLAm – minimum cell lumen area;

MLAx – maximum cell lumen area;

RGVI – vessel grouping index;

vpd – vapour pressure deficit;

tmx – maximum temperature;

tmp – mean temperature;

tmin – minimum temperature;

soil – soil humidity index;

pre – mean precipitations;

Spei 1-12 – monthly standardized precipitation index.

INTRODUCTION

The actual reality, dominated by the uncertainties generated by climate change (Lee et al. 2023), underscores the necessity of identifying the ecological limitations of forest species (Benito Garzón et al. 2019), which is essential for evaluating the adaptive potential, the basis of strategies to reduce the negative impacts of climate. Given the complexity of environmental factors (Booth et al. 1988), that influence the physiological processes of tree species (Case et al. 2005; Holt et al. 2004), estimating their adaptive potential requires a multidirectional approach based on the analysis of adaptive processes.

The testing of the adaptive potential of tree species can be efficiently conducted by using the provenance trials (Mátyás 1996), which allows the separation of the genotype and environment effect and (White et al. 2007) and, thus, facilitating identification of populations with specific adaptation, which can be used as a source of genetic material in assisted migration strategies (Chakraborty et al. 2024), developed to ensure the survival of species under the pressures of climate change (Ste-Marie et al. 2011).

Fagus sylvatica L. is known as the most important tree species in Europe (Leuschner et al. 2006) and an emblematic one for Romanian forests (Drăcea 2018). The vast environmental conditions across the entire distribution range have shaped specific adaptations (Șofletea & Curtu 2008), and testing different beech populations from Europe is becoming necessary to understand the particularities of this species' adaptation (Von Wuehlisch 2004). Therefore, implementing an international network of provenance trials made it possible to test the adaptive potential across diverse environmental conditions and to realise forecasts regarding the future of the species (Robson & Garzón 2018).

To address the need for a better understanding of beech tree behaviour in various environmental conditions in Romania, this study aims to estimate the species' adaptive potential using a comprehensive approach. This approach is designed to efficiently capture the different aspects of this process. Specifically, the research involved four international provenance trials established in typical environmental conditions across the national distribution range of beech. The study focused on several key areas: evaluating growth performance, quantifying phenotypic plasticity, analysing the impact of provenance transfer, modelling height growth, examining phenological characteristics, and conducting anatomical analysis of the wood.

The obtained results, published in several journal articles (Besliu et al. 2024a; Besliu et al. 2024b; Besliu et al. 2024c), make a modest contribution to the knowledge of the species' adaptive particularities and support the idea of adjusting the management of beech forests to ensure future persistence and productivity. Beyond these, the study offers new information on the transfer of forest reproductive material and, at the same time, highlights the need for a deep understanding of species' adaptation at the local scale.

CHAPTER 1: THE CURRENT STATE OF KNOWLEDGE

1.1. Adaptive potential of tree species

1.1.1. Interaction between genotype and environment

The adaptive potential of species is defined as a function of a complex of biological, physiological, and ecological factors, as well as of the evolutionary process, which act simultaneously and differently in time and space (Royer-Tardif et al. 2021), providing species with the ability to acclimatise to new environmental conditions (Glick et al. 2011). These factors are determined by the phenotypic plasticity of individuals, the genetic diversity of populations, the evolutionary capacity of species, as well as by genetic exchange within populations or between different populations (Alfaro et al. 2014; Jump et al. 2009; Menon et al. 2020; Nicotra et al. 2010; Savolainen et al. 2007).

Adaptation to environmental conditions is considered part of the evolutionary process, driven by environmental selection, thereby promoting the most resilient genotypes. The emergence of more performant genotypes is fundamentally driven by gene exchange between populations (Bussotti et al. 2015).

The current context, in which climate change is at the forefront, has renewed the need to test the ability of tree species to withstand and, consequently, to adapt to new environmental conditions (Benito Garzón et al. 2019). The study of adaptability depends on analysing the interactions between environmental factors and the biological characteristics of species, and to obtain concrete results, the entire complex of factors must be analysed.

One of the fundamental laws of genetics holds that the phenotype results from the interaction between hereditary potential and the totality of external factors. From this law arises the issue of distinguishing between genetic and environmental control of trait variation. Thus, the relationship G (genotype) × E (environment) involves determining the genetic potential underlying a trait and the productive potential expressed by the phenotype under environmental influence. More explicitly, the genetic potential of a tree is fully expressed in the phenotype only under favourable environmental conditions. If these optimal conditions are not met, the phenotype will be clearly inferior, even if the individual's genetic capacity is high (Enescu 1972).

White et al. (2007) define the G × E relationship as the deviation of a genotype from the continuity of its growth performance under different site conditions. Therefore, the occurrence of phenotypic differences within a genotype when the environment changes indicates a significant interaction between genotype and environment.

Based on the fact that the phenotype is the result of the interaction between genotype and environment, Fiorani & Schurr (2013) stated that the determination of phenotypic characteristics involves a series of measurements and techniques which ultimately provide a clear answer regarding the response of species to different conditions. Thus, the analysis of the phenotype represents an efficient way to determine growth performance and adaptation.

The analysis of differences between populations or species in growth performance and adaptive potential is based on the study of genotype-environment relationships. Some of the concepts derived from this relationship include phenotypic plasticity, the analysis of population responses to transfer to other site conditions, the particularities of species migration, the evaluation of phenological behaviour, and wood anatomical analysis.

1.1.2. Implications of genetic variability in the adaptation process

The adaptation of forest species to environmental changes is one of the most intensively studied topics, and genetic variability plays a key role in this battle for adaptation, as it determines the natural evolution process of species (Ciocîrlan & Șofletea 2013).

Genotype specialisation is an integral part of species adaptability and involves changing it by determining new reaction norms that renew the acclimatisation capacity of the old genotype. This adaptation process is a mechanism of evolution and involves changes in the genetic structure of tree species, based on the genetic variability of populations (Enescu & Ionită 2000). Adaptive potential is mainly determined by the interaction between gene flow and selection, and the potential for acclimatisation to new environmental conditions is influenced by genetic variability and dispersal (Savolainen et al. 2007).

The geographical differentiation of populations in terms of genetic variability is the result of genetic factors such as mutations, genetic drift, natural selection, or gene exchange (Booy et al. 2000).

Low genetic variability in populations can negatively influence adaptation due to reduced gene exchange; thus, fragmented populations or those with poor geographical representation are at risk of extinction (Alberto et al. 2013; Keir et al. 2011).

The adaptation process occurs both between different populations of a species and within the same population when site conditions differ. Thus, adaptation to local conditions can be effective when genetic variability is high. Therefore, genetic diversity is essential in the adaptation and evolution of tree species (Booy et al. 2000).

The analysis of genetic variability is particularly important in determining differences between populations, as this information forms the basis for quantifying the adaptive potential of species and for justifying human interventions aimed at maintaining balance in their geographical distribution and persistence. Furthermore, this genetic variability encompasses both phenotypic variability and genomic structural variability across species.

1.1.3. Phenotypic plasticity

The ability of a genotype to exhibit different phenotypes under the influence of varying environmental conditions is known as phenotypic plasticity (Bradshaw 2006). Therefore, phenotypic plasticity refers to a genotype's ability to survive under different environmental conditions by modifying its phenotype, and the extent to which these changes occur determines an organism's degree of plasticity (Bradshaw 1965). Thus, phenotypic plasticity refers to the adjustment of the functional traits of tree species, both morphologically and physiologically, in order to adapt to new environmental conditions (Bussotti et al. 2015).

Phenotypic plasticity can be analysed at the trait level or at the genotype level; it is genetically controlled and can be influenced by selection. Furthermore, this ability of plants is directly involved in the adaptation process and is particularly influenced by environmental impulses (Bradshaw 1965). Crispo (2008) presents phenotypic plasticity as a process closely linked to divergent selection and gene flow between populations. The importance of this natural process arises from the fact that it can lead to the rapid adaptation of genotypes to new environmental conditions, thereby enabling populations to survive under various environmental conditions while reducing the risk of extinction (Benito Garzón et al. 2011).

Plasticity is determined by epigenetic factors that lead to changes in gene expression without altering the organism's DNA (Nicotra et al. 2010), and the limitations of this process arise when environmental pressure exceeds the plasticity of the species' adaptive traits, a phenomenon observed in marginal populations at the edge of their range (Bussotti et al. 2015; Chevin et al. 2010; Thuiller et al. 2008).

The concept of phenotypic plasticity has two meanings: one refers to the genotype's ability to maintain fitness by adapting the phenotype, while the other refers to a diametrically opposed approach, indicating a lack of adaptability or a lack of fitness (Bradshaw 2006).

Phenotypic plasticity is further divided by Ghalambor et al. (2007) into adaptive and non-adaptive plasticity. Adaptive plasticity is defined as the ability of a genotype to colonise a new environment, facilitating the attainment of a new phenotypic optimum at which natural selection will act. Non-adaptive plasticity is the genotype's response to interaction with limiting conditions, resulting in the expression of a phenotype that is far inferior to the species' ecological optimum.

The concept of phenotypic plasticity encompasses complex genetic processes that remain largely unexplored, particularly in forest vegetation. However, phenotypic differentiation can provide valuable insights into the level of plasticity of species, which is of crucial importance in the context of environmental change.

1.1.4. Migration

Migration is the natural phenomenon involving the exchange of genes between populations (Enescu 1972). More precisely, migration is defined as the movement of alleles between populations (White et al. 2007). This process can be achieved naturally through pollen transfer (gene migration) and seed transfer (genotype migration) (Enescu 1972), or artificially through seedling transplantation (Wright 1976). Thus, the effects of migration can lead to diversification of population genetic structure, but the persistence of this phenomenon over several generations can affect genetic differentiation between populations (White et al. 2007).

The phenomenon of migration is considered to be part of the adaptive potential of species to environmental changes (Aitken et al. 2008). Therefore, this process occurs when the ecological requirements of the species are exceeded, and the adaptation mechanism uses migration to identify and colonise new habitats that can ensure the species' persistence (Thurman et al. 2020).

The limitations of this process arise mainly due to the biology of tree species, which does not favour rapid dispersal. These limitations stem from the reproductive capacity, which occurs at a very advanced age in the most important species (Giesecke & Brewer 2018) and has a long periodicity, and the dispersal of seed material is difficult (Svenning et al. 2008; Svenning & Skov 2007). In addition, the rapid pace of climate change predicted for the future could exceed species' migration capacity, and under these conditions, certain species could become extinct (Aubin et al. 2018; Boisvert-Marsh & de Blois 2021). However, tree species with high reproductive capacity and easy dispersal could replace species with low migration potential (Boisvert-Marsh et al. 2020), but this would lead to the loss of economically valuable species.

Taking these aspects into account, human intervention is necessary in these natural processes, which have been disrupted by anthropogenic practices, to reduce, as far as possible, the consequences of future environmental changes. One mechanism that can be used in this case is to support species migration by identifying the most valuable and resilient populations and species.

1.1.5. Assisted migration

Assisted migration is defined as the artificial support of the movement or expansion of species or populations in order to mitigate the negative effects of climate change (Ste-Marie et al. 2011). This concept derives mainly from two phenomena: assisted gene transfer and assisted colonisation of new territories. Assisted gene movement involves human intervention in the transfer of genotypes between populations, but only within the species' natural range. The artificial transfer of species or populations outside their natural range corresponds to the phenomenon of assisted colonisation (Aitken & Whitlock 2013). In addition, the possibility of introducing exotic species is considered another branch of assisted migration and can be carried out through intercontinental or transcontinental species transfers (Johnston 2009).

Therefore, assisted migration is a technique that involves human intervention to support the transfer of populations from areas where they are at risk of extinction due to environmental changes to other areas where current and future climatic conditions may favour the survival of the species and the maintenance of its ecosystem services (Sansilvestri et al. 2015).

In the forestry sector, assisted migration is considered to be very useful in maintaining the viability and productivity of established stands (Leech et al. 2011), using seed sources adapted to the climate, thus ensuring the maintenance of the forest throughout the production process (Gray et al. 2011), preventing the disappearance of species and protecting biodiversity (Hewitt et al. 2011), as well as preserving the various ecosystem services provided by the forest (Pedlar et al. 2012).

However, the use of assisted migration also involves potential dangers, such as: the risk of invasions, difficulty of implementation, interspecific hybridisation, the possibility of poor adaptation of southern populations to conditions in the northern range, as well as economic and ecological losses that may occur (Benito-Garzon et al. 2013; Hewitt et al. 2011).

1.2. Provenance trials

Genotypes selected from natural populations within a specific area of the species' range are known as provenance, which is also defined as source, origin, or natural origin (Wright 1976). White et al. (2007) defined provenance as the geographical location of the population from which the reproductive material was harvested.

The growth and adaptation performance of selected provenances from different populations is tested in specialised trials, known as comparative trials or tests. The main purpose of these tests is to observe the genetic contributions and environmental influences that lead to variation in woody plants at the phenotypic level (White et al. 2007).

Provenance trials are defined by Wright (1976) as experiments in which seeds collected from different stands, generally natural, are used and the seedlings are planted in similar conditions. The only method that can be used to determine the growth and adaptation performance of different provenances under diverse environmental conditions and, implicitly, decisions regarding the transfer of reproductive materials, is the use of long-term provenance trials (White et al. 2007).

Mátyás (1996) defines provenance trials as one of the best methods for testing the adaptability of forest species to different environmental conditions, thus highlighting an important use of these trials, which have become significantly more relevant in forestry research in recent years.

1.3. European beech (*Fagus sylvatica* L.)

From a systematic classification perspective, the species *F. sylvatica* L. belongs to the order *Fagales*, family *Fagaceae*, genus *Fagus* (Manos et al. 2001; Milescu et al. 1967; Șofletea & Curtu 2008).

The genus *Fagus* is one of the most important plant genera in the temperate zone of the northern hemisphere, where it is represented by 10 species of trees, distributed throughout Europe, eastern North America, and Asia (Denk et al. 2002; Shen 1992).

Regarding the origin of the *Fagus* genus, some of the oldest fossils identified are 45 million years old and were discovered in western North America (Manchester & Dillhoff 2004), and about 30 million years ago, it is believed that this genus was widespread from North America to Asia and western Europe (Denk et al. 2005). On the European continent, more precisely in Saxony, fossils of *Fagus prisca* Ett. dating back to the Cretaceous period have been identified (Milescu et al. 1967).

In Romania, the most common species of the genus *Fagus* is *F. sylvatica* L., but, *F. orientalis* Lipsky and *F.* × *taurica* Popl. also occur sporadically (Șofletea & Curtu 2008).

During the ice ages, the beech tree survived in several refuges on the European continent, from which it later spread throughout the entire area. Slovenia and the eastern part of the Alps, as well as southern Moravia and Bohemia, are considered to be the main refuges where the beech tree retreated during the ice ages. In addition, research has revealed the existence of smaller refuges in southern France, central and southern Italy, the northern Iberian Mountains, and the southern Balkan Peninsula (Magri 2008; Milescu et al. 1967). The colonisation of territories after the glaciation period was influenced by local and regional factors that limited the expansion of this species and ultimately contributed to the completion of its natural range (Magri 2008; Magri et al. 2006).

In Romania, researches has shown that in the second half of the postglacial period, beech had a significant expansion (Milescu et al. 1967), and the genetic structure of populations confirms that the Carpathian beech belongs to the European haplotype (Magri 2008).

Other studies have noted that, during its expansion in Romania, beech competed with spruce in high-altitude areas and with hornbeam in lowland areas. In addition, it is believed that the expansion of this species began in the Maramureș Mountains 5110 years ago. It appeared in the south-west and north-west of the country about 4500 years ago, in the south-east 3000 years ago, and in the south-west 4800-5000 years ago. There is also a hypothesis of the existence of a glacial refuge in the Apuseni Mountains, but this has not been confirmed by other research (Fărcaș et al. 2013).

Fagul (*F. sylvatica* L.) The beech is one of the most important tree species in European forests (Leuschner & Ellenberg 2017; Peters 2013), where it covers over 910.000 km^2 (Bohn & Gollub 2007).

The natural range extends from the Cantabrian Mountains in the west to the Carpathian Mountains and the Balkan Mountains in the east, and in the south of the range, it appears from Sicily and spreads north to southern Sweden and Norway (Magri 2008).

Beech covers a wide range of environments, being a lowland and hill species in the northern part of its natural range, where it descends to sea level, and in the south and east it grows in mountainous areas, reaching altitudes of over 2000 m (a.s.l.) (Magri 2008; Șofletea & Curtu 2008; Von Wuehlisch 2008).

Of the total European range of this species, one-third is found in the Carpathian Mountains region (Biriș 2014), and if it had not been artificially replaced by promoting coniferous species, it would have occupied around 65% of all deciduous and mixed forests in Europe (Knapp & Fichtner 2011).

In Romania, beech is the most widespread forest species, accounting for over 30% of the forest area (Ifn 2024) and 10% of all European beech forests (Biriș 2014). The largest areas are found in the Carpathian Mountains, but it also occurs in Banat, Transylvania, and the central area of the Moldavian Plateau (Milescu et al. 1967).

In conclusion, *F. sylvatica* is a species of particular importance on the European continent due to its extensive range and, consequently, its significant implications for ecological, social, and economic aspects. These implications are also known in Romania, where it is the most common forest species. Romania is described by the distinguished professor Marin Drcea as a huge beech forest and is therefore called the country of beeches (Drăcea 2018).

The natural range of the species *F. sylvatica* is determined by local factors, especially climatic ones (Fang & Lechowicz 2006; Magri 2008). Thus, the distribution area of this species can be grouped into two zones from a climatic point of view, one under the influence of the oceanic and Atlantic climate (western and central Europe) and the other under the influence of the continental climate (northeastern and southeastern Europe) (Șofletea & Curtu 2008).

In southern and eastern Europe, the expansion of beech is limited by high temperatures and low rainfall (Czúcz et al. 2010; Jump et al. 2006a), and in the northeastern part of the European continent, low temperatures, combined with late frosts and rainfall of less than 500 mm/year, prevent the species from spreading into northern regions (Bolte et al. 2007).

The climate requirements of beech trees include average annual temperatures ranging between 4.5 °C and 10 °C, average annual rainfall of 500-1000 mm, a growing season of 110-150 days, with wet summers and mild winters (Bolte et al. 2007; Giesecke et al. 2006; Packham et al. 2012), and in terms of drought resistance, it is considered to be a moderately sensitive species (Leuschner 2020).

Given its wide distribution and the great variation in vegetation conditions within its range, *F. sylvatica* is considered to be the most successful plant species in Central Europe (Leuschner et al. 2006).

CHAPTER 2: AIM AND OBJECTIVES

2.1. Aim of the research

Current concerns in forestry research focus on assessing the adaptability of tree species and their responses to imbalances caused by environmental fluctuations. These targets of the research community are absolutely necessary because knowledge and testing of the ecological limits of species are essential in the issue of adaptation. With the emergence of uncertainties about the future of Earth's climate, the forestry sector has entered a period of paradigm shift. Thus, concerns centred on forest productivity have been progressively transformed into objectives oriented toward the adaptive potential of forest ecosystems. However, the two perspectives can be easily merged, as there can be no productivity without adaptability, and productivity is, in fact, one way to validate adaptability. The mechanism of testing tree populations and species, corresponding to quantitative genetics, comes into play in achieving these targets. Thus, by modifying environmental conditions, genotypes are evaluated based on phenotypic responses, and productivity and adaptability can be assessed to increase the potential of forests to meet the needs of the human community. Given that F. sylvatica is emblematic of Romanian forests and that improvement programs have favoured coniferous species, determining its adaptive potential is essential for the future of the species in the Carpathian region. In conclusion, we can state that:

The aim of the research was to evaluate beech provenances from Europe, tested under different local environmental conditions in order to estimate their adaptive potential and the possibility of their use in the conditions found in Romania.

2.2. Objectives

This research study, focused on European beech, aims to achieve the following objectives, established according to current research needs:

1. Evaluating growth performance in two series of provenance trials, using phenotypic response variability analysis, quantifying phenotypic plasticity, and testing their reaction to transfer to different environmental conditions;
2. Experimental modelling of height growth for international beech provenances under Romanian environmental conditions for the test period, but also in different climate scenarios;
3. Study of phenological processes at the level of provenances tested in the Sacele trials;
4. Anatomical analysis of wood for selected provenances from the Fantanele trial.

CHAPTER 3: MATERIAL AND METHODS

3.1. The international beech provenance trials installed in Romania

From the analysed data, the first concerns regarding beech testing in Romania arose with the launch of European projects to establish two series of international provenance trials between 1995 and 1998. As a result of these projects, two provenance trials were established in the spring of 1995 in Sacele (Curvature Carpathians – Baiului Mountains) and Carbunari (Eastern Carpathians – Gutaiului Mountains), and another two in Alesd (Western Carpathians – Plopis Mountains) and Fantanele (Moldavian Subcarpathians – Pietricica Crest) in the spring of 1998 (Figure 3.1). The 1995 trials contain a total of 16 common provenances, but the number of provenances per trial differs. A total of 44 provenances were introduced in the Sacele trial, and 26 provenances in the Carbunari trial. As for the 1998 series, 32 provenances were installed in the two trials, of which 31 are common (Mihai 2009). Therefore, the establishment of this series of international provenance trials was mainly aimed at testing the species' level of adaptation to different environmental conditions by including populations from the entire range of the species (Robson & Garzón 2018; Von Wuehlisch 2004).

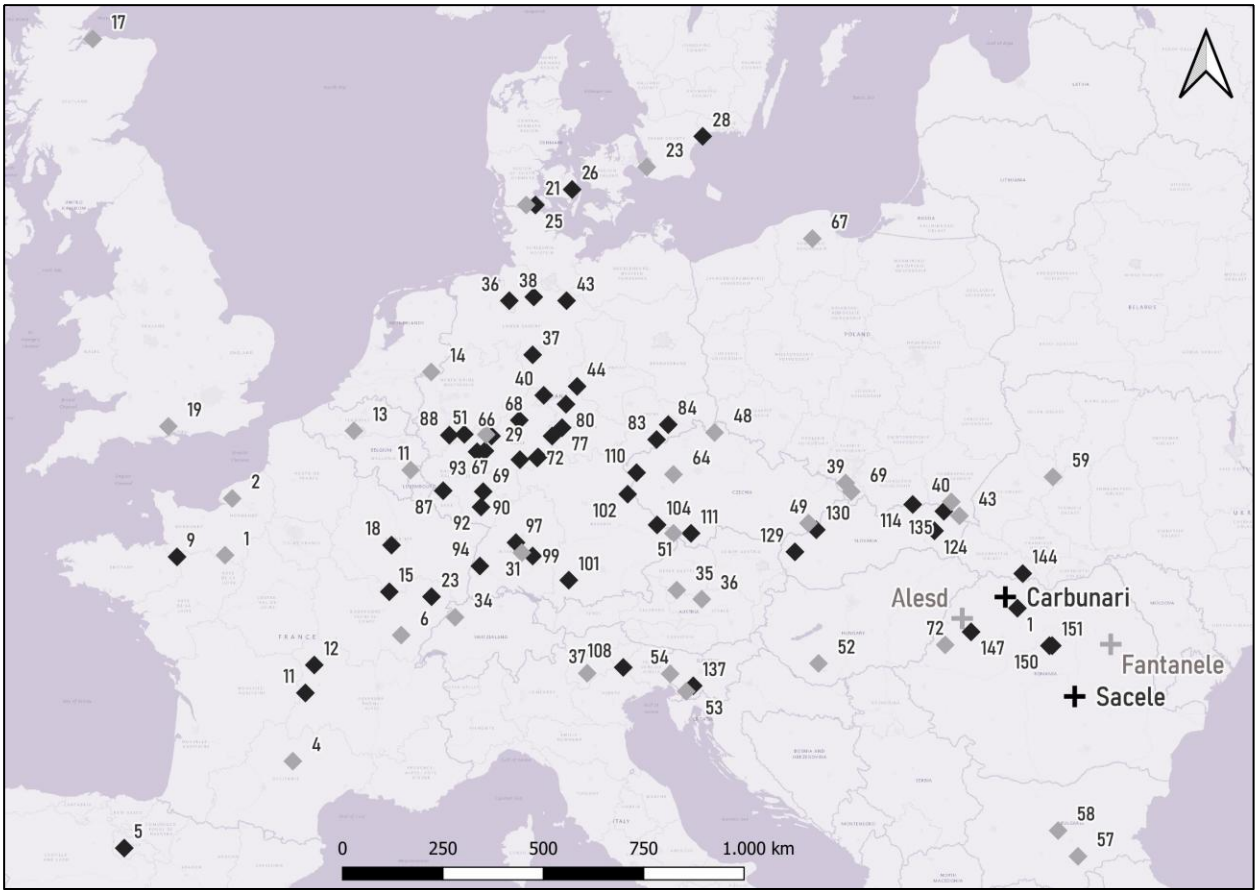


Figure 3.1. Locations of provenances (black diamonds for the 1995 series and grey for the 1998 series) and trials (black plus for the 1995 series and grey for the 1998 series) (Robson & Garzón 2018).

The experimental design used to set up the four provenance tests is a completely randomised block design 10 x 10, with three replicates and a total of 50 seedlings/block, planted at a 2 x 1 m spacing (2 m between rows and 1 m between seedlings in a row). Each block covers 100 m2 (Liesebach 2017; Von Wuehlisch 2004).

Given the large number of provenances tested and their separation into trial series, individual codes were assigned to each provenance and each trial in order to facilitate reporting in the text. These codes refer to the series (95=1995 and 98=1998), the trial code (A=Aleșd), the country of origin code (Fr=France), and the provenance number (1=1). Therefore, to refer to provenance 1 France from the Alesd crop, we will use the code 98-A-Fr-01.

The provenances tested in the first series come from 12 countries in Europe, respectively from diverse environmental conditions, and the two trials in Romania are installed in the natural area of the beech, but in different environmental conditions (Robson & Garzón 2018).

The Romanian provenances 150 Sovata (25) and 151 Sovata (26) were analysed as a single provenance (150 Sovata) in this study, as they originate from similar site conditions, both climatically and geographically (same watershed and similar altitude).

In the trials established in the 1998 series, the provenances originate from 18 European countries, and the two experiments, Alesd and Fantanele, are located in contrasting station conditions. The Fantanele trial is located at the eastern limit of the natural range of beech, while the one at Alesd is located in the ecological optimum of the species. Also, a provenance of *F. orientalis* from Bulgaria was included in this series (57 - Gramaticovo) (Robson & Garzón 2018).

3.2. The environmental conditions at the four testing sites

Based on annual temperature and precipitation averages reported in the species' ecological requirements (Stănescu et al. 1997), a climatic analysis of the trial sites was performed, thus facelifting comparisons between test sites and, at the same time, providing a clearer picture for understanding the reaction of beech provenances to interaction with different climatic conditions. A similar type of characterisation was also used by Petrík et al. (2022) for the climatic separation of provenances tested in international beech trials. The climate data used was extracted from the *B4est* database using *Climate Downscaling Tool* (B4EST 2024). This tool is based on downscaling climate variables using a dynamic adjustment of the altitudinal gradient at a resolution of 1 km, based on data provided by the CRU and UKCP18 databases (Marchi et al. 2024). In addition, to test the accuracy of the climate data, the temperature recorded by Hobo Prov2 sensors installed in each crop was used.

Analysis of climate data for the 95 series, extracted for the period between the year of installation (1995) and the year in which the measurements were taken (2022), indicates, on the one hand, the existence of similar values for average annual precipitation and, on the other hand, a higher difference in average temperature. In the case of the Sacele crop, the average precipitation was 873 mm, while in the Carbunari crop, precipitation totalled 906 mm. The average annual temperature in the Sacele crop (7.2 °C) was 2.4 °C lower than that recorded in the Carbunari crop (9.6 °C). Thus, the climatic conditions place the two experiments within the species' ecological optimum.

At the level of the 98 series, the analysis of climate data showed a clear difference between the two test sites. Thus, in the Alesd trial, the average annual precipitation was 877 mm, and the average temperature was 8.3 °C, which is within the ecological optimum for the species. In the Fantanele trial, the average annual rainfall was 591 mm, and the average temperature was 10.0 °C, placing this experiment within the ecologically limiting conditions.

3.3. Measurements

In 2022, 27 years after the installation of the experiments in series 95 and 24 years after those in series 98, the four international beech cultures installed in Romania were identified, and the limits of the trials, repetitions, and provenances were marked using yellow paint. At the same time, artificial pruning was carried out to improve accessibility in the Sacele trial, and sensors for recording air temperature and relative humidity (Hobo Prov2 Temp/RH) were installed in all tests. These sensors were installed in trees, at a height of 2.5 – 3 m above the ground, on the northern side, and the data were recorded at intervals of between 30 minutes and one hour over a period of three years.

The working methodology involved the schematic selection of five trees per provenance, respectively per repetition, following a pre-established scheme (selection of trees diagonally). If the tree indicated by the scheme was missing, another nearby tree was selected. Therefore, a total of 15 trees were selected from each provenance per trial.

Measurements were performed according to the *Treebredex* manual (Ducci et al. 2012) and aimed to determine the following phenotypic characteristics:

- Breast height diameter (*Db*);

This trait was measured using a forestry caliper. For each selected tree, two measurements were taken in different (perpendicular) directions at a height of 1.3 m, and the final value was obtained by calculating the average of the two values.

- Total height (*Ht*);

Ht was measured using the Haglof Vertex IV ultrasonic hypsometer at the level of each selected tree.

- Forking (*Fk*);

The forking was evaluated according to the *Treebredex* protocol, which proposes the use of a 7-class scale.

- Branch diameter (*Dr*);

For this trait, the diameter of the average branch located at a height of 2.2 m on the trunk was measured using an electronic caliper.

- Stem quality (*Ct*);

It was assessed based on the *Treebredex* protocol, adapted specifically to the rectitude of the tree's stem.

- Survival (*Sr*).

To determine this trait, all remaining trees from each provenance and replication were counted, and the Sr value was obtained by calculating the ratio between the current number of trees and the number of trees initially planted, which was multiplied by 100 to obtain percentages.

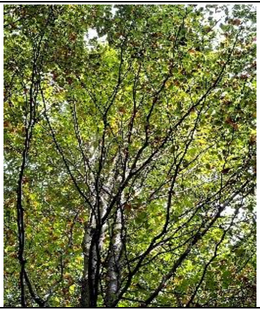
In addition to the measurements taken on the biometric traits of the trees, observations were made in the Sacele trial on the phenological processes of leafing and senescence. These observations were made over a period of three years (2022-2024), at intervals of approximately seven days. For these observations, three predominant trees were selected from each provenance (except for provenance 95-Ge-92 in the second replication, for which the last two surviving trees were selected), with well-developed crowns. These trees were selected in the first replication of the Sacele trial (the most homogeneous) in the spring of 2022, and in the following year (2023), the observations were extended to the second replication. Therefore, these observations were made for a total of 262 trees. Binoculars were used to increase visibility, and the observations focused on the upper part of the crown, made from the same position (the upstream side of the tree).

To make these observations, the phenological scales used in international beech trials established in Europe were used (Robson & Garzón 2018; Robson et al. 2013) established by Du Cros et al. (1988), with seven classes for leafing and five for senescence (Tabelul 3.4).

Table 3.4. Phenological scales used to assess the stages of leafing and senescence (Robson & Garzón 2018) (foto: Beșliu E.V.).

Leafing		
Class	**Stage**	**Visual description**
1	Dormant buds	

2	Buds swollen and elongated	
3	Budburst	
4	Partial opened leaves	
5	Total opened leaves	
6	Folded leaves	
7	Mature leaves	
Senescence		

Class	Stage	Visual description
1	Green leaves	
2	5% Yellowing	
3	50% Yellowing	
4	100% Yellowing	
5	Winter state	

For the anatomical analyses of wood, the Fantanele trial was chosen because it is located at the edge of the natural distribution area of F. sylvatica, where aspects of the species' reaction to drought can be more precisely identified and studied. For this study, the performance of the tested provenances was taken into account (Figure 4.12), choosing provenances at the extremes in terms of growth performance, as well as the native provenance tested in this plantation. Provenance 98-Fr-04 was selected due to its low performance, and provenance 98-Au-36 for its highest performance. The Romanian provenance, 98-Ro-72, showed a performance around the average.

The extraction of growth samples was carried out at the beginning of 2025 (in the first days of January) and was performed mechanically, using a *Pressler* drill driven by an electric threading machine, following the methodology proposed by Schweingruber et al. (1990). For the three selected provenances, a minimum of three samples (one core per tree) were extracted from each replication, the number being limited by the small number of trees that survived in provenance 98-Fr-04.

For anatomical analysis, three growth samples per repetition were selected, totalling nine samples for each of the three sources. The methodology for analysing these samples involved several steps, as follows (Figure 3.2):

1. Straightening and cutting samples

In the first phase, the wood samples selected for inclusion in the analysis were straightened using a core-microton (Gärtner & Nievergelt 2010). Subsequently, these were cut into two segments, up to 5 cm long, using a bistoury, ensuring that the cut was made at the level of a visible ring and was oblique. This ensured that the sample would be correctly reassembled for analysis.

2. Performing microsections

The microsections were cut using the Thermo HM 340E Electronic Rotary Microtome. The thickness of the microsections was 10 µm.

3. Cleaning microsections and preparing slides

After cutting, the microsections were washed successively with distilled water and chlorine, and then stained using a solution based on safranin and astrablue. The next step was to wash with ethanol at concentrations ranging from 75% to 100%. Finally, the microsections were glued onto slides and pressed for 24 hours using magnets (Gärtner & Schweingruber 2013).

4. Scanning samples

The slides were scanned using the Digital Slide Scanner ZEISS Axioscan 7, which produced images with a resolution of 2.9 pixels/micrometre.

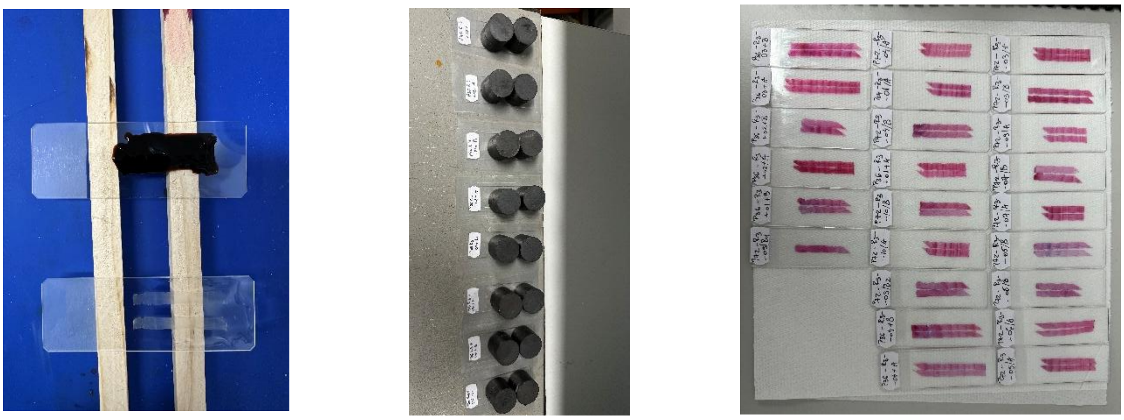
5. Image analysis

The images were edited with the soft ZEISS ZEN 3.11 and analysed with the ROXAS v3.0.250 software (Prendin et al. 2017; von Arx & Carrer 2014).

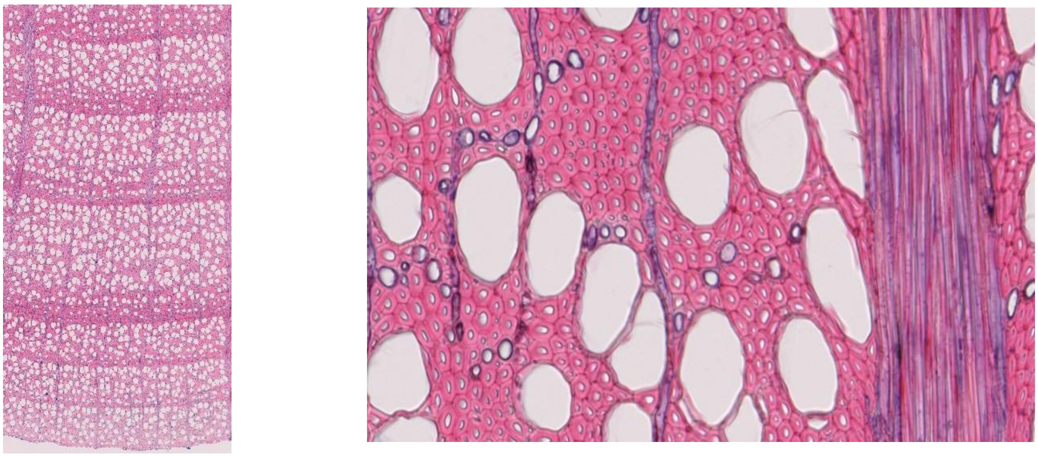
6. Measuring the ring width

The ring width was measured using Corecorder software (Maxwell & Larsson 2021), and the dating was performed using COFECHA software (Holmes 1983).

Cutting samples Performing microsections Cleaning microsections



Colouring microsections Gluing the slides Preparing the slides for scanning



Resulted imagines

Figure 3.2. The working methodology applied in the anatomical analysis of wood (foto: Beșliu E.V.).

3.4. Statistical analysis

Given the complexity of the analyses performed, which required different statistical approaches depending on the nature of the data used and the purpose of the research, they were separated into several subchapters, with each type of analysis used being described. All statistical analyses were performed using the *R statistics* program (R 2024), in which different work packages were used, as highlighted below. The manipulation of data relating to the locations of provenances and trials, and the preparation of the maps used in this paper, were performed using the *Qgis* program (Team 2024).

3.4.1. Analysis of survival and biometric traits

Due to the differentiation between the two series of trials in terms of the tested provenances, these analyses were performed separately for each series, and the graphical representation of the results followed the same distinct approach. The linearity of the data was tested using the *Shapiro Wilk* test (Shapiro & Wilk 1965), and the accuracy of the model used was tested based on the residual value graphs.

To study the variability in *Sr* levels and characteristics: *Ht*, *Db*, and *Dr*, a linear statistical model was applied, run using the *methan* work package (Olivoto & Lúcio 2020):

$$Yijk \;=\; \mu \;+\; \alpha i \;+\; \tau j \;+\; (\alpha\tau)ij \;+\; Yjk \;+\; \varepsilon ijk \;(1),$$

where: Yijk = response variable (i = provenance, j = trial, k = replication); μ = mean; αi = provenance effect; τj = trial effect; (ατ)ij = the effect of the interaction between provenance (i) and trial (j) ϒjk = the effect of replication on the trial level; εijk = random error.

The graphs were created using the packages *ggplot2* (Wickham 2011) and *metan* (Olivoto & Lúcio 2020), and the results of the T-test were represented on the graphs to highlight the significance of the differences between the two test sites in each trial series, as well as the standard error values.

For the *Fk* and *Ct* characteristics, given the nature of the data (categorical variables), variability was tested using the χ^2 (Chi-square) test, and graphical visualisation was performed using mosaic graphs created with the *vdc* package (Meyer et al. 2024).

The performance of the provenances was studied at the trial level, using a graphical representation in the form of quadrants, created with the *ggplot2* package (Wickham 2011), in which the *Sr* and *Ht* averages were considered selection criteria and assessed as representative of growth and adaptation performance (Engel et al. 2023; Matisons et al. 2018).

3.4.2. Analysis of phenotypic plasticity

The ability of trees to adapt to different site conditions was quantified based on the *Relative Distances Plasticity Index (RDPI)* described by Valladares et al. (2006). This index involves calculating the absolute value of the differences between the phenotypic characteristics of a provenance that is tested under different environmental conditions. The index takes values between zero (no plasticity) and one (maximum phenotypic plasticity), and the calculation was performed using the *Plasticity* package (Ameztegui 2017). The analysis of phenotypic plasticity (*Pf*) was performed separately on the two series, analysing only the common provenances, and in the graphical representation, analysis of variance (*ANOVA*) was used to generate the overall level of differentiation, and the *Tukey* test was used to highlight the differences between provenances by including them in homogeneous groups. The characteristics *Sr*, *Ht*, and *Db* were included in the *Pf* calculation.

3.4.3. Transfer analysis

The analysis of the reaction of provenances to transfer to other environmental conditions was performed using the *Ecological Transfer Distances* method (Mátyás et al. 2009a; Mátyás & Yeatman 1992). This method is based on the assumption that the phenotypic response of provenances is influenced not only by the test environment but also by the transfer distance. Therefore, the method allows visualisation of the macroclimatic adaptation of provenances by comparing the climatic conditions at the test site with those at their place of origin. The calculation of climatic favorability was performed based on the *Ellenberg quotient* index (*EQ*) (Ellenberg 1988), and the difference between the *EQ* value of the test site and the *EQ* value of the place of origin represents the transfer distance value (ΔEQ). The climate data used were those presented above, extracted from the *B4est* portal (B4EST 2024) for the period 1995/1998-2022. To visualise the influence of transfer distances on phenotypic traits, it was necessary to eliminate the effect of the test site by correcting the values of the analysed traits using the difference between the trial average and the overall average, which includes both test sites. (Mátyás et al. 2009a). Finally, the regression equation graph between transfer distance values and phenotypic traits was drawn using a polynomial function and tested with a simple linear model. *Sr*, *Ht*, and *Db* were included as dependent variables in this analysis, and ΔEQ was used as the independent (explanatory) variable. The transfer function was applied in the case of common origins of the two series, and the graphical representation was performed using the *ggplot2* package (Wickham 2011).

3.4.4. Universal Response Function modelling

The Universal Response Function (*URF*) model was selected for modelling the adaptive response of the provenances (Wang et al. 2010). This prediction model uses phenotypic traits as a simultaneous response function to the influence of the climatic conditions at the test sites and the genotype's particularities. The reaction of provenances is recorded in provenance trials, and based on this, the model can generate predictions about the species' adaptation to any climate.

To achieve this goal, it was necessary to use a database with previous measurements of these trials published by Robson & Garzón (2018) and widely used in modelling studies. This database, with repeated measurements in the juvenile stage (up to 2006), was supplemented with measurements taken in this study (2022), thus establishing the growth response of the provenances much more accurately, as it also includes measurements taken 24-27 years after planting. With regard to the climate dataset, the *URF* model used climate data for both the current period and simulations up to the year 2100, extracted from the ECLIPS 2.0 database (Chakraborty et al. 2021) due to the accuracy of the methods used to define climate variables.

Ht was included as a dependent variable in the *URF* model, but in order to eliminate the effect of the different ages of the two series, this variable was normalised (*Hn*) by relating it to the interval between the maximum and minimum values. Thus, the value 1 indicates the best provenance, and 0 the worst, for height.

In order to estimate *Hn* for beech in Romania, a *Random Forest* regression model was applied (Breiman 2001), which was implemented based on the *randomForest* package (Liaw & Wiener 2002). In this model, the predictor variables used were age and climate variables specific to the testing site and provenance origins. The climate variables were identified using the same work package, and their importance was tested numerous times to identify those that best explain the variability of *Hn*. The importance was assessed by reducing prediction accuracy, thereby identifying the variables that play a significant role, and by the Gini index, which indicates the degree to which variables contribute to separating the data within the decision trees. In addition, the final decisions on the use of climate predictors included a careful review of their ecological importance for the species *F. sylvatica*, by consulting the specialised literature. The climatic variables used as predictors and separated for the test area (*site*) and for the provenance origin (*prov*) were: maximum summer temperature *(site_Tmax_sm* and *prov_Tmax_sm*), spring precipitation (*site_PPT_sp* and *prov_PPT_sp*), annual temperature and moisture index (*site_AHM* and *prov_AHM*), January precipitation (*prov_PPT_01* – only at provenance level), and continentality index (*prov_TD* – only at provenance level). The *URF* model used 500 decision trees for training, and at each split, a subgroup consisting of three variables was considered. The model's performance was evaluated using the OOB (Out-Of-Bag) value, which represents the error rate computed on observations not used in training the decision trees and serves as an internal estimate of the model's accuracy.

Finally, the spatial distribution of height (*He*) for the species *F. sylvatica* was estimated by reducing the predictions to the borders of Romania (Crăciunescu 2009) and overlaying the local natural distribution of the species (Doniță et al. 2008), and the final graphs were adapted using the *ggplot2* package (Wickham 2011).

3.4.5. Phenological analysis

In order to determine as accurately as possible, the adaptive potential of international beech provenances, spring phenology (leafing) and senescence were analysed to identify the climate sensitivity of the provenances tested in the Sacele trial. The air temperature data used in the analyses were recorded over three years using two HOBO sensors, one installed in each replicate of this crop. Finally, based on the recorded temperatures, the average daily temperature and the minimum and maximum temperatures (°C) were calculated. Also, to quantify the thermal requirements corresponding to the onset and end of vegetation growth for beech provenances, two indices were calculated: growing degree days (*GDD*) and senescence degree days (*SDD*). These indices were calculated on a daily basis by taking the difference between the average temperature and the base temperature (Ciocîrlan et al. 2024; McMaster & Wilhelm 1997). Finally, to identify the thermal requirements, these indices were cumulated to achieve each class of leafing and senescence. For the base temperature, thermal thresholds of 5 °C for *GDD* and 15 °C for *SDD* were used.

The onset of vegetation growth was assimilated with the budburst stage, and the end of vegetation growth was considered to be marked by reaching the 50% yellowing stage (Ciocîrlan et al. 2024; Schieber et al. 2013). The length of the growing season was calculated as the difference in days between the start and end of vegetation (Ciocîrlan et al. 2024; Drobyshev et al. 2010).

At the level of data derived from observations made on phenological processes, the *Kolmogorov-Smirnov* test (Conover 1999) was used to test their distribution. This was selected due to the large size of the data set, which did not allow the use of the *Shapiro Wilk* test (Shapiro & Wilk 1965).

Due to the fact that the data distribution was not normal, the analysis of differences between origins, years, and repetitions was performed using the nonparametric *Kruskal–Wallis* test (Kruskal & Wallis 1952), where the dependent variable was *DOY* (day of the year). Complementarily, the Dunn test (Dunn 1964) was applied to quantify the differences in all analysed variables.

To identify variation in *DOY* as a function of temperature, a generalised linear mixed model (GLMM) was applied, using the Gamma distribution, which requires a logarithmic transformation of the dependent variable. The Gamma distribution is recommended for this type of calendar data, as well as for non-parametric data. The influence of temperature was captured by applying a spline function at the annual level (with three degrees of freedom), thereby accounting for the nonlinear effect of temperature on phenology and its annual variations. The model was generated using the *glmmTMB* package (Brooks et al. 2017):

$$log(\mu ij) = \beta 0 + f(Tij) + u0j + u1jTij\ (2),$$

where: µij = expected value of *DOY*; β0 = the value of *DOY* estimated by the model, independent of the temperature effect and annual variation of it; f(Tij) = spline function of temperature; u0j și u1j = intercept and random slope for each year (j).

A similar model was used to analyse the thermal requirements of provenances for the onset (budburst) and end (50% yellowing) of vegetation. This time, the dependent variable was *GDD*, respectively *SDD* (cumulative), and provenance was set as a fixed effect and year as a random effect. The same model was used to analyse the length of the growing season. For optimal visualisation of the differences between provenances, the values generated by the model were adjusted using the *Holm* method to generate homogeneous groups, using the *emmeans* package (Lenth 2023).

In other words, for the graphical representation of thermal requirements by class, a step-wise progression graph was used, generated from *GDD* and *SDD*. All graphical representations related to the analyses of leafing and senescence were created using the packages *ggplot2* (Wickham 2011) and *metan* (Olivoto & Lúcio 2020).

3.4.6. Anatomical analysis of wood

The analysis of differences in radial growth and lumen area was performed using a linear model fitted with the *lmerTest* package (Kuznetsova et al. 2017):

$$Yijkl \; = \; \mu \; + \; \alpha i + uj + vk + wkl \; + \; \varepsilon ijkl \, (3)$$

where: Yijk = reponse variable (i = provenance, j = year, k = replication, l = tree); μ = mean; αi = effect of provenance; uj = effect of year; vk = effect of replication; wkl = effect of tree; εijkl = residual error.

Correlations between anatomical parameters and climate were performed using the *dendroTools* package (Jevšenak 2020), and the climate data used in these analyses were extracted from CRU (Harris et al. 2020) and TerraClimate (Abatzoglou et al. 2018) databases.

The chronological data analysis was performed using the *dplR* package (Bunn 2008), and the *GAM* (General Additive Model) model for testing the interaction between the average area of the vessels and climate at the sector level was generated using the *mgcv* package (Wood 2017):

$$Ym \; = \; \mu \; + \; \alpha\{i(m)\} \; + \; \gamma\{g(m)\} \; + \; f\{i(m), g(m)\}(xm) \; + \; b\{t(m)\} \; + \; \varepsilon m \, (4)$$

where: Ym = mean vessel variable; μ = mean; αi = effect of provenance; Yg = effect of climatic group; xm = relative position on the tree ring; f{i,g}(x) = the smooth function specific to the interaction provenance:climate group; bt = effect of tree; εm = residual error.

The differences between provenance, shown in the model graphs, were calculated using the *Kolmogorov-Smirnov* test (Conover 1999).

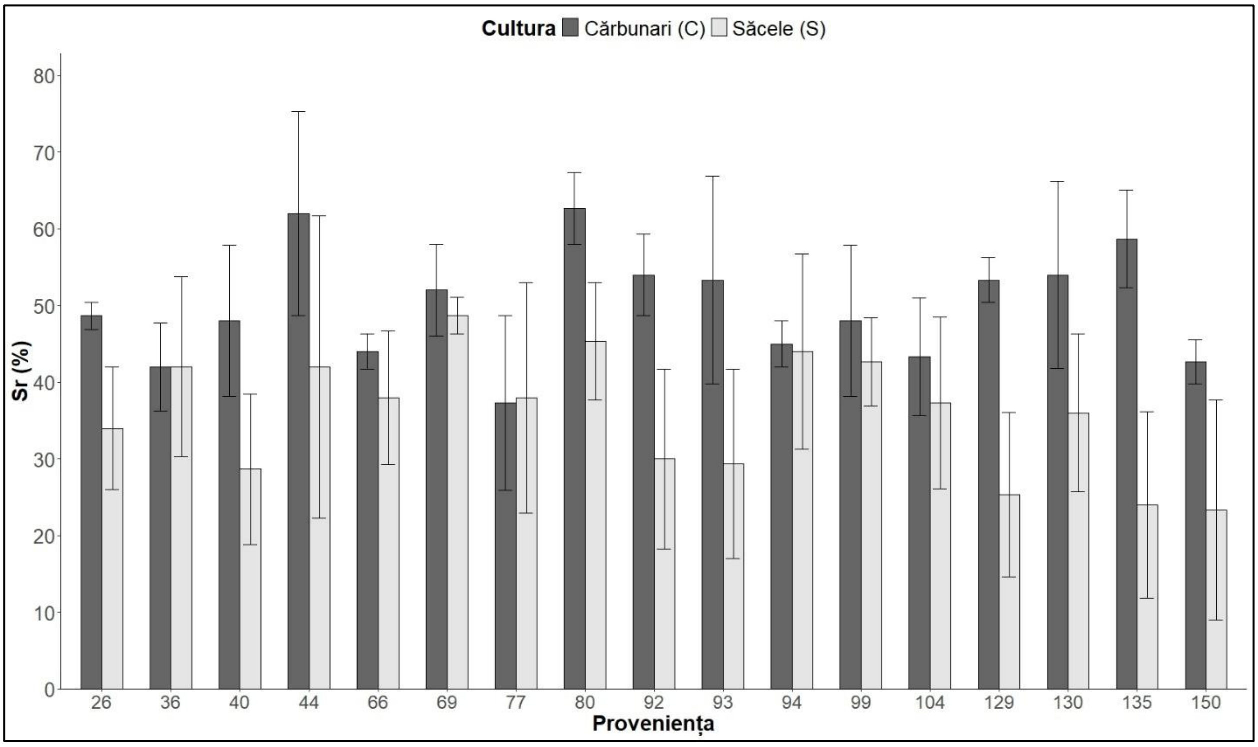
CHAPTER 4: RESULTS AND DISCUSSIONS

4.1. Survival and biometric traits

4.1.1. Survival

The evaluation of survival (*Sr*) variability at the 95 series level revealed significant differences in terms of replications and trials, but the differentiation between provenances within trials, respectively the provenance x locality (test site) interaction, was not significant. *Sr* recorded an average value of 50% in the Carbunari trial, significantly higher ($p<0.001$***) than the values obtained in the Sacele trial (35.8%). In the case of series 98, the differences were significant at all levels, thus suggesting the involvement of all the factors analysed in *Sr* performances. In the Alesd trial, the *Sr* average was 7.8% higher than in the Fantanele test, a difference that was statistically significant ($p<0.001$***).

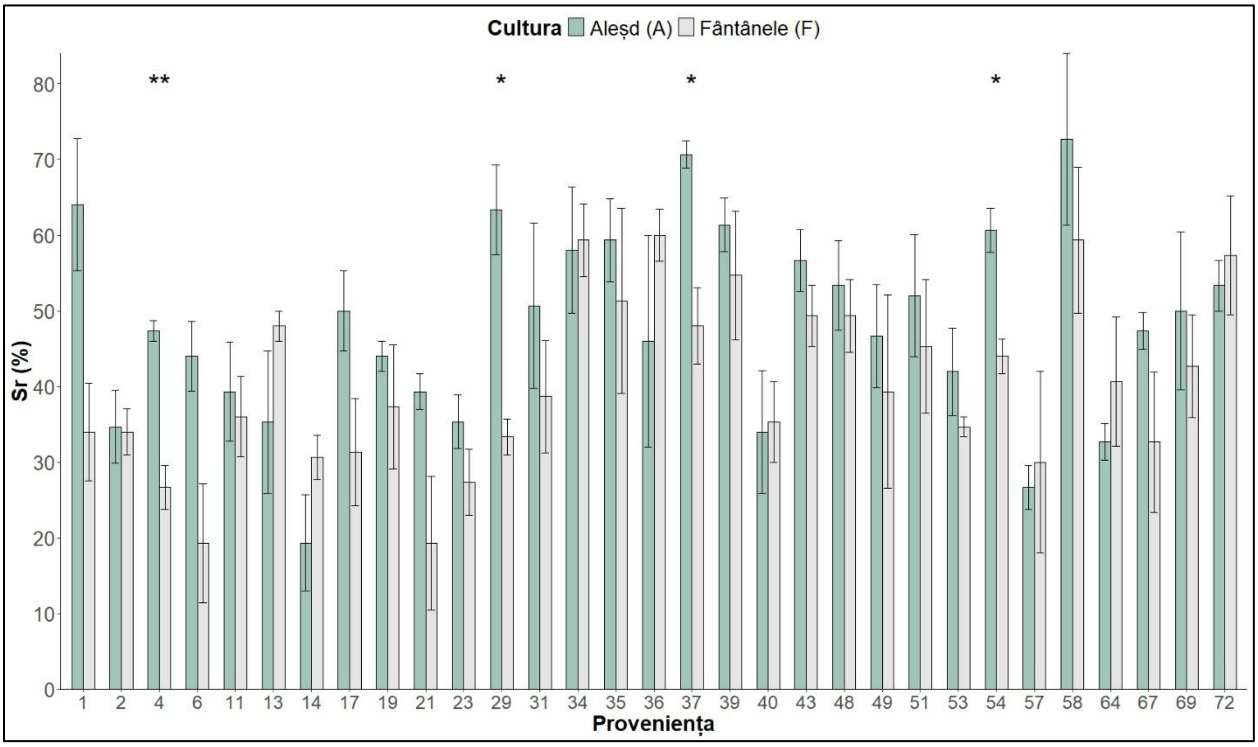
In the case of series 95 (Figure 4.1), the highest *Sr* values were obtained in the Carbunari trial, where 15 of the 17 common provenances recorded higher values than in the Sacele test. The 95-Ge-80, 95-Ge-44, and 95-Sk-135 provenances exhibited the highest *Sr* values, whereas the lowest performance was recorded by the 95-Ro-150, 95-Sk-135, and 95-Sk-129 provenances in the Sacele trial. Similar reactions were observed at the two test sites for provenances 95-Ge-36, 95-Ge-77, and 95-Ge-94, but high variation, ranging from 18% to 35%, was recorded for provenances 95-Ge-92, 95-Ge-93, 95-Sk-129, 95-Sk-130, and 95-Sk-135. The local provenance 95-Ro-150 obtained *Sr* values below the average in both experiments.



The black lines positioned above the bars of the chart represent the standard error values.

Figure 4.1. Survival analysis in series 95, modified after Besliu et al. (2024c).

The *Sr* evaluation at series 98 (Figure 4.2) highlighted the superiority of the Alesd crop, where the highest values were obtained by provenances 98-Bg-58 and 98-It-37 with over 70%, respectively, 98-Fr-01 with 64%. At the opposite end of the pole, the lowest *Sr* performances (19%) were recorded by provenance 98-Ol-14 in the Alesd trial and by provenances 98-Fr-06 and 98-Dk-21 in the Fantanele trial. Large variations in *Sr* were observed for provenances 98-Fr-04, 98-Ge-29, 98-It-37, and 98-Sl-54. These obtained significantly higher values ($p < 0.05$*) in the Alesd environment. Although most provenances recorded higher values in the Alesd trial, provenances 98-Be-13, 98-Ol-14, and 98-Au-36 obtained higher values under the more restrictive vegetation conditions of the Fantanele test, but these were not statistically significant. The provenances 98-Fr-02, 98-El-34, and 98-Pl-40 yielded very similar *Sr* values at both test sites, highlighting their consistent behaviour and stability across different environments. The reaction of the local provenance, 98-Ro-72, proved to be similar in the two experiments, where it obtained values above 50%, which indicates good performance in terms of *Sr*.



The black lines positioned above the bars of the diagram represent the standard error values; '' represents the significance of the t-test (* for $p < 0.05$; ** for $p < 0.01$; *** for $p < 0.001$; **** for $p < 0.0001$).*

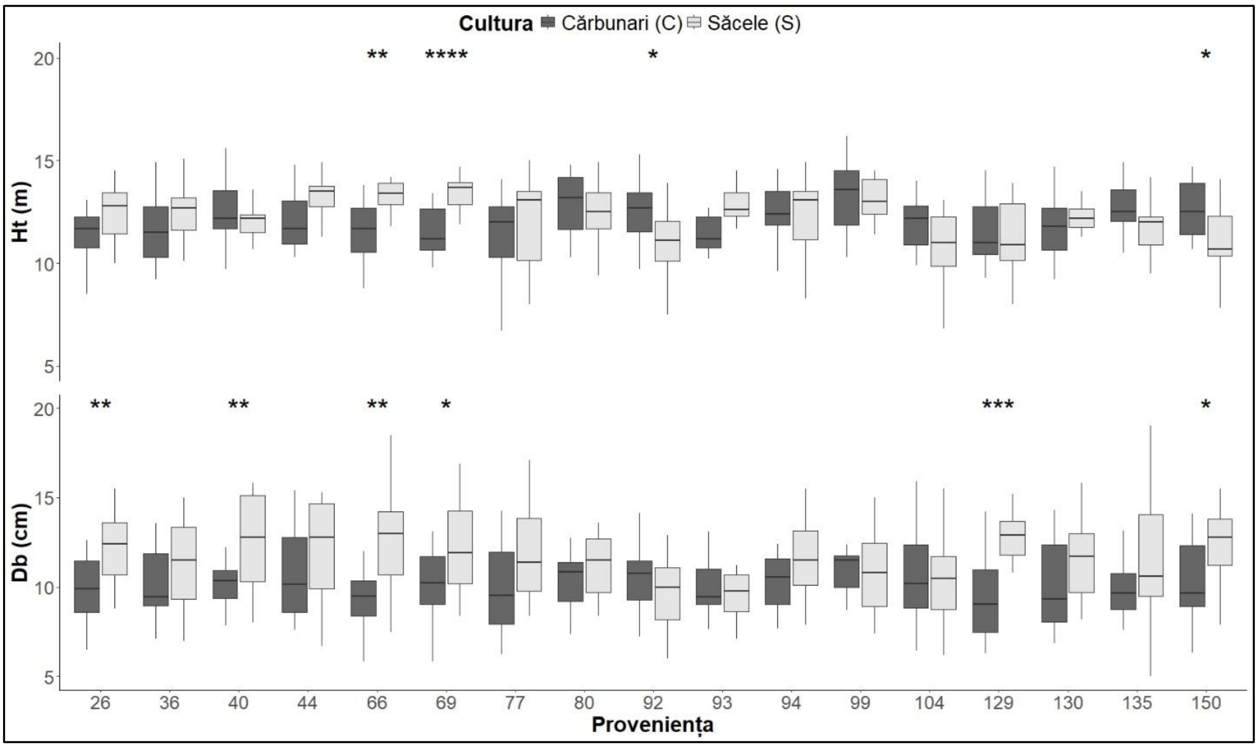
Figure 4.2. Survival analysis in series 98, modified after Besliu et al. (2024b).

4.1.2. Height and diameter

In series 95, *Ht* variability was high for both trial and for the provenance x location interaction, but insignificant for the difference between the two test sites. Therefore, this trait is clearly influenced by genetic factors of provenance and by replication. With regard to *Db*, no significant variation was observed between provenances at the trial level, and the provenance x location interaction was close to the significance threshold. The factors that significantly influenced this trait were replication and trial. In series 98, variability in *Ht* was high at almost all levels, except for the replication in the Fantanele trial. Thus, the *Ht* values in the Alesd test were on average 1 m higher than in the Fantanele trial. In contrast, only the test site (the trial factor) had a significant influence on *Db*, while within the experiments, high homogeneity was achieved, with neither the genetic factor (provenance) nor the environmental factor (replication) having a statistically significant influence.

Although the differences between the two trials in the 95 series are insignificant for *Ht*, certain provenances showed contrasting reactions between the two test sites, which is also supported by the significant provenance x location interaction ($p < 0.001$***). Therefore, it can be observed that the 95-Ge-66 and 95-Ge-69 provenances recorded significantly higher performances in the Sacele trial, while the 95-Ge-92 provenance and the native 95-Ro-150 provenance had significantly better performances in the Carbunari trial. Also, the highest average *Ht* values were obtained for provenances 95-Ge-66 and 95-Ge-69 in the Sacele test, and for provenance 95-Ge-99 in the Carbunari trial. In the Sacele trisl, the lowest *Ht* averages were observed in the 95-Ge-92, 95-Ge-104, and 95-Sk-135 provenances (Figure 4.3).

Regarding *Db*, significantly higher average values were recorded in the Sacele trial ($p < 0.001$***), and the highest values were obtained by provenances 95-Ge-40, 95-Ge-44, and 95-Ge-66. The lowest average values were observed in the Carbunari test for provenances 95-Dk-26, 95-Ge-66, and 95-Sk-129. The average *Db* for the native provenance 95-Ro-150 was significantly higher in the Sacele trial (Figure 4.3).

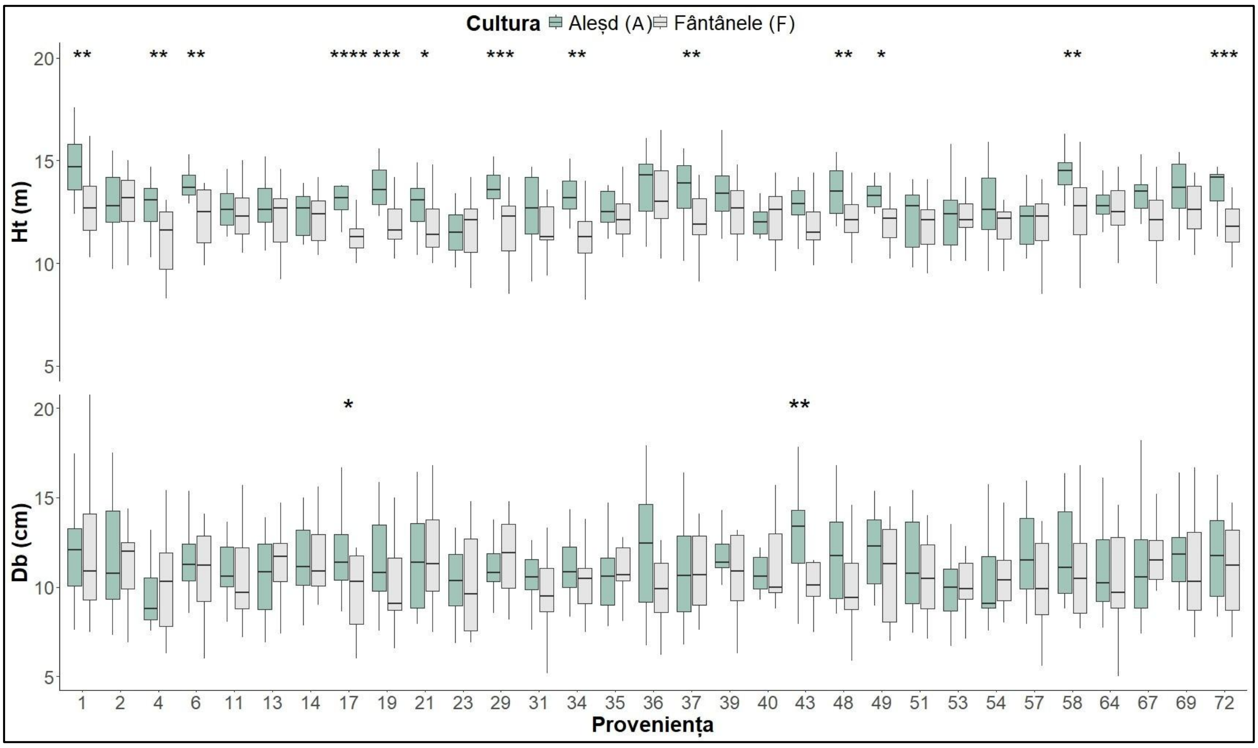


The black lines positioned above the bars of the diagram represent the standard error values; '' represents the significance of the t-test (* for p < 0.05; ** for p < 0.01; *** for p < 0.001; **** for p < 0.0001).*

Figure 4.3. Analysis of total height and breast height diameter in the 95 series, modified after Besliu et al. (2024c).

A high degree of variability was observed in series 98 for Ht. The graphical representation of the results (Figure 4.4) indicates the levels of differentiation between provenances and between the two test sites. For 13 provenances, the differences were statistically significant ($p < 0.05$* to $p < 0.0001$****), indicating a clear influence of the test environment on *Ht* performance. The highest average *Ht* values were recorded in the Alesd trial by provenances 98-Fr-01, 98-Au-36, and 98-Bg-58. On the contrary, the lowest values were recorded by provenances 98-Fr-04, 98-Mb-17, and 98-El-34 under the limiting conditions for beech in the Fantanele trial. However, provenances 98-Se-23 and 98-Pl-40 obtained slightly higher average *Ht* values in the Fantanele test, but these were not statistically significant. Noteworthy is the performance of provenance 98-Au-36, which recorded similar and among the highest performances at both test sites. The local provenance, 98-Ro-72, was significantly influenced by contrasting environmental conditions, obtaining significantly lower values for *Ht* under the limiting conditions of the Fantanele trial.

With regard to *Db*, significant differences between the two trials were observed only in the 98-Mb-17 and 98-Pl-43 provenances, which obtained higher values in the Alesd trial. The most significant performances were obtained by provenances 98-Au-36, 98-Pl-43, and 98-Pl-49 in the Alesd trial, and the lowest by provenances 98-Pl-64 and 98-Ge-31 in the Fantanele experiment. The reaction of the Romanian provenance, 98-Ro-72, was similar at both test sites.



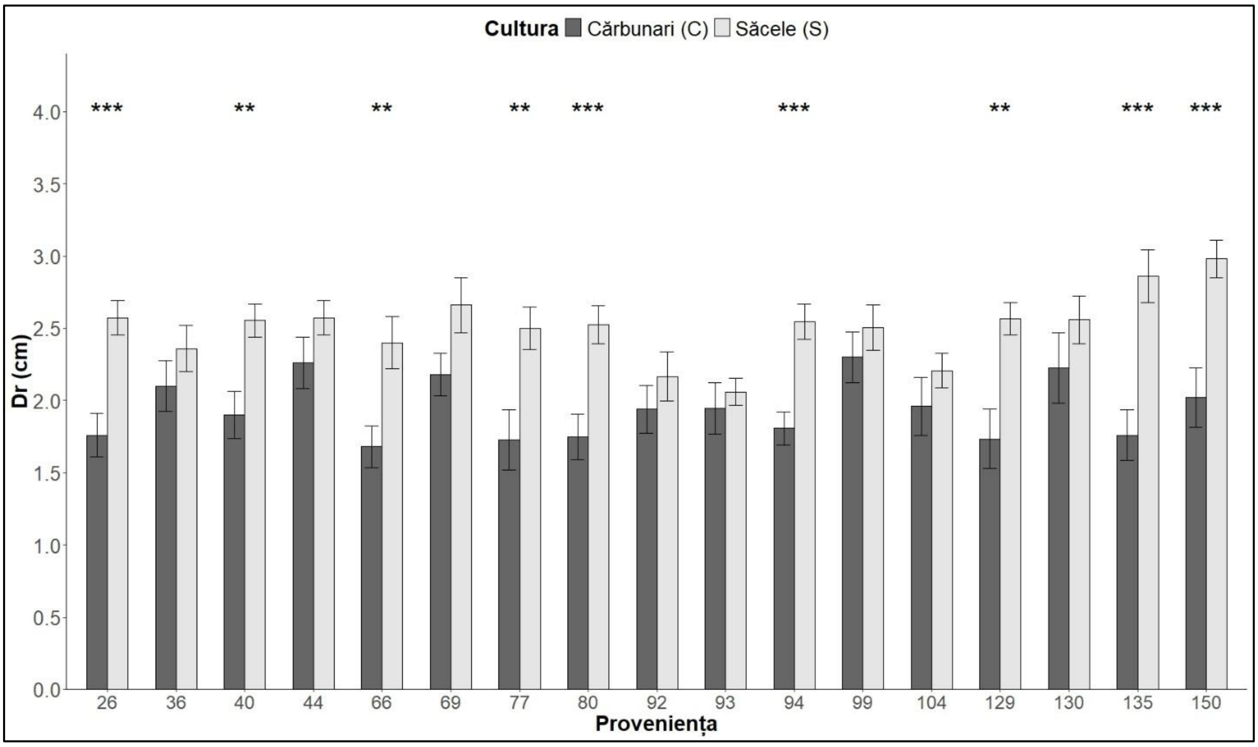
The boxplot diagram shows: the minimum value, quartile 1, median, quartile 3, and maximum value; '' represents the significance of the t-test (* for $p < 0.05$; ** for $p < 0.01$; *** for $p < 0.001$; **** for $p < 0.0001$).*

Figure 4.4. Analysis of total height and breast height diameter in the 98 series, modified after Besliu et al. (2024b).

4.1.3. Brach diameter

At the 95 series level, differences between provenances in the two cultures, as well as their interaction, were significant, indicating that branch diameter (*Dr*) is influenced by both environmental factors and the genetic makeup of the provenances. The mean *Dr* was significantly higher ($p < 0.001$***) in the Sacele trial, by 0.6 cm. In the Carbunari trial, provenance did not have a significant influence, and in the case of the Sacele test, the replication was the insignificant factor in the variation of *Dr*.
Regarding the variation in *Dr* in the 98 series tests, a wide range was observed across all levels. The only insignificant factor was repetition in the Alesd trial. Therefore, in this series as well, *Dr* proved to be both genetically controlled and influenced by testing conditions. The difference between the two environmental conditions was smaller (0.2 cm) but statistically significant ($p < 0.001$***).

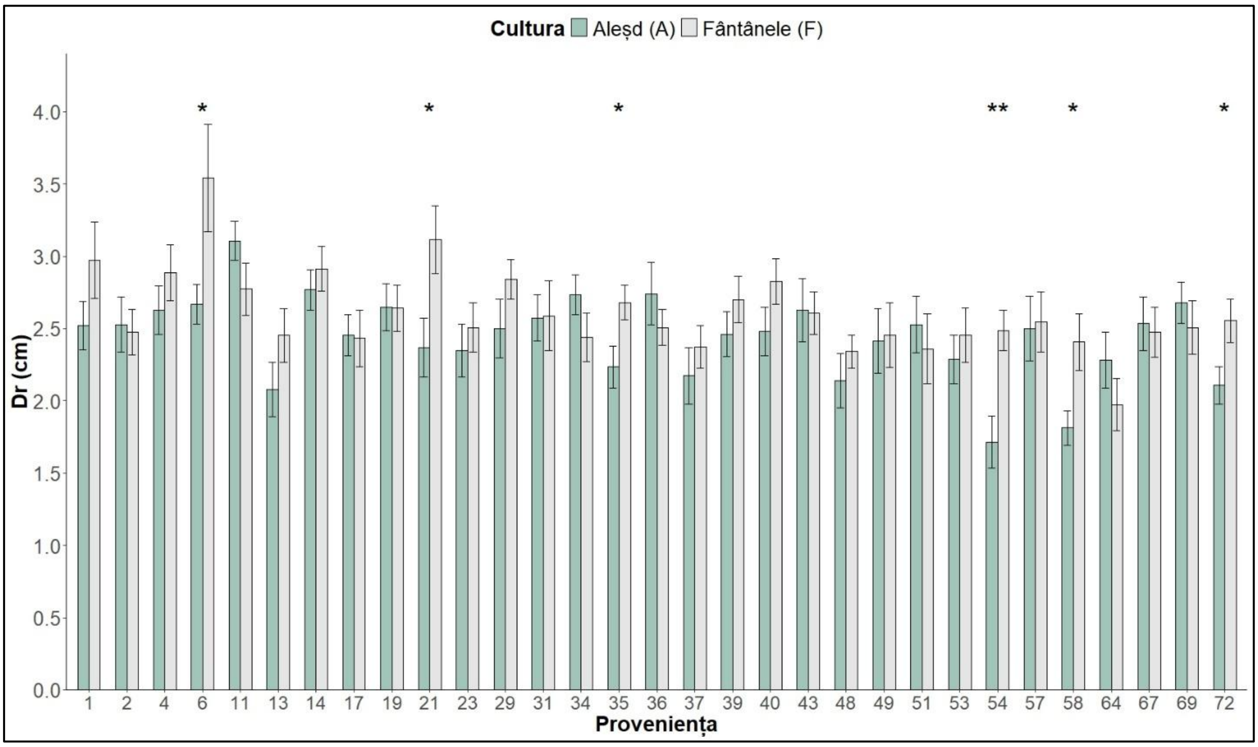
The evaluation of variability in series 95 highlighted the different reactions of provenances in the two experiments. Figure 4.5 shows that all provenances recorded higher *Dr* values in the Sacele trial, and most of the differences are statistically significant. Consequently, the reaction of the provenances draws attention to the local conditions that clearly influenced the performance of the provenances in terms of this trait. The highest average values for *Dr* were obtained by provenances 95-Ro-150, 95-Sk-135, and 95-Ge-69 in the Sacele trial, while provenances 95-Ge-66, 95-Ge-66, and 95-Ge-77 recorded the lowest averages in the Carbunari experiment. The provenances 95-Ge-92, 95-Ge-93, and 95-Ge-104 achieved consistent performance at both test sites.



The black lines positioned above the bars of the diagram represent the standard error values; '' represents the significance of the t-test (* for p < 0.05; ** for p < 0.01; *** for p < 0.001; **** for p < 0.0001).*

Figure 4.5. Analysis of branch diameter in the 95 series, modified after Besliu et al. (2024a).

Regarding series 98, most provenances recorded higher values in the Fantanele experiment, and for six of them the differences were significant ($p < 0.05$), also indicating their sensitivity to environmental conditions (Figure 4.5). Therefore, these results indicate that provenances react to interaction with more restrictive test sites by intensifying growth at the *Dr* level. The highest average values, indicating the poorest performance, were obtained by the 98-Fr-06 and 98-Dk-21 provenances in the Fantanele trial and by 98-Lu-11 in the Alesd trial. Contrary to these, the lowest values of *Dr*, so the best performances, were observed in the 98-Sl-54 and 98-Bg-58 provenances in the Alesd trial, and in the 98-Pl-64 provenance in the Fantanele trial. Some provenances with a very similar reaction in both experiments were 98-Fr-2, 98-Mb-17, 98-Mb-19, and 98-Ge-31, suggesting a low influence of the testing site on their phenotype expression. The 98-Ro-72 (native) provenance performed significantly better in the Alesd experiment, while also highlighting its sensitivity to changing site conditions.



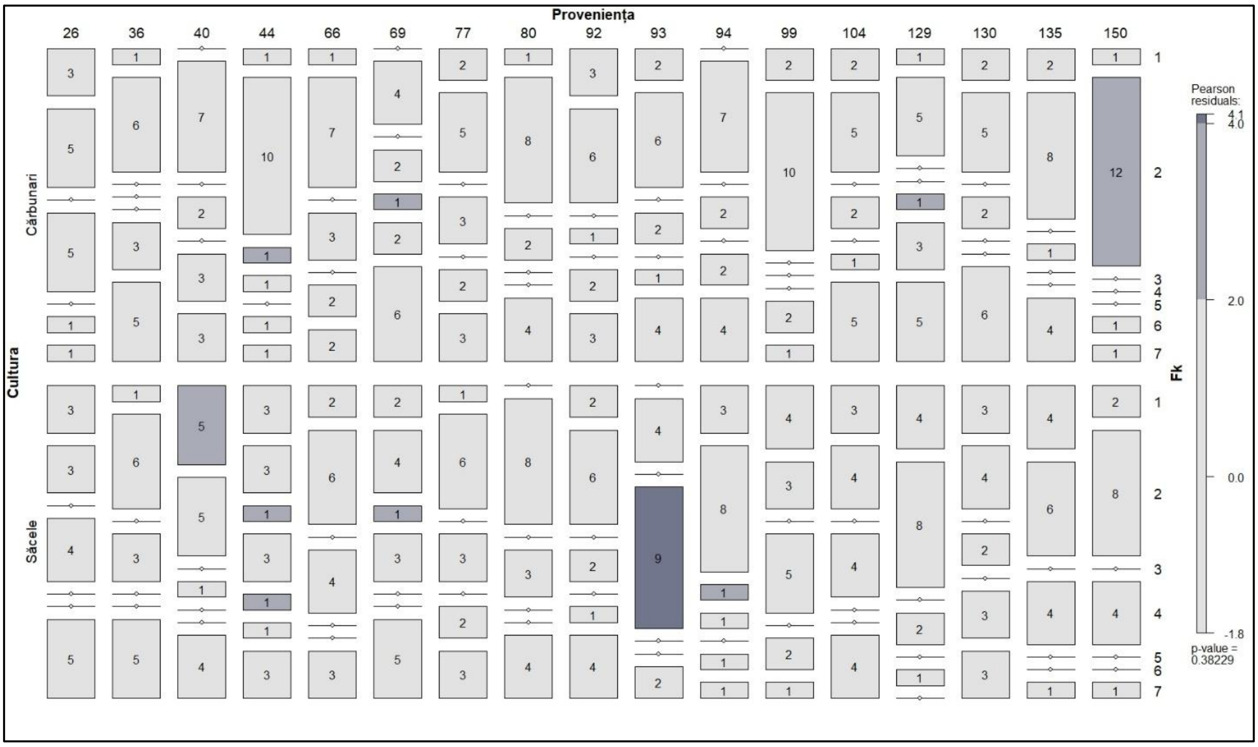
The black lines positioned above the bars of the diagram represent the standard error values; '' represents the significance of the t-test (* for $p < 0.05$; ** for $p < 0.01$; *** for $p < 0.001$; **** for $p < 0.0001$).*

Figure 4.6. Analysis of branch diameter in the 98 series, modified after Besliu et al. (2024a).

4.1.4. Forking

The evaluation of variability for forking (*Fk*) highlighted a similar trend in both trial series. Thus, there are significant differences between trials ($p < 0.001$***) and no differences between provenances, both at the series level and at the level of each trial. Therefore, this trait appears to be clearly influenced by environmental conditions and less by the genetic pattern of the provenances.

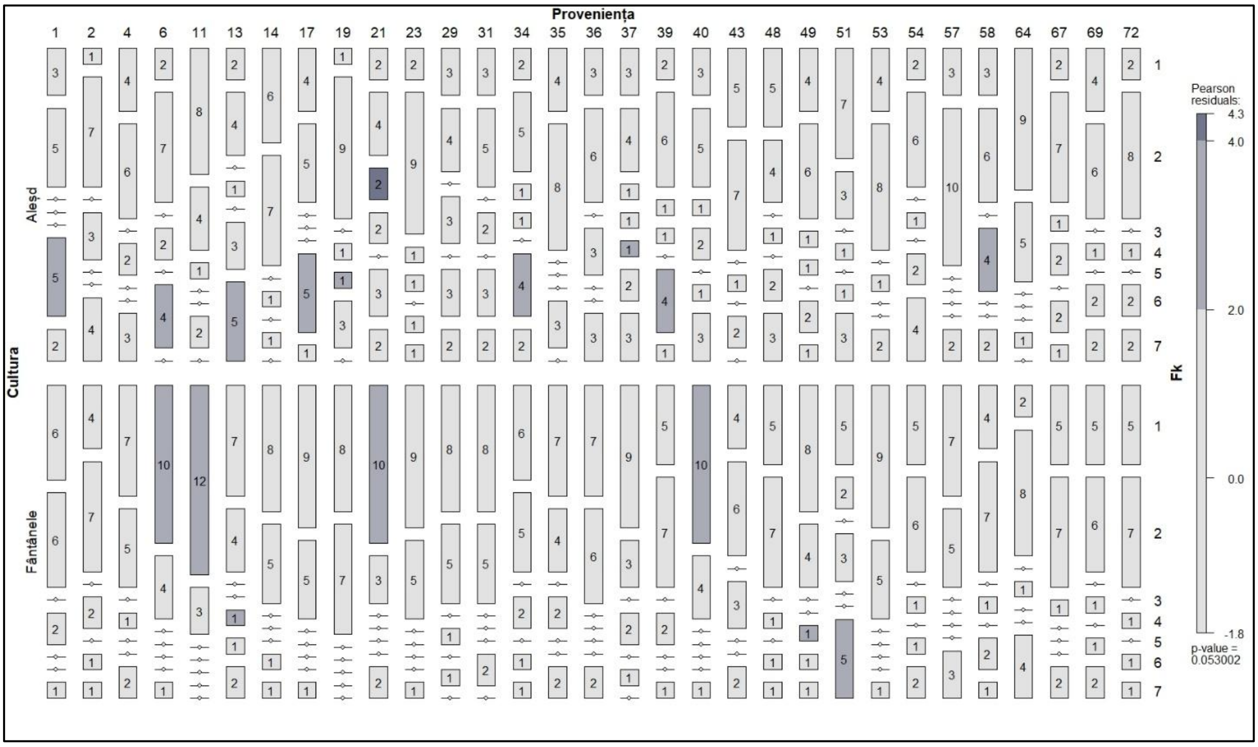
At the 95 series level, the *Fk* values were significantly different between the two test sites, with differences identified in the fourth class of *Fk*. Thus, in the Carbunari trial, significantly fewer trees with a fork in the middle third of the stem (class 4) were found. Also in this experiment, a higher number of trees without forking (class 7) was observed, and in the Sacele trial, a higher number of trees with multiple forks in the first part of the stem (class 1) was observed, but these differences were not marked as significant. At the level of the two trials (Figure 4.7), no statistically significant variations were identified among provenances. However, the lowest performances in terms of *Fk* (class 1) were identified in the Sacele trials at provenances 95-Ge-40, 95-Ge-99, 95-Sk-129, and 95-Sk-135. Conversely, most trees without forks (class 7) were observed in the case of provenances 95-Ge-69 and 95-Sk-130 in the Carbunari trial. In addition, provenance 95-Ge-69 recorded a significant number of trees without forks in both trials. In the case of the native provenance, 95-Ro-150, a large number of trees with forks in the first part of the stem (classes 1 and 2) were observed in both experiments. Similar behaviour in the two tests was also observed in the provenances 95-Ge-36, 95-Ge-66, and 95-Ge-92.



The colours in the graph and their intensity represent the level of significance for the Pearson residuals statistical measure: grey = insignificant, red = significantly lower values, blue = significantly higher values; the values represented inside the boxes indicate the number of observations; the horizontal lines indicate the lack of observations.

Figure 4.7. Analysis of forking in series 95, modified after Besliu et al. (2024a).

In series 98, a significant variation in *Fk* was observed in classes one and six. Therefore, under the more favourable environmental conditions in the Alesd experiment, the number of trees with multiple forks in the first part of the stem (class 1) was lower, and the number of trees with a fork in the upper third of the stem (class 6) was higher compared to the values obtained in the Fantanele trial. Also, under the more difficult vegetation conditions in the Fantanele trial, approximately half (46%) of the trees had forks in the lower part of the trunk (classes 1 and 2), while in the Alesd trial, there were more trees without forks (class 7). This trend of *Fk* was also confirmed in series 95. Although no notable differences were identified between provenances, a large number of trees with multiple forks in the lower third of the stem (class 1) were identified in the Fantanele trial (Figure 4.8). Thus, the provenances with the lowest performance were 98-Fr-06, 98-Lu-11, 98-Dk-21, and 98-Pl-40. On the other hand, most trees without forks (class 7) were identified in the Alesd trial, in the provenances 98-Fr-02, 98-Be-13, and 98-Sl-54. In general, better performance was observed in the Alesd culture, but provenances 98-Ch-51 and 98-Ch-64 recorded a higher number of trees without forking in the Fantanele trial. Provenance 98-Lu-11 performed poorly in both experiments, and the native provenance showed a large number of forks in the lower third (classes 1 and 2) and a small number of trees without forks (class 7) in both test sites.



The colours in the graph and their intensity represent the level of significance for the Pearson residuals statistical measure: grey = insignificant, red = significantly lower values, blue = significantly higher values; the values represented inside the boxes indicate the number of observations; the horizontal lines indicate the lack of observations.

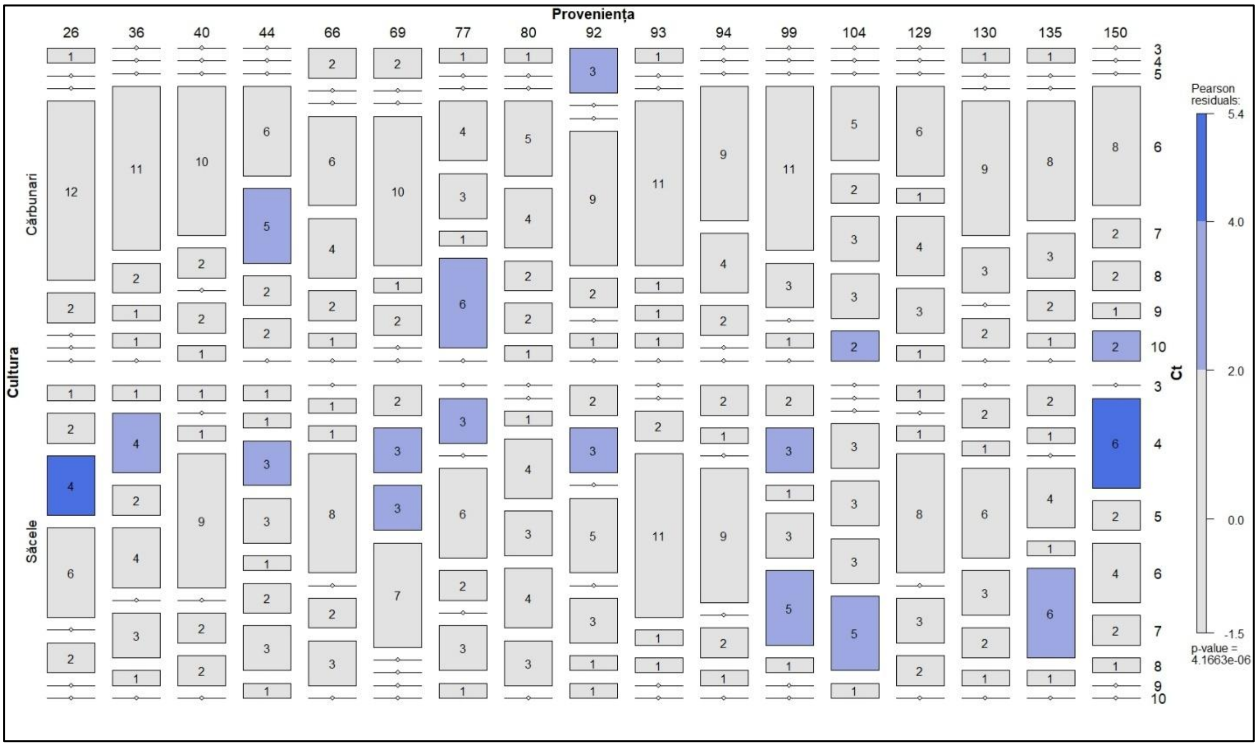
Figure 4.8. Analysis of forking in series 98, modified after Besliu et al. (2024a).

4.1.5. Stem quality

A significant variation in stem quality (*Ct*) was observed in series 95, both between trials and between provenances ($p < 0.001$***). However, at the trial level, differences among provenances were significant only for the Sacele trial ($p < 0.05$*). Therefore, the test site strongly influences this trait, while provenance exerts a lower influence.

Regarding series 98, *Ct* showed high variation at all levels ($p < 0.001$***), which indicates a strong influence of the testing location, but also of the genetic background of the provenances on the phenotypic expression of this trait.

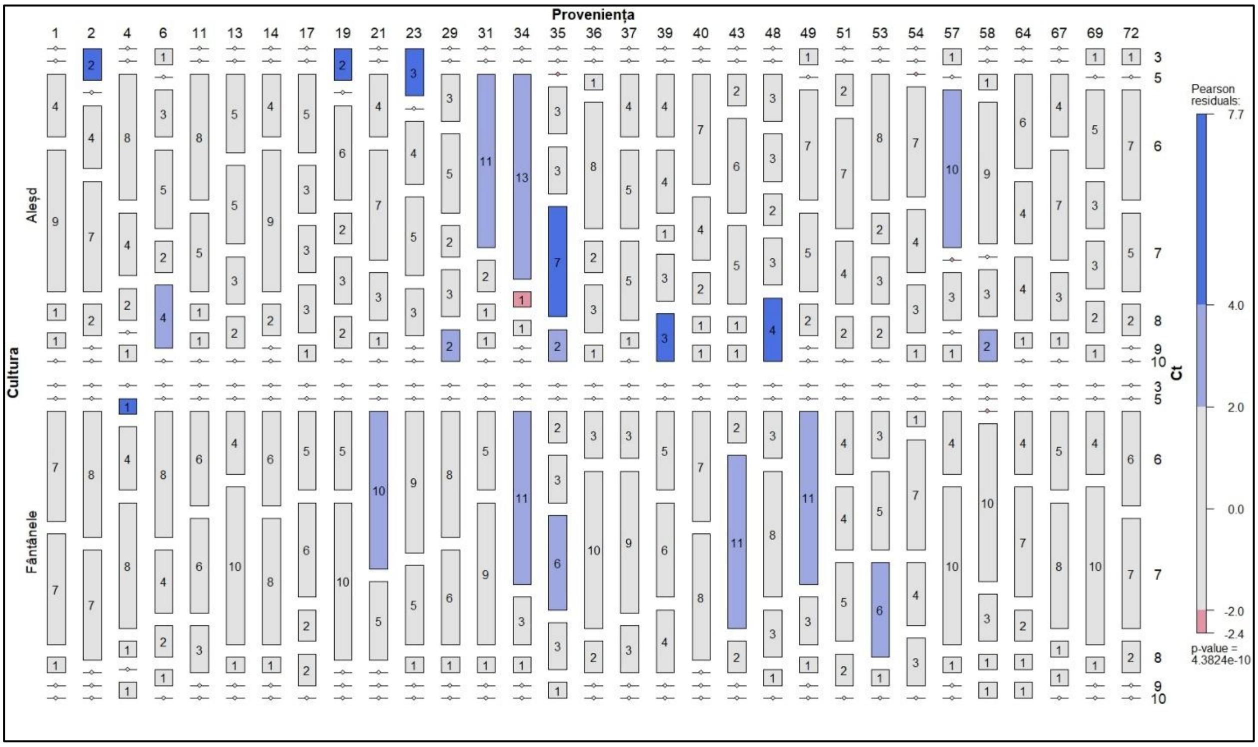
In series 95, the differences between the two test sites were significant in the case of four, five, and seven classes. This result suggests that in the Sacele trial, a significantly higher number of trees with major curvature (class 4) and trees with slightly sinuous stems (class 5) were identified, and a significantly lower number of trees with two medium curvatures (class 7). On the other hand, no notable differences were identified in terms of trees with straight stems (classes 9 and 10). Consequently, a higher proportion of trees with severe defects (classes 3-6) was observed in the environmental conditions of the Sacele trial. At the two test sites, obvious differences were only noted between the provenances of the Sacele trial. Also, in this experiment, a wider representation of classes 3–5 (severe defects) was identified compared to the Carbunari experiment, an aspect observed in provenances 95-Dk-26, 95-Ge-36, and the provenance 95-Ge-69 and the local provenance, 95-Ro-150, which also had the lowest performance. The provenances that performed well (classes 9 and 10) were 95-Ge-77 in the Carbunari trial and 95-Ge-104 in the Sacele trial. Also noteworthy is the reaction of provenances 95-Ge-40, 95-Ge-66, and 95-Ge-93, which had poor but consistent performance in both experiments (Figure 4.9).



The colours in the graph and their intensity represent the level of significance for the Pearson residuals statistical measure: grey = insignificant, red = significantly lower values, blue = significantly higher values; the values represented inside the boxes indicate the number of observations; the horizontal lines indicate the lack of observations.

Figure 4.9. Analysis of stem quality in series 95, modified after Besliu et al. (2024a).

In series 98, the significant differences between the two experiments consisted of a larger number of trees with many major defects (class 3), but at the same time, a large number of straight stems (classes 9 and 10), identified in the Alesd trial. A lower proportion of trees grouped in class 7 (two medium curves) was also observed in the same experiment. These aspects highlight the influence of site conditions on the quality of beech stems. Regarding the reaction of the provenances, it is noteworthy that the best performances (classes 9 and 10) were recorded by provenances 98-Au-35, 98-Pl-39, and 98-Pl-48 in the Alesd test. However, the lowest performance was also observed in the Alesd experiment, in provenances 98-Fr-02, 98-Mb-19, and 98-Se-23. At the same time, it is worth mentioning the very low representation of classes 9 and 10 (straight stem) in the Fantanele trial, but also the high proportion of class six (slightly sinuous stem) in both test sites (Figure 4.10).

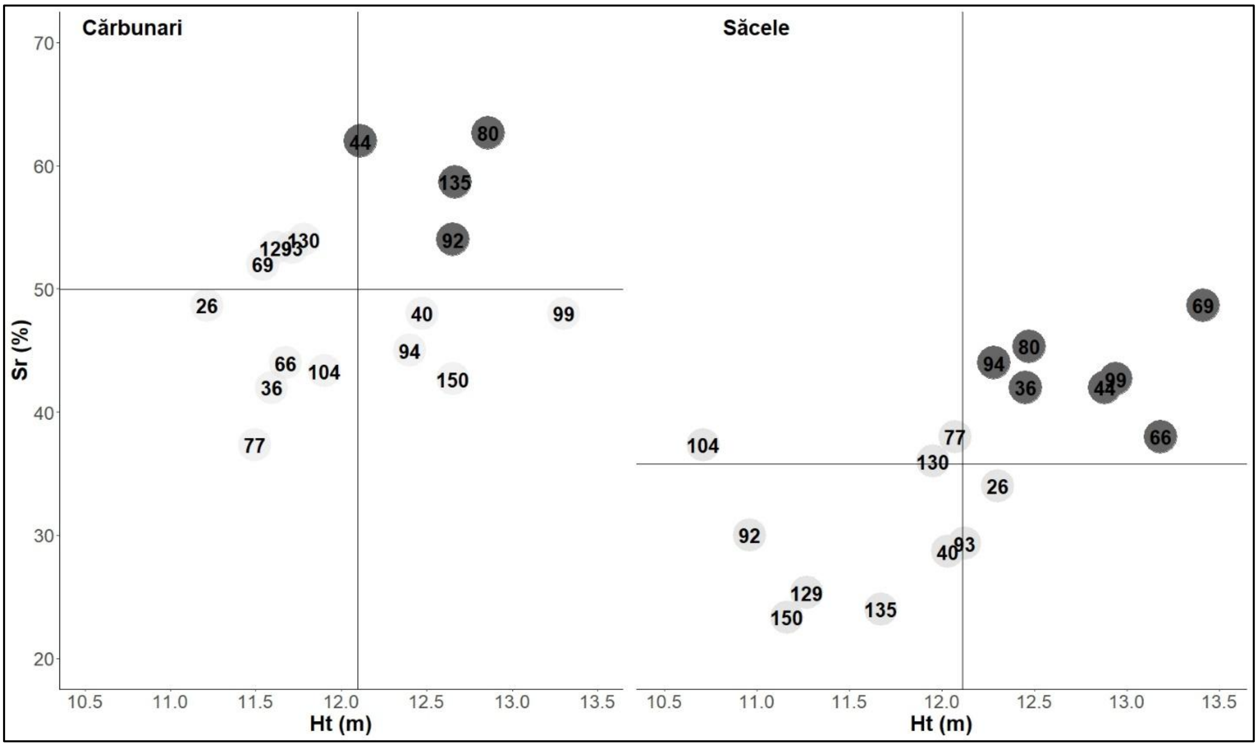


The colours in the graph and their intensity represent the level of significance for the Pearson residuals statistical measure: grey = insignificant, red = significantly lower values, blue = significantly higher values; the values represented inside the boxes indicate the number of observations; the horizontal lines indicate the lack of observations.

Figure 4.10. Analysis of stem quality in series 98, modified after Besliu et al. (2024a).

4.1.6. Growth performance

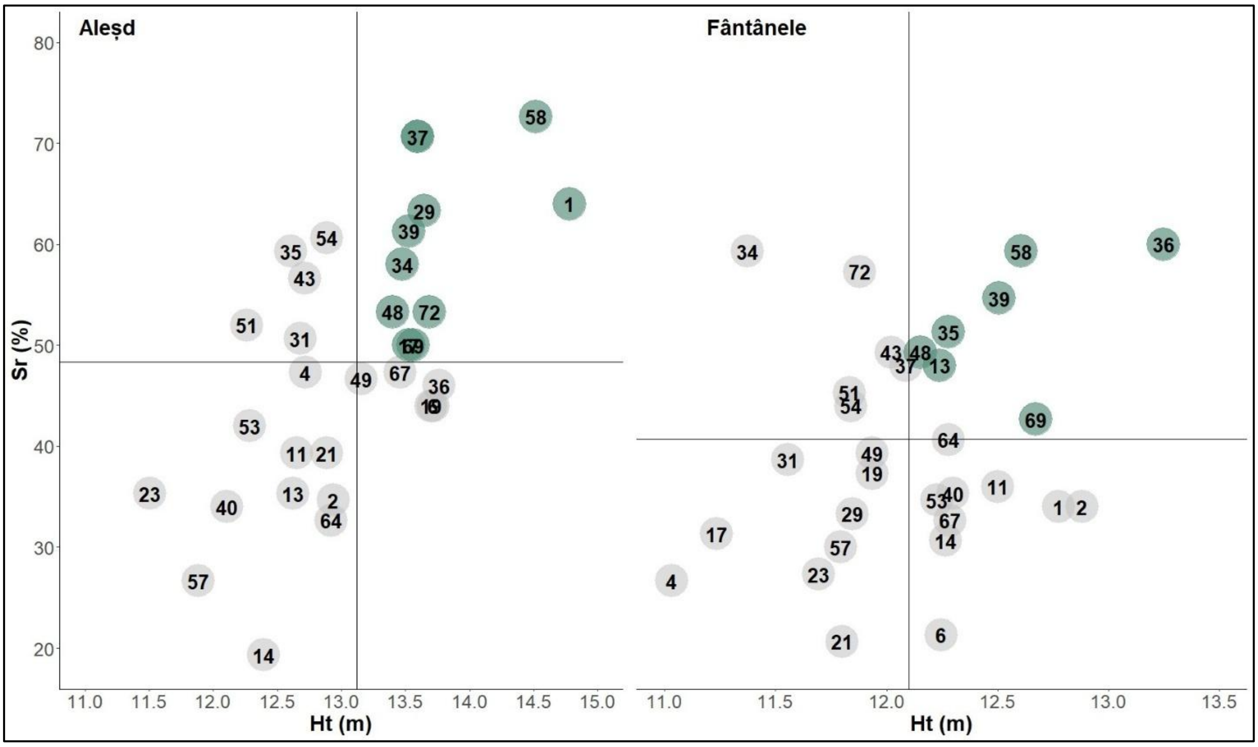
The separation of provenances according to growth performance highlighted the existence of varied reactions in the two experiments in series 95 (Figure 4.11). In the Carbunari trial, only four provenances stood out, 95-Ge-44, 95-Ge-80, 95-Ge-92, and 95-Sk-135, while in the Sacele test, the provenances 95-Ge-44, 95-Ge-66, 95-Ge-69, and 95-Ge-99. Similar reactions in both experiments were observed in the provenances 95-Ge-44 and 95-Ge-80, which were included in the category of the best provenances at both test sites. The provenances 95-Ge-104, 95-Sk-129, and 95-Sk-130 also performed lower in the two trials. At the same time, certain provenances had contrasting reactions in the two experiments. Thus, it can be observed that provenances 95-Ge-66 and 95-Ge-36 had high performance in the Sacele trial, but a low performance in the Carbunari trial, while provenances 95-Ge-92 and 95-Sk-135 reacted in the opposite way, performing better in the Carbunari test but very low in the Sacele test. The local provenance, 95-Ro-150, performed low in both experiments, mainly due to low *Sr* values.



The black circles mark the highest performances of the provenances; the average values of the experiments are marked by horizontal lines for Sr and vertical lines for Ht.

Figure 4.11. Growth performance within the 95 series, modified after Besliu et al. (2024c).

Various reactions of provenances were also observed in the 98 series. In the Alesd trial, 10 provenances with high growth performance were selected. Of these, the top three were 98-Fr-01, 98-It-37, and 98-Bg-58. The lowest performance was recorded by the provenances 98-Ol-14, 98-Se-23, and the oriental beech provenance 98-Bg-57. An important aspect to mention is that these high-performance provenances originate from low-altitude sites (between 40 and 200 m). In the case of the Fantanele trial, only seven provenances were highlighted for superior performance, and of these, provenances 98-Au-36, 98-Pl-39, and 98-Bg-58 were ranked first. The lowest performing provenances were 98-Fr-04, 98-Mb-17, and 98-Dk-21. On the other hand, the provenances 98-Pl-39, 98-Pl-48, 98-Pl-69, and 98-Bg-58 performed well in both experiments, thus being less affected by the contrasting environmental conditions in the two tests. A similar, but underperforming, reaction was observed for provenances 98-Fr-04, 98-Dk-21, 98-Se-23, and 98-Bg-57 in both trials. Different reactions in the two tests were recorded for provenances 98-Mb-17 and 98-Ge-29, which were among the best provenances in the Alesd test but had some of the lowest performances in the Fantanele trial. In contrast, the 98-Be-13 provenance achieved high performance in the more restrictive environment (Fantanele) and low performance under optimal station conditions (Alesd). Regarding the Romanian provenance 98-Ro-72, its high performance in the Alesd trial is notable, and in the Fantanele trial, it was close to being included in the ranking of the best performers. Therefore, this provenance shows stability expressed by *Sr*, but a decrease in *Ht* induced by the transfer to a limiting environment.



The black circles mark the highest performances of the provenances; the average values of the experiments are marked by horizontal lines for Sr and vertical lines for Ht.

Figure 4.12. Growth performance within the 98 series, modified after Besliu et al. (2024b).

4.1.7. Discussions

The survival and growth performances of the provenances can be considered evidence of their ability to adapt to specific site conditions. Site conditions had a significant influence on the stability of the beech provenances tested in the four cultures, with stability being assessed based on the performances obtained for Sr. Under the more favourable (optimal) site conditions in the Carbunari and Alesd trials, the stability of the provenances was significantly higher than that recorded in the Sacele and Fantanele trials, where site conditions are characterised by lower temperatures (Sacele) and high temperatures and low precipitation (Fantanele), respectively. Therefore, a sensitivity of beech provenances to interactions with lower temperatures and precipitation was identified, and this was also confirmed in other reference studies for this species (Leuschner & Ellenberg 2017; Peters 2013). These observations have also been confirmed by other studies conducted on beech forests in Europe, which have highlighted the high stability of provenances in favourable environments (Petkova et al. 2022; Von Wuehlisch et al. 2008). In addition, the significant influence of climatic conditions on the performance of beech provenances has also been reported by Chmura et al. (2024).

Numerous studies conducted on comparative beech trials have reported high variation in growth traits, both between test sites and between provenances (Bogunović et al. 2020; Müller & Finkeldey 2016; Petkova et al. 2022; Stojnić et al. 2015a; Von Wuehlisch et al. 2008). This fact is also confirmed by the results of this research study, in which the analysis of *Ht* variability highlighted the significant influence of the testing sites, as well as the genetic control of this trait. In the case of *Db*, only the influence of the testing location was found to be significant, but the genotype did not show any control over this trait. Thus, in the ecological optimum (Alesd), the provenances recorded higher performance than in the eastern limit area (Fantanele) for *Ht*, and in lower temperature conditions (Sacele), a better increase was observed in terms of *Db* compared to the area with higher temperatures (Carbunari).

The morphological traits of the stem can be used to study the adaptive potential of provenances because they are closely related to other indicators of adaptability (Kembrytė et al. 2022). In this study, the qualitative characteristics evaluated *(Dr*, *Fk*, and *Ct*) were used to observe the adaptation trends exhibited by the provenances.

In the process of analyzing Dr, a trait that determines wood quality (Ducci et al. 2012), a high variation was observed, which was determined both by the specifics of the testing site and by the genetic background of the provenances. The more restrictive testing sites in terms of environment contributed to an increase in *Dr* and, therefore, to a decrease in wood quality. Thus, the site conditions in the Sacele and Fantanele trials favoured an increase in *Dr* and, at the same time, revealed a weaker adaptation of the provenances. This trend was also observed in the case of *Fk*, but this trait was found to be significantly influenced only by the testing site, although it is known that there is also a genetic determinism of forking (Ducci et al. 2012). At the same time, the local conditions in the Carbunari and Alesd trials proved to be more favourable, as a significantly higher number of trees without forking were identified, and the provenances had a higher adaptation response. *Ct* proved to be influenced by both the test site and the genotype, thus agreeing with the results obtained by Del Rio et al. (2004). A high presence of trees with severe defects and a significantly lower number of trees with straight stems were recorded in the Sacele and Fantanele trials. This confirms the low adaptation of the provenances in these experiments, which exposed a qualitatively inferior phenotype, a result also confirmed by other studies (Horváth & Mátyás 2016; Mátyás et al. 2009b).

The performance evaluation indicates the high stability of the 95-Ge-44, 95-Ge-80, 98-Fr-01, 98-It-37, and 98-Bg-58, which had previously been reported by Mihai (2009) as some of the best provenances, thus highlighting the consistent performance of provenances after 16 years of age. The high performance of provenances from Germany was also emphasised by other research conducted on trials planted in that country (Müller & Finkeldey 2016; Müller et al. 2020; Thiel et al. 2014), but Stojnić et al. (2015a) observed poor performance of German populations in experiments in southern Europe. The high performance of provenances from Bulgaria was also highlighted by Petkova et al. (2019), in the trials installed in that country. The same authors note the superiority of local provenances over German ones, but this superiority was reversed in experiments conducted in Germany (Thiel et al. 2014).

Mihai (2009) notes the low stability of the 98-Fr-06, 98-Ol-14, and 98-Dk-21 provenances, which was also confirmed in this study. The low performance of provenance 98-Ol-14 was also reported in the trials planted in the Netherlands (Eilmann et al. 2014) and Ireland (Thompson 2007), thus confirming the low adaptive potential of this beech population. Low performance at the test sites in Romania was also observed for the oriental beech provenance 98-Bg-57. This reaction of this provenance could be caused by limiting factors, such as low winter temperatures, as well as by the shorter growing season.

The low adaptive potential of this beech variety was also observed by Von Wuehlisch et al. (2008) after testing a provenance from Turkey across several European environments.

With regard to *Dr*, the 95-Ge-66 and 98-Sl-54 provenances stood out with the best performance, while 95-Ro-150 and 98-Fr-06 were at the opposite pole. However, opposite results were obtained in Sweden, where the provenance from Romania (95-Ro-150) was at the top of the performance rankings, and the one from Germany (95-Ge-66) ranked among the weakest in terms of the percentage of knots in the wood (Vanícek 2021). Provenance 95-Ge-69 stood out due to a large number of trees without forking, but with poor stem quality, while 98-Lu-11 was one of the provenances with the highest presence of forking, a fact also noted by Bergkvist (2019) in the Swedish experiment, where it showed the highest predisposition to forking. This author also highlights provenance 98-Au-35 for its high *Ct* value, a result confirmed in the present study.

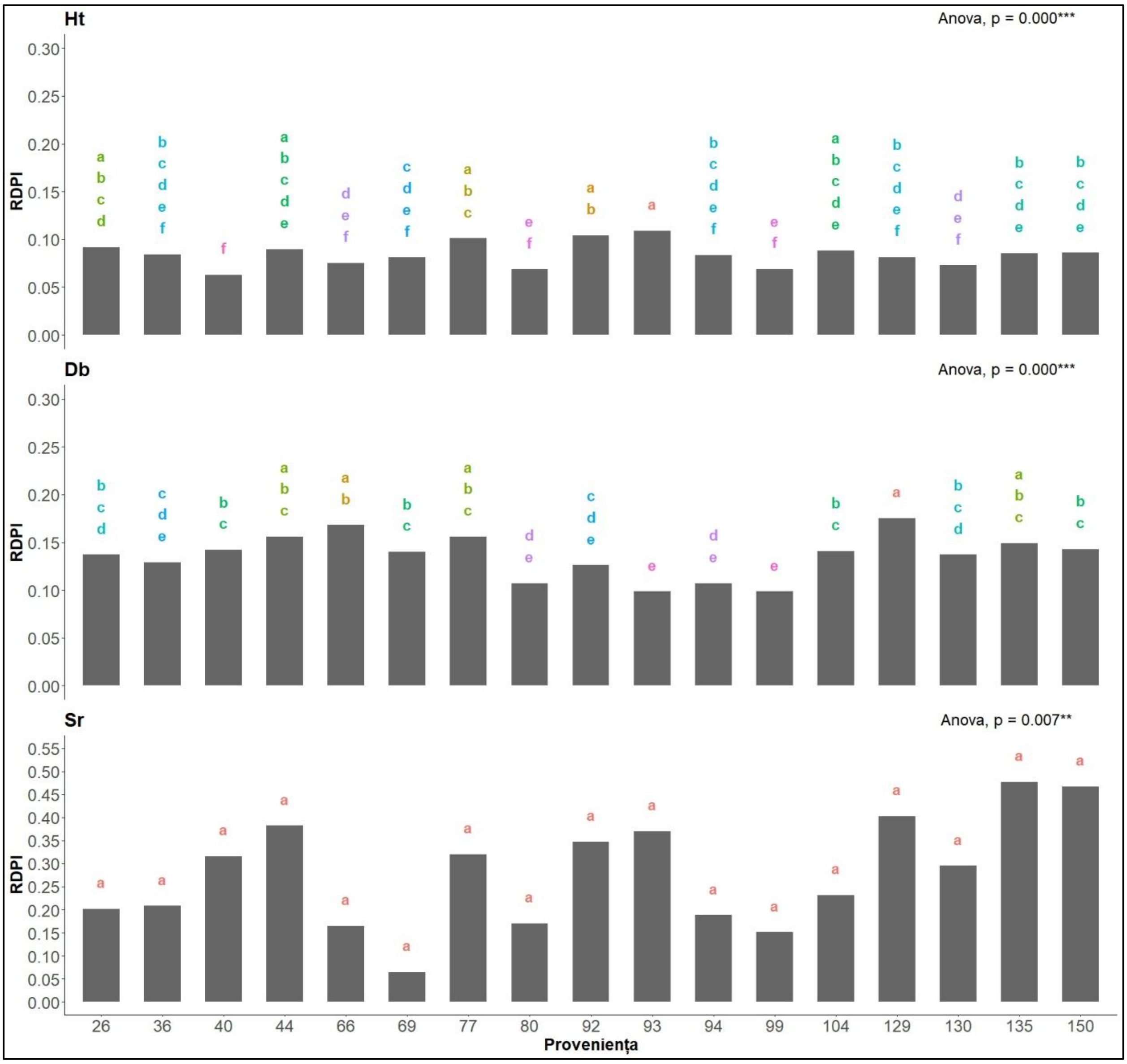
Another important aspect to mention is the reaction of the local provenance, 95-Ro-150, which recorded low levels of *Sr*, *Fk*, and *Ct* at both test sites, with performance far surpassed by international provenances. This result is confirmed by a previous study on these trials (Mihai et al. 2008), but also by Hofmann et al. (2015), which highlighted the low frost resistance of this provenance in a crop planted in Germany, within the same series (95). On the other hand, the local provenance from series 98, 98-Ro-72, obtained constant values above the experiment averages, indicating good performance. This performance was also reported in a previous study conducted on these trials (Mihai et al. 2008), but also in a trial from Ireland (Thompson 2007). However, in provenance tests conducted in Bosnia and Herzegovina, Serbia, and Croatia, this provenance did not perform well, and Konnert & Ruetz (2001) also noted its low genetic variation.

Considering the increasingly intense environmental changes, which have intensified the need to identify populations with high growth potential under limiting conditions (Dounavi et al. 2016; Knutzen et al. 2015; Nguyen et al. 2017; Rose et al. 2009), the results obtained in this study indicate that some provenances would have this capacity. Thus, under the limiting conditions of the Fantanele trial, provenances 98-Au-36, 98-Pl-39, and 98-Bg-58 showed high performance, and provenance 98-Be-13 proved to be more efficient than in the ecological optimum of the species (Alesd), which indicates the existence of a high adaptive potential of these populations that needs to be studied in detail.

Analysis of the results obtained at the European level in the trial series highlighted a high level of interaction between genotype and test sites, as well as the high adaptive potential of certain provenances (Von Wuehlisch et al. 2008). These remarks are supported by the results of this study and by other research (Krajnc et al. 2022; Thiel et al. 2014). Taking these aspects into account, as well as those relating to the contrasting reactions of some provenances that have been shown to be represented by different phenotypes under various site conditions (Enescu 1972), there is a clear need to test provenances in as many different sites as possible, including those outside the natural distribution range, in order to quantify more accurately the adaptive potential of beech and, at the same time, to identify populations that are effective even under restrictive site conditions (Benito-Garzon et al. 2013; Benito Garzón et al. 2019; Beșliu et al. 2022; Capdevielle-Vargas et al. 2015; Hewitt et al. 2011).

4.2. Phenotypic plasticity

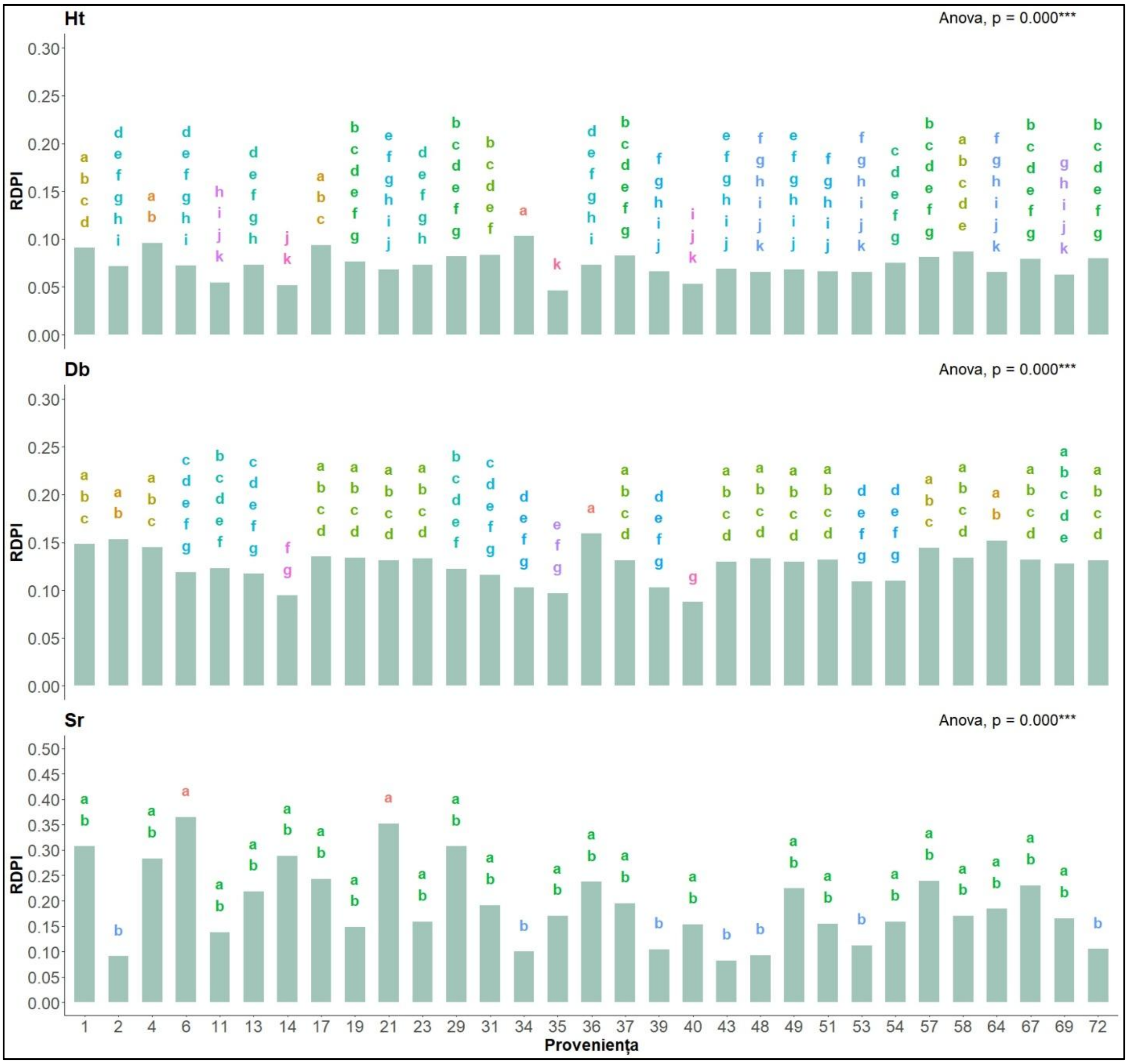
The evaluation of phenotypic plasticity (*Pf*) in series 95 (Figure 4.13) revealed significant variation among provenances, particularly for the Ht and Db traits, thereby highlighting differences among beech populations in their adaptation to different site conditions. In general, *Pf* values were low. For *Ht*, the most plastic response was observed at provenance 95-Ge-93, and the lowest at provenance 95-Ge-40. For *Db*, provenance 95-Sk-129 was noted to have the highest *Pf* value, and provenances 95-Ge-93 and 95-Ge-99 the lowest. At the *Sr* level, the differentiation between provenances was lower, and they were grouped into a single category. However, a low *Pf* level was observed for the 95-Ge-69 provenance, whereas the highest value was observed for the 95-Sk-135 provenance. If we refer to the average *Pf* for all the analysed traits, the highest values were recorded by provenances 95-Sk-129, 95-Sk-135 and the local provenance, 95-Ro-150.



The letters positioned above the bars of the diagram represent the results of the Tukey HDS test, and homogeneous groups are marked with the same letters and colours; the right side of the diagram shows the results of the ANOVA test (for p < 0.05; ** for p < 0.01; *** for p < 0.001).*

Figure 4.13. Evaluation of phenotypic plasticity in series 95.

At the level of series 98 (Figure 4.14), the degree of variability among provenances was high for all analysed traits, with a trend similar to that of series 95 regarding the differentiation of beech populations from Europe. The highest level of plasticity was obtained by provenances 98-El-34 (for *Ht*), 98-Au-36 (for *Db*), 98-Fr-06, and 98-Dk-21 (for *Sr*). At the opposite pole, the lowest *Pf* values were recorded for provenances 98-Au-35 (for *Ht*), 98-Pl-40 (for *Db*) and 98-Pl-43 (for *Sr*). The average plasticity (for all analysed traits) was highest for provenances 98-Fr-01, 98-Fr-04, 98-Fr-06, and 98-Dk-21, and the lowest *Pf* was recorded by provenances 98-Pl-39, 98-Pl-40, 98-Pl-43, and 98-Sl-53. The local provenance, 98-Ro-72, was included in the group of provenances with low *Pf* values for *Sr*, but for the other traits, the values were grouped around the average value.



The letters positioned above the bars of the diagram represent the results of the Tukey HDS test, and homogeneous groups are marked with the same letters and colours; the right side of the diagram shows the results of the ANOVA test (for p < 0.05; ** for p < 0.01; *** for p < 0.001).*

Figure 4.14. Evaluation of phenotypic plasticity in series 98, modified after Besliu et al. (2024b).

4.2.1. Discussions

Simulating adaptive potential is one of the most notable benefits of *Pf* because it can identify the ability of different tree populations to adapt more quickly to various environmental conditions compared to natural selection, which is a slower process of adaptation (Crispo 2008). Therefore, the evaluation of Pf depends on identifying the degree of phenotype modification when interacting with different station conditions (Bradshaw 1965; Bussotti et al. 2015).

The method of assessing beech plasticity may involve a simple analysis of the variability of growth traits between different environmental conditions (Capdevielle-Vargas et al. 2015; Müller et al. 2020; Wortemann et al. 2011), or it may be quantified on the basis of plasticity indices (Frank et al. 2017; Stojnić et al. 2015b), as determined in this study. The evaluation of plasticity in the two series of trials was considered appropriate due to the significant differences between the four test sites, including limiting vegetation conditions for beech, thus favouring the observation of adaptation trends of the international provenances. The results obtained indicate a higher plasticity for *Sr* than for growth characteristics (*Ht* and *Db*). Therefore, it can be said that the provenances showed a plastic reaction to the interaction with the test sites in the Carpathian region of Romania, but their productivity was reduced in the limiting areas, which indicates the presence of *Pf*, which determines the reduction of the phenotype's performance for the purpose of adaptation (Benito Garzón et al. 2011; Lauteri et al. 2004). Similar results were obtained by Stojnić et al. (2015b), who observed that the plasticity of the anatomical characteristics of beech leaves contributed to the adaptation of provenances to harsh site conditions. In addition, Frank et al. (2017) note that the high plasticity of beech seedlings, as measured by growth characteristics, enables this species to withstand even restrictive vegetation conditions.

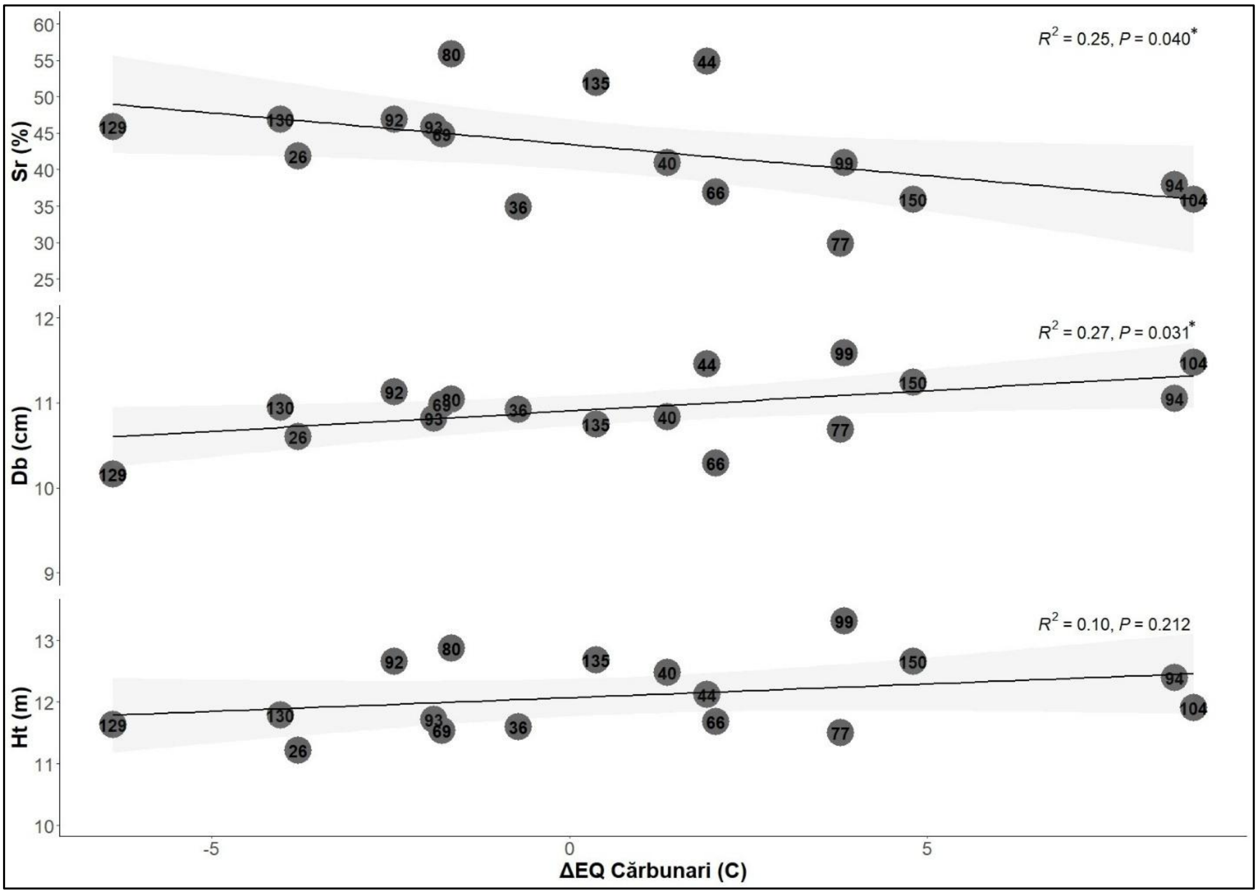
In this study, the *RDPI* index was used to evaluate *Pf*, enabling a more complex statistical approach than other plasticity indices used in the aforementioned studies. Therefore, this index (*RDPI*) is considered to be more appropriate for use in the study of plasticity at the level of provenance tests (Valladares et al. 2006). The results showed that the provenances with the highest average plasticity were: 95-Sk-129, 95-Sk-135, 95-Ro-150, 98-Fr-01, 98-Fr-04, 98-Fr-06, and 98-Dk-21. This indicates a higher adaptive potential in these beech provenances. However, given the complexity of the adaptation process of forest species, more accurate studies need to be initiated to certify the adaptive potential of beech (Stojnic et al. 2013), and these should focus on separating adaptive plasticity from non-adaptive plasticity (Ghalambor et al. 2007).

4.3. Transfer analysis

Linear regression analysis at the Carbunari trial level (Figure 4.15) showed a significant correlation ($p < 0.05^*$) for *Sr* and *Db*, but with opposite trends. With regard to *Sr*, it can be seen that as transfer distances increase, the stability of provenances at this test site decreases. Thus, the approach that transferring provenances from diametrically opposite stations can lead to a decrease in stability is statistically confirmed in this case. Under the conditions of the Carbunari trial, a decrease in stability was observed for provenances transferred from areas with lower temperatures and higher precipitation (95-Ge-104, 95-Ge-94), but an increase in *Sr* for provenances transferred from more restrictive environmental conditions (95-Dk-26, 95-Sk-129, and 95-Sk-130). This may be the result of the climatic conditions in the Carbunari trial, characterised by higher temperatures, which favoured the adaptation of provenances with a genetic predisposition for vegetation in similar environmental conditions. Also, some of the provenances with similar climatic origins recorded the best performances (95-Ge-44, 95-Ge-80, and 95-Sk-135), but this was not confirmed for provenances 95-Ge-36 and 95-Ge-66, which again highlights the very divergent response among beech populations from Europe.

On the other hand, the increase in transfer distances significantly influenced the increase in *Db*, a trend also observed for *Ht*, but without statistical significance for the latter. The opposite trend identified between *Sr* and *Db* can be explained by the reduction in growing space and, implicitly, competition between trees (generated by a low level of *Sr*), which favoured the increase in *Db*.

No significant linear regression values were identified for the transfer of provenances to the Sacele trial, highlighting the low influence of transfer distance on the analysed traits in this experiment.

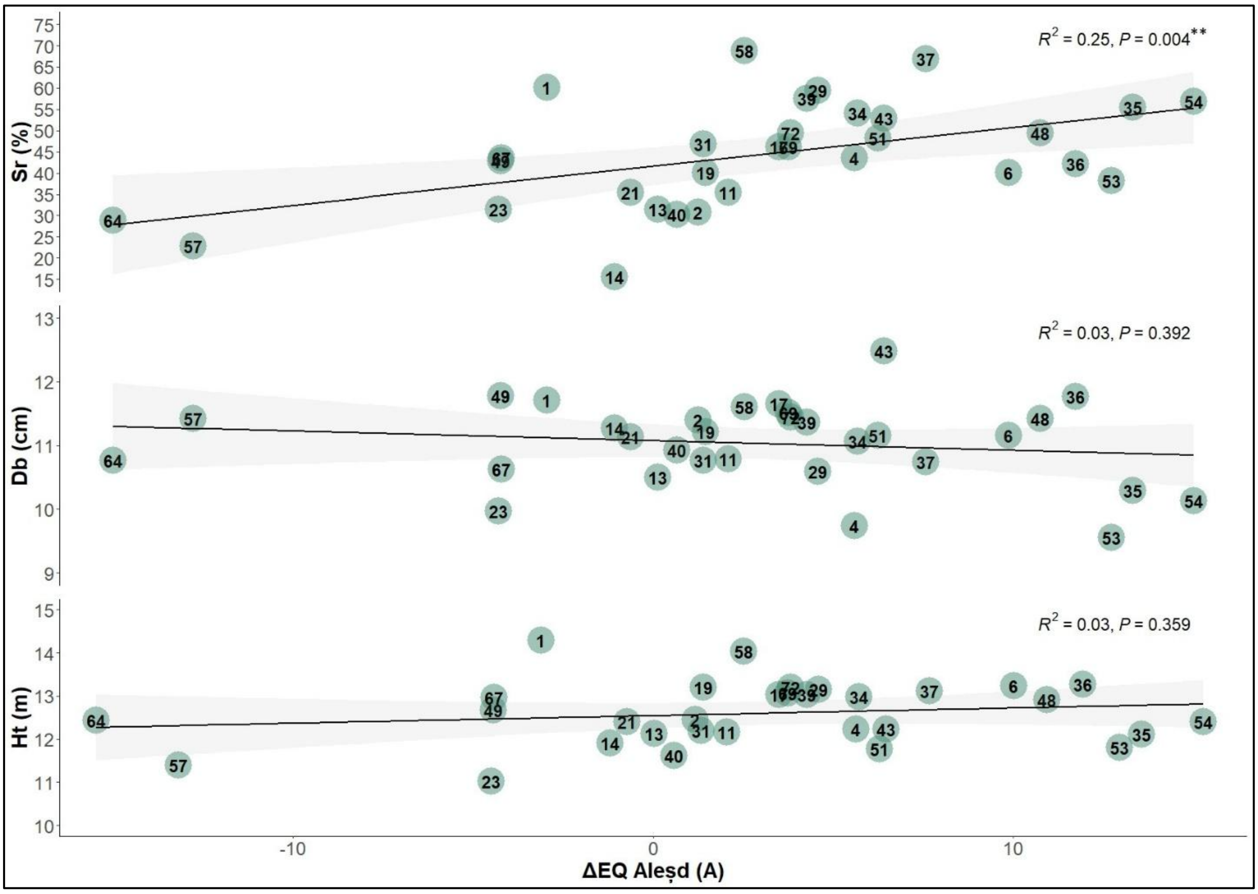


The provenances are represented by black circles containing their numerical codes; on the right side of the diagram are shown the results of the regression equation (R) and the level of statistical significance (for p < 0.05; ** for p < 0.01; *** for p < 0.001).*

Figure 4.15. Analysis of the transfer at the level of the Cărbunari trial, modified after Besliu et al. (2024c).

The significant influence of ecological distances on *Sr* was also observed in the Alesd trial (Figure 4.16). Provenances transferred from colder and wetter environments had higher stability than those transferred from more arid areas. Therefore, optimal conditions proved to be more favourable for provenances from colder stations and even for those from the alpine zone (98-Au-35, 98-Au-36, 98-It-37). Populations transferred from opposite site conditions exhibit contrasting reactions in the Alesd trial. Thus, the provenance transferred from the warmest environment (98-Ch-64) recorded a *Sr* value 28% lower than the provenance originating from the coldest environment (98-Sl-54). Provenances transferred from climatic conditions similar to those of the test showed varied reactions. Some proved to be unsuitable (98-Ol-14, 98-Lu-11, 98-Be-13), but others (98-Fr-01 and 98-Bg-58) were among the top performers in this experiment. For growth characteristics (*Ht* and *Db*), no direct influence of transfer distances was observed, indicating a constant reaction of the provenances.

In the case of the Fantanele trial (Figure 4.18), no significant influence of transfer distances on the analysed traits was identified. However, in the case of Sr, the influence was very close to being significant, indicating that the trend observed in the Alesd environment was maintained.



The provenances are represented by black circles containing their numerical codes; on the right side of the diagram are shown the results of the regression equation (R) and the level of statistical significance (for p < 0.05; ** for p < 0.01; *** for p < 0.001).*

Figure 4.16. Analysis of the transfer at the level of the Alesd trial.

4.3.1. Discussions

The phenotypic response to interaction with different test sites is considered to be conditioned not only by the adaptive potential of the provenances, but also by the magnitude and direction of the transfer (Mátyás et al. 2009b). Therefore, analysing the transfer of provenances to different locations under climatic conditions can be considered a simulation of assisted migration (König 2005; Sansilvestri et al. 2015), a process aimed at increasing the stability and productivity of forests (Gray et al. 2011; Leech et al. 2011), but also at preserving the ecosystem services provided by forests (Pedlar et al. 2012). In this regard, assisted provenance transfer is considered a complex process, which includes precise studies on climate sensitivity and provenance performance in comparative trials (Mátyás 2021).

In the present study, testing the effect of transfer in the case of international beech provenances was carried out by applying the concept of ecological transfer distances (Mátyás 2021; Mátyás et al. 2009a; Mátyás et al. 2009b; Mátyás & Yeatman 1992). This approach uses the Ellenberg quotient index to characterise the climate of the test site and the environment of provenance origin. The *Ellenberg quotient* index is considered to be a suitable indicator of site suitability for beech (Czúcz et al. 2011) and has also been used in other studies which tested the resilience of this species (Budeanu et al. 2016; Dujka & Kusbach 2023).

The assessment of the overall effect of the transfer of international beech provenances to the test sites in Romania revealed two types of response. Thus, the lack of influence of transfer distances on the analysed traits was assimilated with a similar reaction of the provenances and, therefore, a good adaptation to the site conditions of the test sites in series 95. Similar results were obtained by Petkova et al. (2019), who studied the impact of transfer in beech trials in Bulgaria and highlighted the absence of a significant link between survival, height, and transfer distances. However, in the analysis of series 98, it was observed that provenance stability was significantly influenced by the magnitude and direction of the transfer. In this regard, an increase in the stability of provenances was indicated in relation to the increase in transfer distances from colder and wetter environments to warmer and drier ones, which highlights the ability of populations growing in colder site conditions and, implicitly, at higher altitudes, to perform well in warmer environments. This aspect was also mentioned by Liepe et al. (2024) in the study of beech provenances tested in three trials in Germany. Moreover, Chmura et al. (2024) observed a positive influence on diameter growth when provenances were transferred to test sites with milder winters.

At the level of the four trials, a significant transfer effect was observed in the Carbunari trial, where provenance survival was influenced by increases in the transfer distances. Therefore, the transfer of provenances from colder environments to the test site, where temperatures are higher (Carbunari), significantly affected survival, but in the case of provenances transferred from warmer site conditions, the *Sr* values increased. This trend of the influence of transfer distances was also identified in a study conducted on two comparative trials in Slovakia and the Czech Republic at the level of leaf morphological traits (Petrík et al. 2020). In addition, the authors mention the good adaptation of the provenances to the conditions of the test sites.

An important aspect to note is the sensitivity of the provenances to temperature change, which was observed between the two test sites in the 95 series. Thus, while no significant transfer effects were observed in the Sacele trial, which is characterised by lower temperatures, in the Carbunari trial, where temperatures are 2.4 °C higher, the effects were significant for *Sr* and *Db*. Therefore, as precipitation was equivalent between the two experiments, the factor that produced this change is considered to be temperature.

In the case of the Alesd trial, the increase in transfer distances had a positive influence on the stability of the provenances, indicating better performance of provenances transferred from colder and wetter areas, a trend also observed in the limiting site conditions from the Fantanele trial, but not statistically significant. The acclimatisation of beech provenances to warmer environments than their origin was also observed by Petrik et al. (2022). Therefore, the adaptation of provenances is conditioned more by ecological than geographical criteria, indicating the need for a macroclimate-based approach in defining the rules for the transfer of reproductive materials (Mátyás et al. 2009a; Mátyás et al. 2009b).

The provenances tested in the four cultures showed different reactions to the transfer. Some of the provenances transferred from similar conditions performed very well, highlighting the need to transfer provenances to climatically equivalent environments (Konnert et al. 2015). On the other hand, the similar reactions of provenances transferred from completely opposite environments, as well as the large differences between provenances with very similar climatic origins, indicate the existence of a high variation in climatic receptivity among beech populations in Europe (Gömöry et al. 2010; Konnert & Ruetz 2001; Stojnić et al. 2015a; Stojnić et al. 2016; Vettori et al. 2004). The decline in local beech populations predicted by Chakraborty et al. (2024) for the future, as well as the performance of alpine populations, are confirmed in this study. Native beech provenances were significantly outperformed by international provenances, and alpine provenances showed good adaptation, even under the most difficult conditions.

The need to test the adaptive potential of beech in limiting site conditions, a process supported by Benito Garzón et al. (2019), is also confirmed by the results obtained in this study, as the good adaptation response of the provenances even under limiting conditions (Fantanele trial) indicates the need to explore the requirements of this species and confirm its adaptive potential through provenance tests conducted under limiting vegetation conditions. The adaptation of provenances even under restrictive conditions highlights the high adaptive potential of the species *F. sylvatica* (Kramer et al. 2017; Roibu et al. 2022) and indicates a possible stable response to projected environmental changes (Gárate-Escamilla et al. 2019; Meier & Leuschner 2008; Stojnić et al. 2015b).

4.4. Testing of the Universal Response Function model

4.4.1. Modelling height growth for the current period

In developing the *Universal Response Function* (*URF*) for the current period, with normalised height (*Hn*) as the response variable, 500 decision trees were used to train the model, and a subgroup of three variables was considered for each split. The model explains approximately half of the variation in the dependent variable (*Hn*) given the selected predictors, indicating moderate performance. The main factor determining the model's moderate performance is the very small number of test sites (four), as well as their limited differentiation in site conditions. The analysis of the importance of the variables used as predictors highlighted the decisive role of the climate of origin of provenances in explaining the variability in tree height. Analysing the climatic predictors, the strongest influence was identified for the maximum summer temperature (*prov_ Tmax_ sm*), corresponding to provenance origin, while the annual aridity index (*site_AHM*), corresponding to the test site, had the lowest involvement in the variation of the dependent variable. On the other hand, tree age was identified as the predictor with the least influence, highlighting that it plays a secondary role in the species' climate adaptation.

The graphical representation of the beech height growth in Romania (Figure 4.17) highlights the areas that are favourable and those that are less favourable for this species. Therefore, high growth potential (yellow) can be observed in the Carpathian and Subcarpathian areas, as well as in the central part of Transylvania and the Moldavian Plateau. A higher concentration of high growth was also identified in the Western Carpathians. In these sites, an estimated growth (*He*) of over 70% is indicated. Thus, if regeneration were carried out in these areas using reproductive material from the provenances included in the model, at the age of 20 the installed stands' height growth would reach approximately 70% of the current growth. In contrast, in the south of the country, in the western and eastern areas, and in the high mountain areas, very low growth rates are estimated.

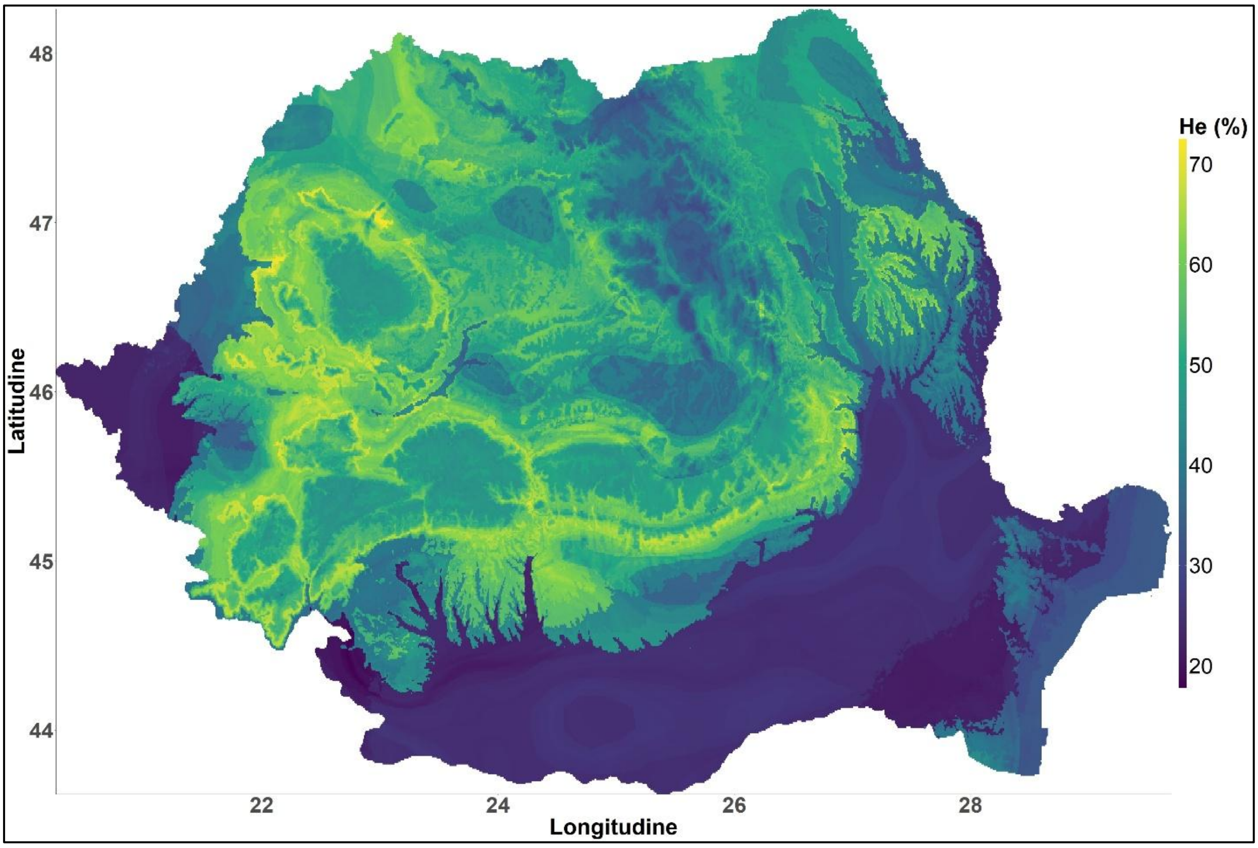
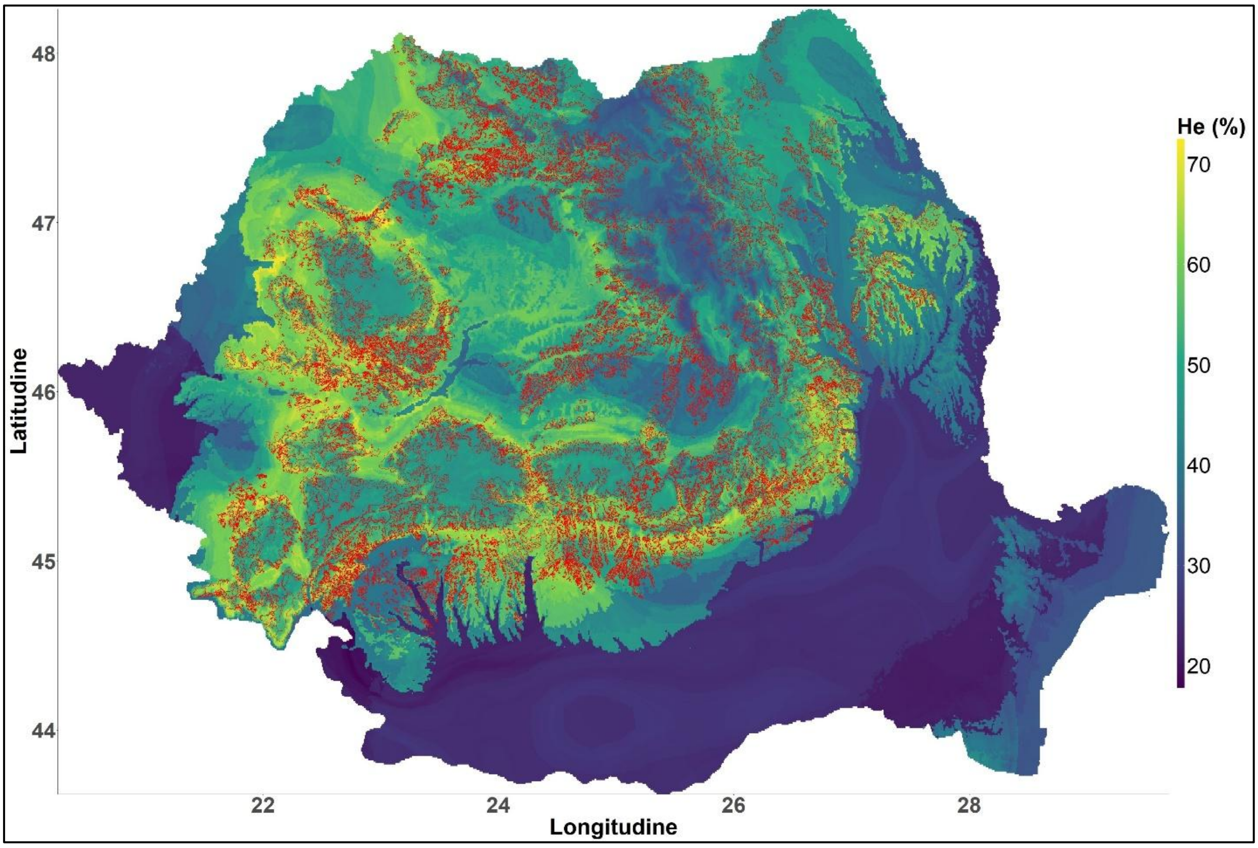


Figure 4.17. Model of the current distribution of the species *F. sylvatica* in Romania.

Overlaying the current distribution of beech in Romania on the *URF* model (Figure 4.18) highlights certain important aspects. One of these is the model's accuracy, which delimits favourable areas from unfavourable ones with a high degree of accuracy, as is the case in the Moldavian Plateau or the southern Carpathians. However, there are also areas where the species is not present, and its ecological requirements could not be met, such as the north-eastern part of the country. On the other hand, this graphic representation also highlights potential sites where the species could grow, if a similar trend in climatic conditions were to continue. The areas with the potential to support high growth are mainly located around mountain formations, in the Subcarpathian area and in the hilly area. Parts of the Transylvanian Plateau are also indicated as possible areas where beech could grow.



*The distribution of the species F. sylvatica in Romania is shown in red. (*Doniță et al. 2008*).*

Figure 4.18. Comparative analysis between the current distribution of the species and the model results for the current period.

4.4.2. Modelling height growth in different climate scenarios

Based on the *URF* model generated for the current period, the beech distribution model was developed in two climate scenarios, RCP 4.5 and 8.5, separately for specific time intervals. Only climate predictors specific to the test site were used in this model, but the explained variability was significantly lower, with an average of 4.70% and varying according to the climate data specific to each period, respectively to each scenario. This low performance of the model is due to the limitations of the data used, as discussed in detail in the previous section, and in particular to the exclusive use of climate predictors specific to the test site, which have a low weight in explaining the variance of *Hn*.

Graphical representation of the distribution obtained based on the model for the period 2021-2040 (Figure 4.19), corresponding to the RCP 4.5 scenario, shows a significant reduction in the estimated height (*He*) of beech, with differences of approximately 20% compared to the maximum increases obtained for the current period (2011-2020). In Romania, there is a marked decrease in growth in the areas outside the Carpathian chain and, at the same time, a transfer of this growth to the higher areas of the Carpathian Mountains. The forecast for the forests in the eastern and Subcarpathian areas shows a significant reduction in growth, mainly due to changes in site suitability, which will no longer support beech growth. As for the mountain forests, they are expected to move to higher elevations, and many of the currently unfavourable high-altitude sites for beech will become suitable migration areas. There is also a decline in marginal forests in low-altitude areas, whose future is uncertain based on this forecast. It is worth noting the speed with which environmental changes will affect this species, given the imminent nature of these reductions in growth.

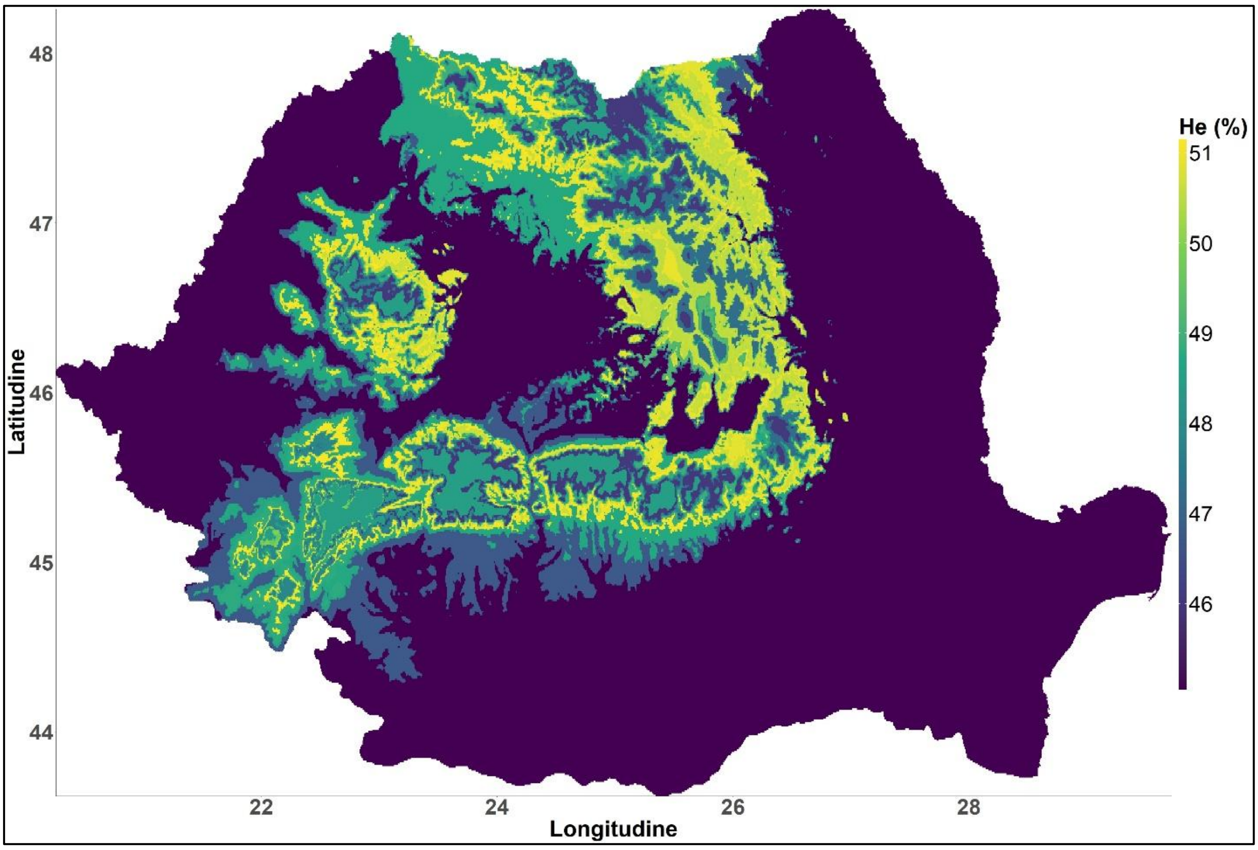


Figure 4.19. Distribution model *F. sylvatica* in Romania in the context of RCP 4.5, period 2021-2040.

The last period analysed in the RCP 4.5 climate scenario predicts a further reduction in potential beech height growth in Romania. The graph shows a reduction across all high mountain areas of the Carpathians. However, the Eastern Carpathians have the largest areas with more intense growth compared to other mountainous areas of the country. In addition, there is some reduction in growth in the low mountainous areas of the species' range, but, to the same extent, an increase in the favourability of high-altitude mountain sites, as is the case in the Southern Carpathians and the northern Eastern Carpathians (Figure 4.20).

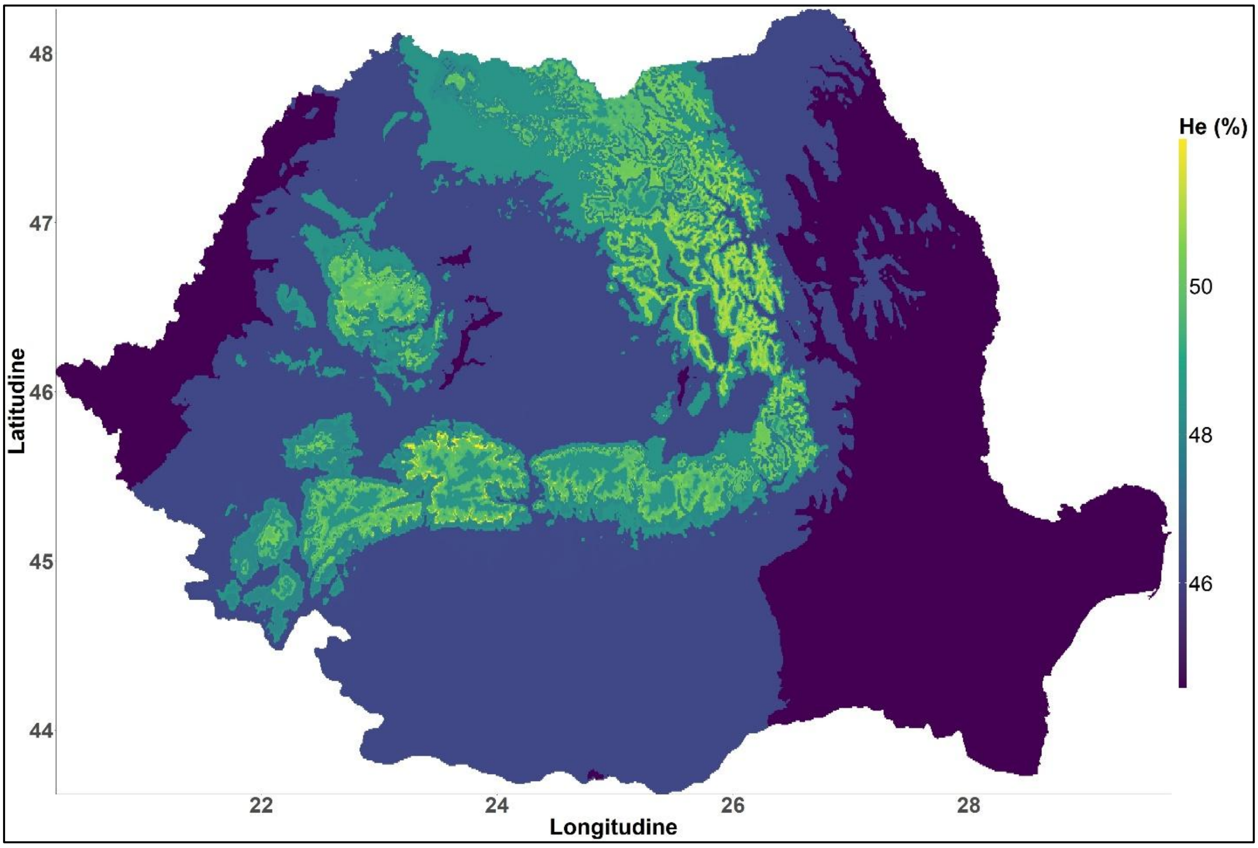


Figure 4.20. Distribution model F. sylvatica in Romania in the context of RCP 4.5, period 2081-2100.

The first period analysed in the RCP 8.5 climate scenario indicates a 20% reduction in height growth compared to the current distribution (Figure 4.21). There is a reduction in height similar to that of the corresponding period in the RCP 4.5 scenario, but the most intense increases occur at higher altitudes. While the RCP 4.5 scenario indicated high increases at certain points in the eastern Carpathians, in this case, these are represented by smaller increases. With regard to mountain areas, there is a more pronounced increase at higher altitudes, as well as a concentration of the largest areas with more intense increases in the Eastern Carpathians. Therefore, the Southern and Western Carpathian divisions are expected to experience a decline in growth for the species *F. sylvatica*. Growth in the southern part of the distribution range, as well as in the eastern part, is narrowing dramatically, and significant decreases in tree height are expected in the Subcarpathian and hilly areas.

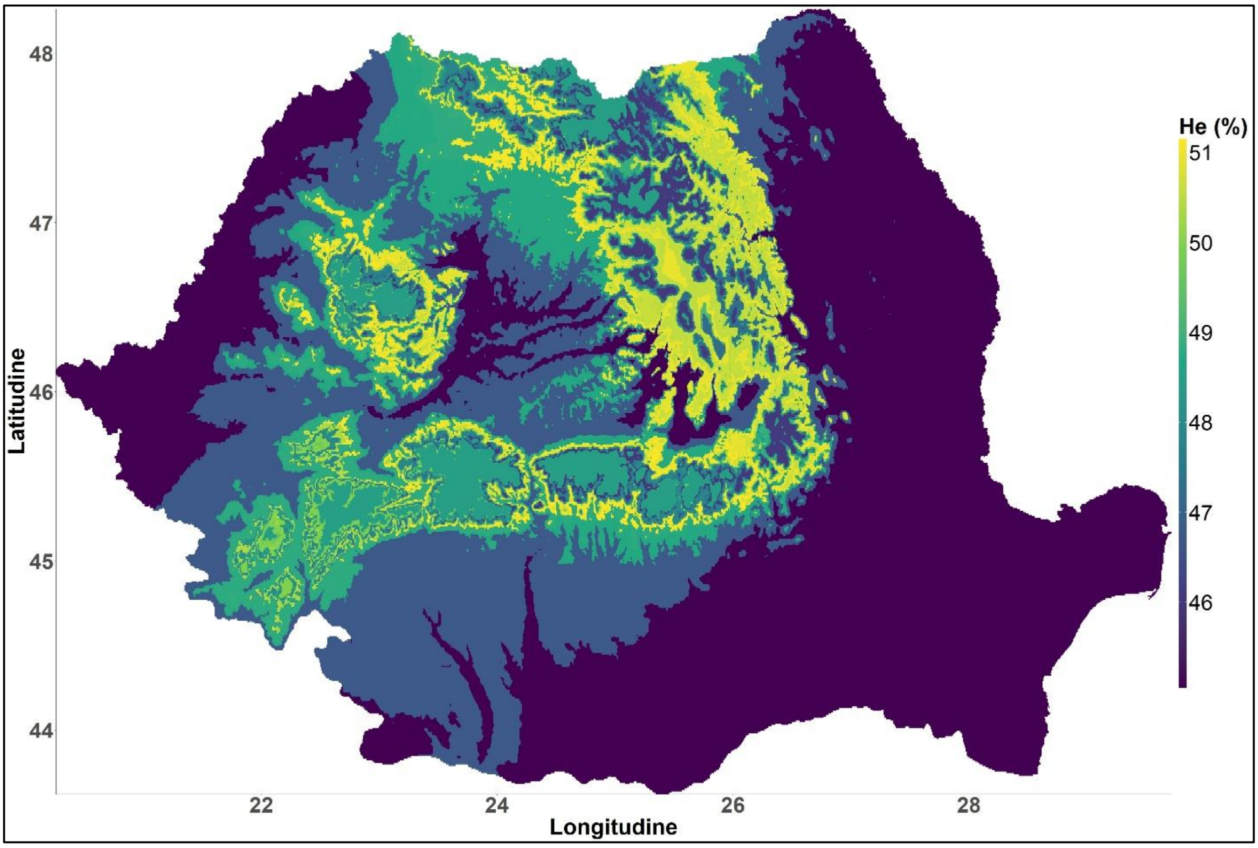


Figura 4.21. Distribution model F. sylvatica in Romania in the context of RCP 8.5, period 2021-2040.

For the final period of the RCP 8.5 scenario, with a 2100 horizon (Figure 4.22), an extreme reduction in areas with growth in the beech range is forecast. This period is associated with an intensification of the fragmentation of mountain environments favourable to beech growth, thereby limiting the species to only a few high-altitude areas. While in the previous period the most significant growth was attributed to the eastern division of the Carpathians, in this case, growth is very limited in this part of the Carpathians (Ceahlău and Rodnei Mountains), but they also appear in high-altitude areas of the Southern Carpathians (Șureanu, Parâng, and Lotrului Mountains), as well as isolated in the Apuseni Mountains. Compared to the similar period in the RCP 4.5 scenario, there is a drastic decrease in areas favourable to growth in height, as well as a pronounced fragmentation.

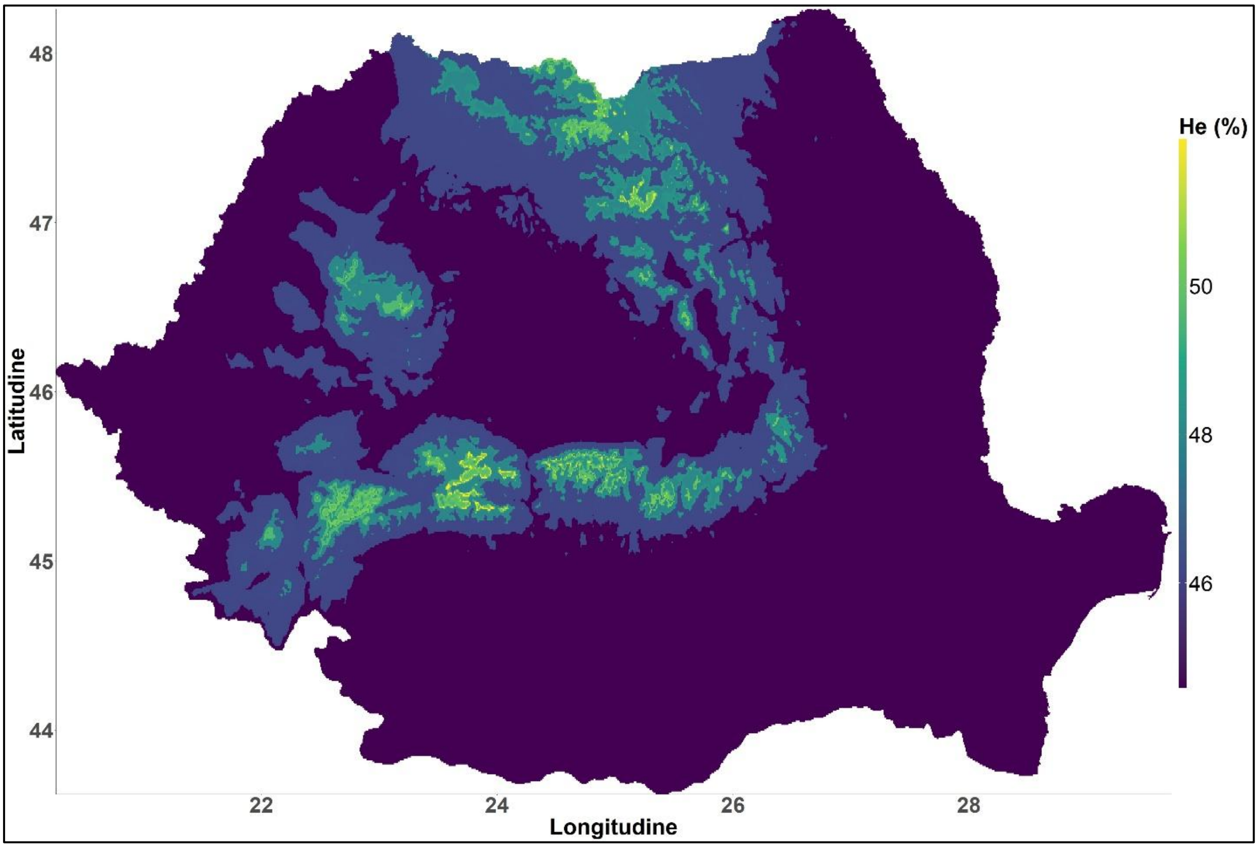


Figure 4.22. Distribution model F. sylvatica in Romania in the context of RCP 8.5, period 2081-2100.

4.4.3. Discussions

The results obtained for the distribution of the model's estimated height growth (*He*) in Romania assimilate the highest growth potential with the mountainous, Subcarpathian, and hilly areas, corresponding, for the most part, to the species' current natural range (Beșliu et al. 2022; Doniță et al. 2008; Marin et al. 2020; Milescu et al. 1967; Șofletea & Curtu 2008). Moderate and low increases were identified in the extracarpatic regions, in areas at the edge of the distribution range, as well as in high mountain areas, which are less favourable to the species (Beșliu et al. 2022; Șofletea & Curtu 2008). It is worth mentioning the potential for maximum height growth, approximately 70% of current growth, which could be achieved in future beech stands until they reach 20 years of age, assuming current climatic conditions remain unchanged (2011-2020 period). Therefore, a decrease in the growth of this species over time is indicated, as pointed out by Martinez del Castillo et al. (2022) in a reference study, which highlights the significant downward trend in the growth of beech forests (including those in Romania) between 1995 and 2016, caused by rising temperatures. This decrease in estimated growth is also supported by the increase in temperatures over the last decade (2011-2020), which exceeded the 1 °C threshold compared to the period 1850-1900 (IPCC 2023).

On another note, the territories marked by the model through sustained increases in height (e.g., the centre of the Transylvanian Plateau or the northwestern part of the country), where beech is not present or appears in isolated stands, can be considered areas where beech grew in the past, as large areas occupied by this species have been confirmed in Romania (Drăcea 2018), and subsequently reduced due to anthropogenic pressure. Due to the desire to expand agricultural areas and communities (Urșanu et al. 2024), the need for wood supply (Reinhardt-Imjela et al. 2018) sau datorită or the introduction of other more valuable species (especially conifers) (Bouriaud et al. 2016; Knapp & Fichtner 2011; Tudoran & Zotta 2020), natural forests have lost significant areas. It is also possible that beech trees did not survive in these areas due to intense competition with other forest species (Fărcaș et al. 2013). At the same time, in certain situations (such as in the northeast of the country), the model overestimates growth, while also highlighting certain limitations mainly due to the nature of the data used.

The model used in the predictions performed low due to the climate predictors associated with the test site, which have very little influence in explaining the variability of *Hn*, making this analysis an exploratory one. Although these results are limited, they are largely consistent with studies that have pursued the same objectives. Thus, the low increases outside the Carpathian chain, predicted for both climate scenarios, but with a significantly higher intensity in the case of RCP 8.5, follow the same direction as studies indicating a high sensitivity of beech, which will contribute to a gradual elimination or fragmentation of populations growing at the lower limit of the species' range (Dolar et al. 2023; Gessler et al. 2024; Jump et al. 2006a; Jump et al. 2006b; Roibu et al. 2022; Sánchez-Gómez & Aranda 2024). Alongside this phenomenon, the results of this study indicate a future migration process of the species towards higher altitudes in the Carpathian Mountains, a fact confirmed by other research that forecasts an ascent to higher altitudes where climatic conditions will be able to support the growth of forest species (Fuchs et al. 2025; Noce et al. 2023; Pauli et al. 2012; Pavlović et al. 2019). These observations were also made in Romanian research on beech, where marginal populations were found to be highly sensitive to drought and low growth rates were predicted for them (Chira et al. 2003; Klesse et al. 2024; Leifsson et al. 2024). A vulnerability of beech forests to climate change has also been identified, characterised by intensified drought, leading to an altitudinal migration of beech (Barnoaiea 2017; Budeanu et al. 2016; Kermavnar et al. 2023). In view of these drastic changes in climatic conditions, Kasper et al. (2022) indicate a future replacement of beech in the Western Carpathians with other species that are more resistant to drought, such as those of the genus *Quercus*. This conclusion is supported by the results of the present study, which indicate a possible reduction in beech height growth in this area and a concentration of growth in the Eastern Carpathians.

The limitations of the results obtained appear mainly from the constraints of the database, but also from the model used. Thus, because this model considers only tree height as the dependent variable and, for environmental variables, data on soil or other site characteristics are not included, the results are limited. These limitations of modelling are also recognised in other studies, which identify the complexity of forest ecosystems as one of the main impediments, generated by the difficulty of quantifying all natural processes at the level of these ecosystems, and propose the development of integrated study methods (Anderson-Teixeira et al. 2022; Boukhris et al. 2025).

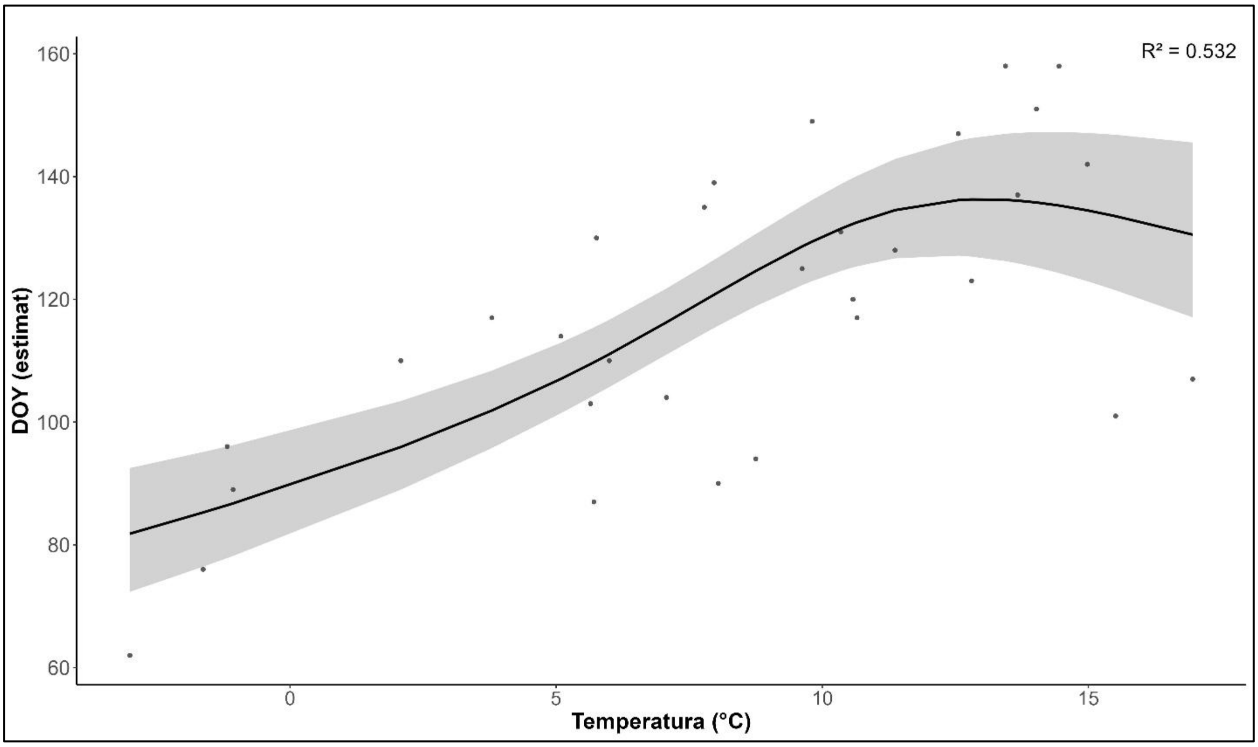
Considering: (a) the very widespread distribution of the species *F. sylvatica* in Europe (Bohn & Gollub 2007; Leuschner & Ellenberg 2017), where (b) it grows in diverse environmental conditions (Magri 2008; Von Wuehlisch 2008), (c) it has populations with genetic particularities (Ciocîrlan et al. 2017; Sánchez-Gómez & Aranda 2024; Șofletea & Curtu 2008), (d) exhibits high phenotypic plasticity (Besliu et al. 2024b; Capdevielle-Vargas et al. 2015; Frank et al. 2017; Gárate-Escamilla et al. 2019; Vitasse et al. 2010), (e) certain provenances have shown increased resilience (Dounavi et al. 2016; Meier & Leuschner 2008; Stojnić et al. 2021; Thiel et al. 2014), and (f) can grow very well in mixtures with other forest species (Pretzsch et al. 2020; Vanhellemont et al. 2019; Vannoppen et al. 2020), it can be considered that the forecasts in the context of climate change could be more optimistic. However, the speed and intensity of these environmental changes (Aubin et al. 2018; Boisvert-Marsh & de Blois 2021) are raising an alarm for the intervention of specialists to implement techniques known to be effective in mitigating the negative effects as much as possible. Therefore, this modelling method (*URF*) can be used to prevent certain imbalances that may be caused by climate change, as it combines environmental and genetic effects to provide predictions of provenance performance. At the same time, the method allows the identification of future species migration areas, as well as the optimal provenances for vegetation under specific conditions, and can also be used to select species that should be introduced in future production cycles (Jump et al. 2006b; Wang et al. 2010), thus forming the basis of the assisted migration process (Chakraborty et al. 2024).

4.5. Analysis of phenology

4.5.1. Leafing

Analyses of leafing (spring phenology) revealed variation across all tested sources, with particularities at the phenological stage level. The most significant variations were observed for the "year" factor, with very significant differences ($p < 0.0001$****) among the three years analysed across all phenological stages, indicating the strong influence of annual variations of the site conditions on spring phenological processes. In terms of replications, very significant differences ($p < 0.0001$****) were identified for classes two and three, respectively, at the last two stages (six and seven). The weakest differentiation was observed at the provenance level, which showed significant differences ($p < 0.01$**) only in stage three (assimilated with the actual onset of vegetation) and weakly significant differences ($p < 0.05$*) in the case of stages five and six (assimilated with the leaf formation stages).

The model applied highlighted the existence of a nonlinear relationship between the two variables, indicating that temperature strongly influences beech leafing (Figure 4.23). The results show that 53% of the variance in *DOY* is explained by temperature. At the same time, it was observed that temperature does not have a constant effect on *DOY*, because in certain intervals (5–10 °C), a small increase in temperature produces faster changes in the leafing processes. Thus, it is found that after exceeding the 5 °C threshold, the provenances begin their physiological activity. In practice, the model indicates that the stages of leafing begin earlier when spring temperatures are higher, but these changes are not constant. Therefore, in years with an earlier onset of leafing, the increase in temperature does not accelerate this process as much, and may even slightly delay some stages, compared to years when leafing begins later, indicating that spring phenological processes have a constant duration. On average, the stages of leafing advance by 2.6 days for every +1 °C. The highest sensitivity was observed in the 5–10 °C temperature range, where, after passing the 5 °C threshold, the stages of leafing advance by about five days and, about three days after reaching the 10 °C threshold, by +1 °C. On the other hand, this advance is small at lower or higher temperatures. For example, at temperatures of 15 °C, the advance decreases to less than one day, suggesting that the final stages of leafing (classes six and seven), which occur in early summer, are not as temperature-dependent as the early stages (classes three and four), and that the factors conditioning these processes may be precipitation, light intensity, etc.

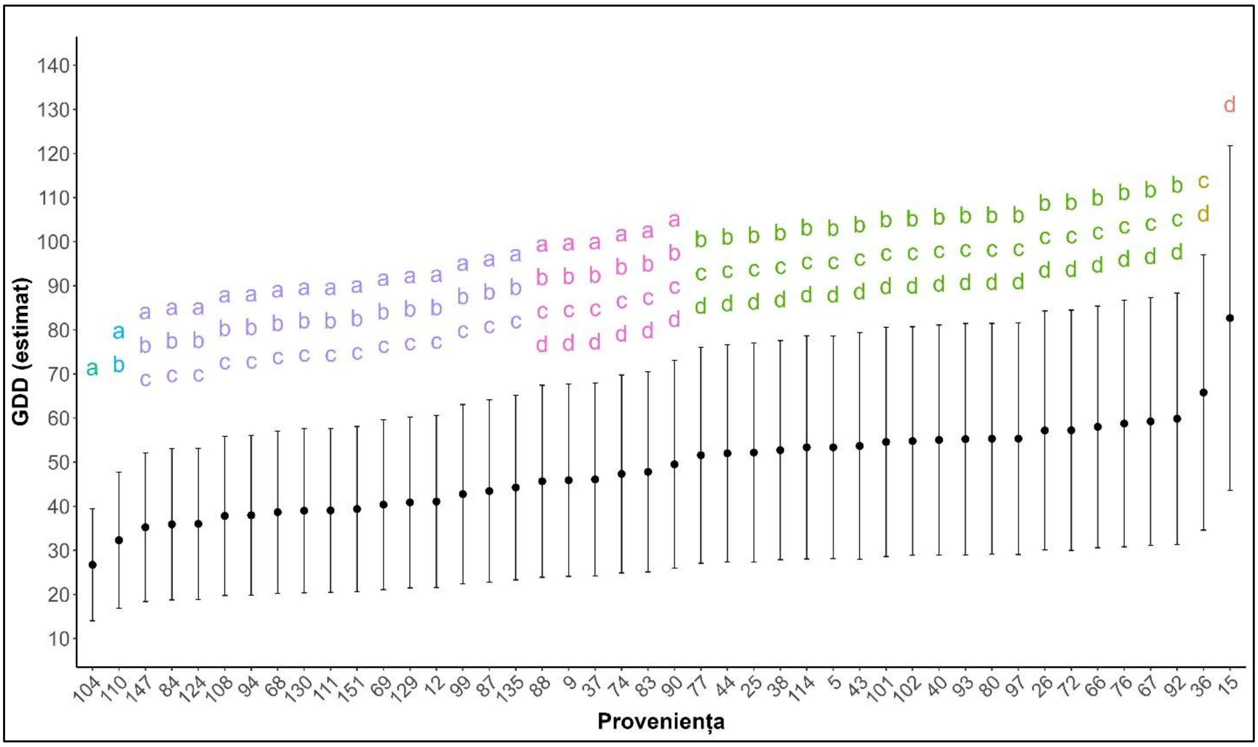


The right side of the diagram shows the result of the variability explained by the model (R2>0.5 - high significance).

Figure 4.23. Interaction between day of year (*DOY*) and temperature.

To analyse the temperature conditions required for the provenances to begin the leafing process, a nonlinear model was applied, in which the variation of the provenances was tested according to the cumulative *GDD*, in the calculation of which the base temperature was set at 5 °C. The *GDD* range within which the tested provenances enter vegetation is between 27 and 83, indicating significant differences among provenances. Therefore, the estimated onset of vegetation differs between the earliest and latest provenances by approximately 11 days, with an average temperature of 10 °C (56 *GDD*). On average, vegetation begins when the thermal requirement threshold (*GDD*) of 53 units is reached, at which point budburst begins for 50% of provenances. This result, expressed in *DOY*, anticipates vegetation onset beginning around April 23.

According to the results obtained (Figure 4.24), the earliest flush provenance is 95-Ge-104, followed by 95-Ch-110, both originating from central Europe. In the opposite pole, the latest budburst was observed at provenance is 95-Fr-15, from eastern France, and 95-Ge-36, transferred from northern Germany. The reference provenance for budburst is 95-Sp-05, originating from Spain, which requires a threshold of 53 *GDD* for this phenological stage, assimilated at the same time as the average threshold for the start of vegetation. The other provenances were grouped into three. The earlier group (provenances 95-Ro-147 - 95-Sk-135) also includes the two Romanian provenances, originating from Sovata (95-Ro-151) and Remeti (95-Ro-147), which had a similar reaction in terms of vegetation start. Most of the provenances were transferred from Germany, but no specific trend was identified in relation to the onset of vegetation.



The black dots represent the GDD mean. The black lines above the bars in the diagram represent the standard error values, and the letters above these bars represent the results obtained after applying the Holm method to the p-value obtained from the model. Homogeneous groups are marked with the same letters and colours.

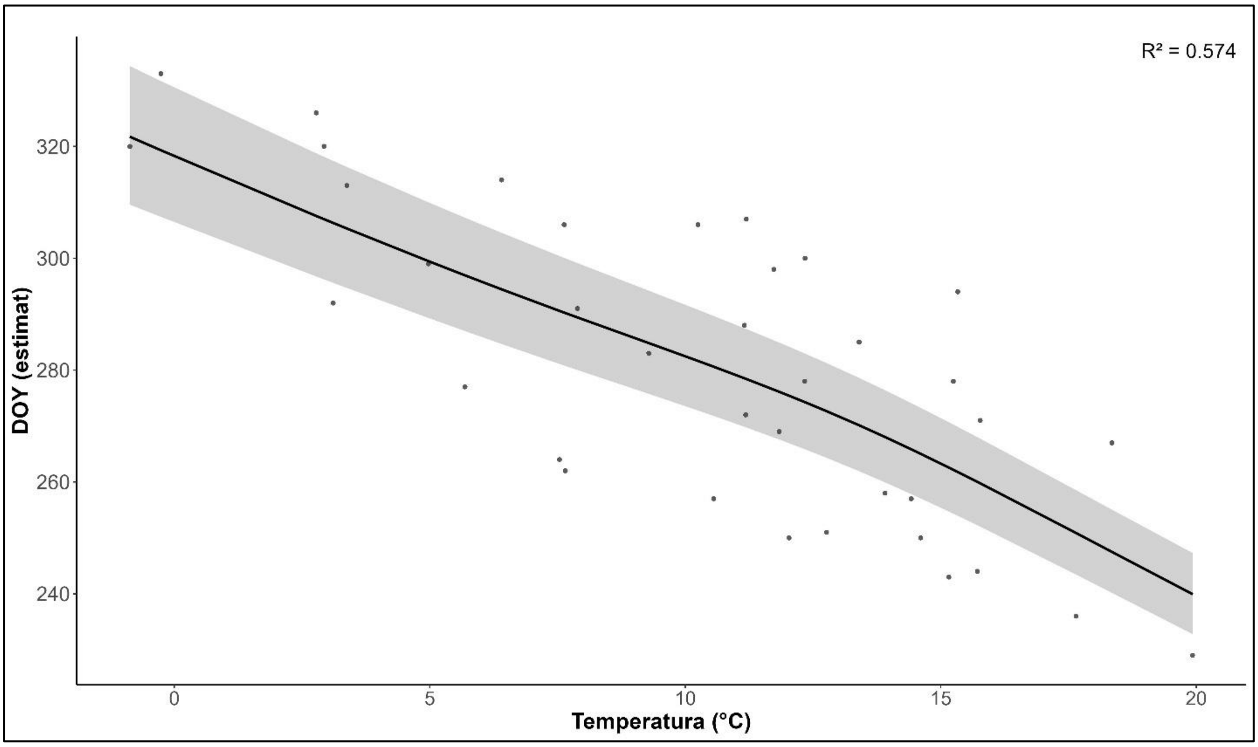
Figure 4.24. The influence of the growing degree days (*GDD*) on the budburst of provenances.

Overall, the differentiation in terms of provenance was more intense in the first part of the leafing process (classes two and three), assimilated with a multi-annual delay that increased to class five, followed by a rapid decrease towards the end of leafing. Therefore, there is a homogenization of the reaction of provenances at the end of spring phenology, in which temperature is no longer the main factor. Consequently, the correct differentiation at the provenance level can only be achieved at the budburst stage (class three), which is also a key point marking the beginning of beech vegetation and indicating, at the same time, the level of adaptation of provenances to local environmental conditions.

4.5.2. Senescence

The processes corresponding to senescence showed high variations for all tested provenances and at all stages, except for provenance in the case of class five. The year was identified as having the highest variation ($p < 0.0001$****), with a constant significant effect across all stages, highlighting the significant influence of annual climatic conditions, whose variations delay senescence. At the replication level, the differences were significant for all stages, but for the 5% yellowing stage, a low variation was recorded ($p < 0.05$*), indicating a weaker differentiation in the onset of senescence compared to the other stages of this process. In terms of provenance, the differences were highly significant ($p < 0.0001$****) for the first four stages, indicating high variation among the tested provenances. In the last stage (winter state), differentiation among provenances was not significant, indicating homogenization of their reactions, suggesting a possible influence of other environmental factors in reaching this class, not just temperature.

The analysis of the interaction between *DOY* and temperature revealed a similar nonlinear trend in senescence, similar to that observed for leafing (Figure 4.25). The applied model explains over 57% of the variation in *DOY*, which translates into high significance, while the rest of the variation can be attributed to other environmental factors that were not analysed in this study. Therefore, temperature is the main factor conditioning the processes corresponding to senescence in the case of the beech provenances tested in the Sacele trial, but the evolution of this process is not linear in relation to the decrease in temperature, indicating certain delays in the process at intermediate temperatures (10-15 °C range). The influence of the year was also significant ($p=0.001$***), with a negative correlation between them (-0.62), indicating that in years when senescence begins more rapidly, sensitivity to temperature is lower, whereas in years when senescence is later, sensitivity to temperature is higher. On average, senescence advances by approximately four calendar days (*DOY*) for every -1 °C recorded, and the nonlinear trend suggests that the advance is slightly higher in the 10–15 °C temperature range, corresponding to the stage associated with the onset of senescence (50% yellowing).



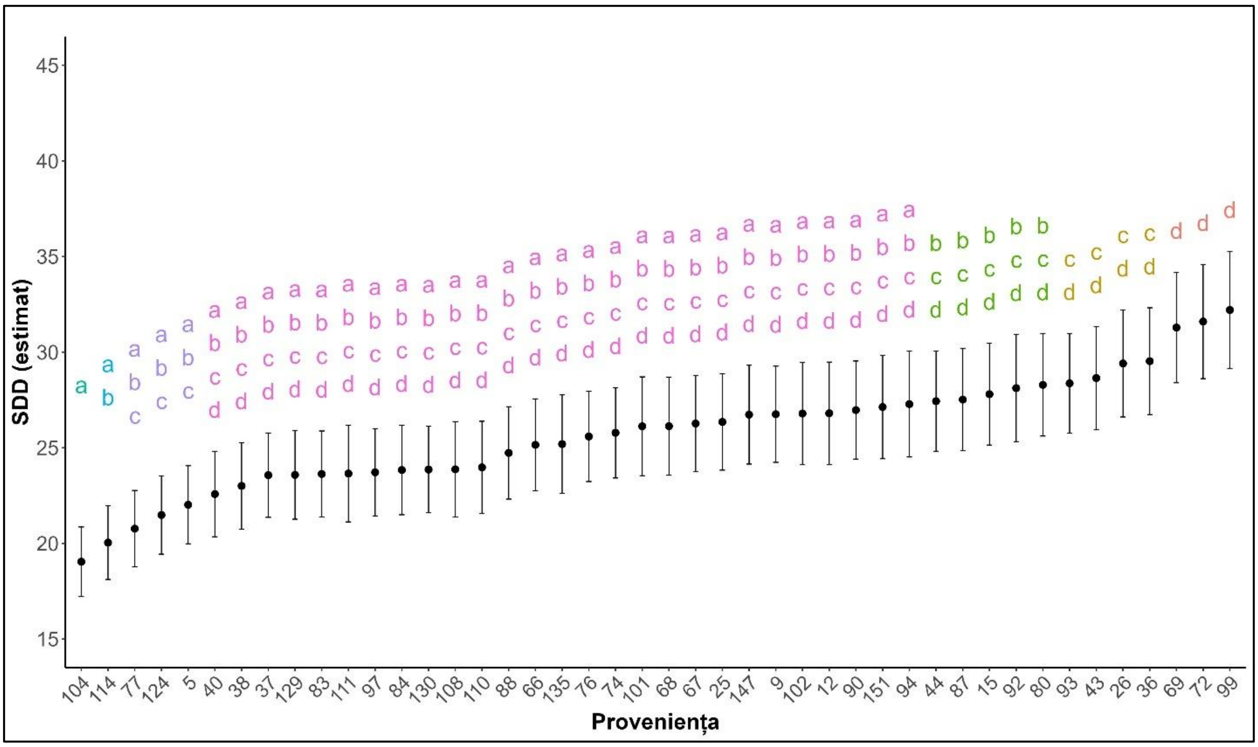
The right side of the diagram shows the result of the variability explained by the model (R2>0.5 - high significance).

Figure 4.25. Interaction between day of year (*DOY*) and temperature.

The defining stage of senescence is considered to be its onset, which marks the end of vegetation. In this study, the moment of vegetation end was assimilated with the 50% yellowing stage (third class), which is why the analyses at the provenance level focused on this.

To identify the thermal requirements for each provenance to initiate senescence, a nonlinear model based on *SDD* (senescence degree days) was used. For the SDD calculation, the base temperature was set to 15 °C. Thus, it was observed that *SDD* is a stable indicator of senescence; annual variations are smaller than those generated by provenance, highlighting the greater importance of genetic differentiation in defining the thermal requirements of the beech populations tested in the Sacele trial. On average, senescence begins after 26 *SDD* have accumulated, a value that has proven stable over the years analysed, which translates into approximately five calendar days with average temperatures below 10 °C or around 26 days with average temperatures of 15 °C. This moment is estimated to occur on day 265 (DOY), i.e., September 21, at which point senescence begins in half of the tested provenances. The *SDD* range, within which senescence begins in the tested provenances, is between 19 and 32 SDD, meaning that the latest provenance requires 68% more thermal forcing (cooling) than the earliest. This highlights a difference of approximately three days with temperatures of 10 °C.

At the level of the Sacele trial (Figure 4.26), the 95-Ge-104 provenance was identified as the earliest, followed by the Polish 95-Pl-114 provenance, with a small difference (only +1 *SDD*). On the other hand, the latest provenances were 95-Ge-99 and 95-Ge-72, originating from southern and central Germany. The reference provenances, whose onset of senescence is identified with the experiment's average (26 *SDD*), are 95-Ge-101 and 95-Ge-68, from southern and central Germany. Most provenances belong to the central group (95-Ge-40 and 95-Ge-94), which is positioned around the reference provenances. This group also includes the Romanian provenances originating from Sovata (95-Ro-151) and Remeti (95-Ro-147), which require a cumulative 27 *SDD* for the onset of senescence.



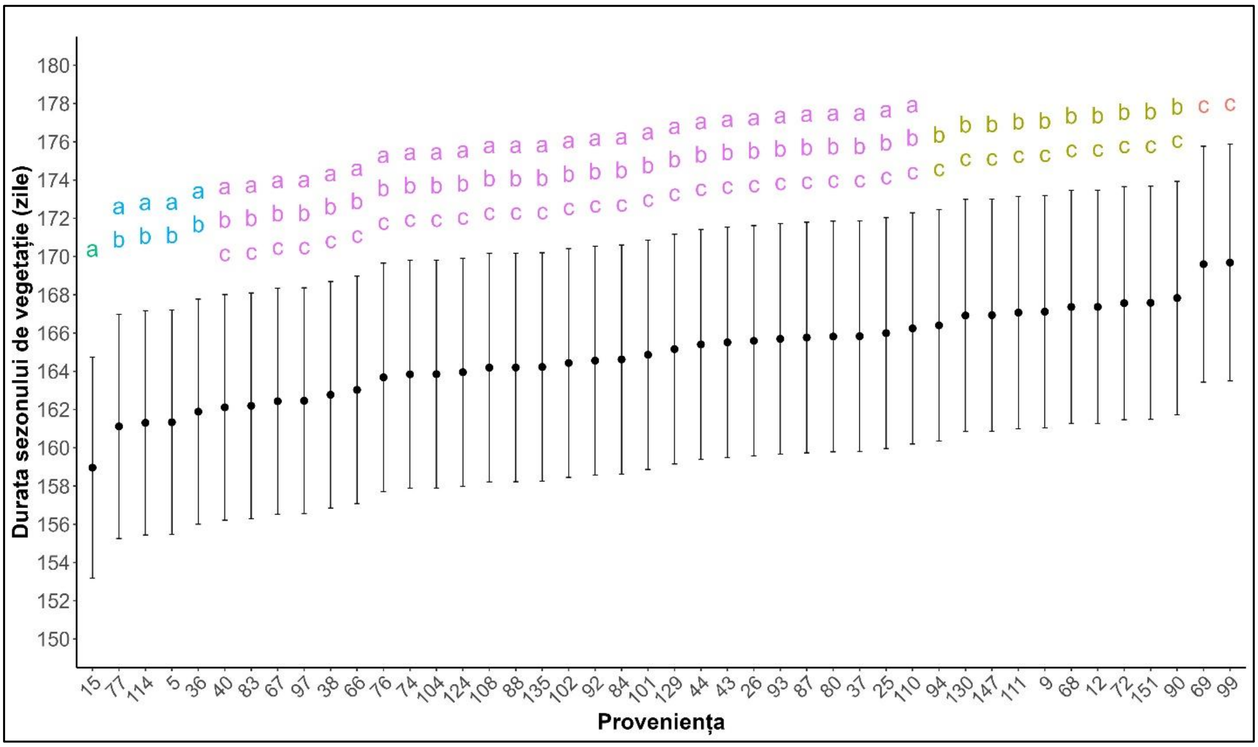
The black dots represent the GDD mean. The black lines above the bars in the diagram represent the standard error values, and the letters above these bars represent the results obtained after applying the Holm method to the p-value obtained from the model. Homogeneous groups are marked with the same letters and colours.

Figure 4.26. The influence of the senescence degree-days (*SDD*) on the 50% yellowing stage of provenances.

4.5.3. Length of the growing season

In order to obtain values for the growing season, the difference was calculated between the day (*DOY*) marking the start of vegetation (budburst) and the day of the end of vegetation (50% yellowing) for each tree analysed. Subsequently, the data were analysed using the nonlinear model.

According to the results, the average growing season lasts 162 days, influenced by annual variations, but especially by provenance, visible at the level of each year. The differences between the length of the growing season amount to 12 calendar days (Figure 4.27). These differences are more noticeable between the groups at the extremes. The shortest growing season was observed in the French provenance 95-Fr-15, which recorded a season approximately 3 days shorter than the average. The German provenances 95-Ge-69 and 95-Ge-99 recorded the longest growing season, with more than eight days above the experiment average. Similar to the analyses on the start and end of the growing season, in this case, there is also a majority group of provenances whose growing season is similar in length (95-Ge-40 - 95-Ch-110). The native provenances (95-Ro-147 and 95-Ro-151) were positioned in the group (95-Ge-94 - 95-Ge-90), i.e., those with a significantly longer growing season (approximately six days longer than the average), close to the provenances with the longest growing season.



The black dots represent the GDD mean. The black lines above the bars in the diagram represent the standard error values, and the letters above these bars represent the results obtained after applying the Holm method to the p-value obtained from the model. Homogeneous groups are marked with the same letters and colours.

Figure 4.27. Length of the growing season of provenances.

4.5.4. Discussions

The phenological processes of spring (leafing) and autumn (senescence) are considered to be part of the determining factors of forest species distribution and, implicitly, of their productivity (Chuine 2010; Chuine & Beaubien 2001), and temperature is known to be the main environmental factor conditioning these processes (Chuine & Cour 1999). Given the current trend of environmental changes affecting the length of the growing season (Corona et al. 2010), forest species are forced to adapt to new conditions by regulating their physiological activity (Aitken et al. 2008; Badeck et al. 2004; Ciocîrlan et al. 2022). Therefore, research in this area is particularly important because it can highlight the requirements of different tree populations regarding the growing season, which are essential for assisted migration processes or for identifying and promoting provenances with high adaptive potential (Vitasse et al. 2009a).

The analyses carried out in this study aimed to quantify the influence of site conditions on the beech provenances tested in the Sacele trial and to identify differences among provenances in the timing of leafing and senescence, and, implicitly, in the length of the growing season. In these interpretations, temperature was the factor used to determine the phenological trends of the provenances, being, in general, the main environmental factor used in numerous phenological studies in the case of *F. sylvatica* (Ciocîrlan et al. 2024; Ciocîrlan et al. 2022; Kramer et al. 2017; Vitasse et al. 2010; Vitasse et al. 2009a).

Variability testing revealed significant annual differences in both leafing and senescence, indicating the direct influence of annual temperature variations on the phenological processes of beech, a fact that is well known and widely reported in reference studies (Badeck et al. 2004; Chuine & Cour 1999; Delpierre et al. 2016; Vitasse et al. 2009a). Another very significant factor was replication, thus justifying the conditioning effects of microenvironmental variations on phenological processes. This implication of the microenvironment in differentiating the reaction of provenances was also observed by Besliu et al. (2022) in a comparative spruce trial. Another factor that was particularly important in these analyses was provenance. In this case, significant differences were observed in the early stages of leafing and senescence, indicating genetic control of phenological processes, which was also confirmed by similar studies in beech provenance trials (Gömöry & Paule 2011; Robson et al. 2013). Therefore, selecting provenances adapted to local vegetation conditions is both feasible and necessary (Von Wuehlisch et al. 1995). However, the effect of provenance was lower than that of year or replication, which may indicate a more decisive influence of test-site conditions over genetic origin in the phenological processes of provenances. This conclusion has been reiterated previously by Schueler & Liesebach (2015), who analysed the phenological processes of international beech provenances planted in two trials in Germany and Austria, from the same series as the Sacele experiment.

The model applied to phenology identified a nonlinear effect of temperature on phenological stages, which explains why, at higher temperatures, phenological onset is faster, but at the same time, the duration of the entire process can be slowed down, thus becoming constant between years with early or late phenological onset. Also, the rate of phenological advance was 2.6 days per +1 °C, with greater sensitivity in the 5–10 °C temperature range, and for the phases defining the final leaf stage, temperature was not the main factor conditioning this process. These results are supported by the conclusions drawn in other studies that have highlighted the influence of temperature on the phenological delay and its nonlinear effect, but also the influence of other factors, such as photoperiod, in phenological processes (Bigler & Vitasse 2019; Menzel et al. 2006; Vitasse & Basler 2013). The advance in phenology is considered to be on average between two and three days for every +1 °C (Jochner et al. 2016; Vitasse et al. 2009b), and the results obtained are therefore consistent with these values.

The average temperature at budburst, as recorded over the three years of observation, was 10 °C. The thermal requirement for 50% of the beech provenances analysed to enter vegetation was on average 53 *GDD*, equivalent to approximately 10,5 days with average temperatures of 10 °C, and the differences between the earliest and latest provenances totalled 11 days. The temperature threshold at which beech in the Carpathian region of Romania begins the vegetation period is considered to be 10 °C (Popescu & Șofletea 2020), and the thermal requirement determined by Ciocîrlan et al. (2022), in a study of beech phenology in the near the Sacele trial, was 60 GDD, accumulated seven days before the start of vegetation, a result very close to that obtained in the present study. In addition, Ciocirlan et al. (2024) note a 15-day delay between the beech populations analysed, which is similar to the delay identified for the extreme provenances in the Sacele trial, thus supporting the wide differentiation between provenances, which is comparable to the difference between populations located at the altitudinal limits of the species' distribution. The provenances selected for the earliest entry into vegetation and, implicitly, for higher thermal sensitivity were 95-Ge-104 and 95-Ch-110, originating from central Europe. The selection for the latest provenances, which require more intense thermal forcing (heating) for a longer period, included provenances 95-Fr-15 and 95-Ge-36, transferred from eastern France and northern Germany. Similar to these results, Horváth (2016) included beech provenances from central Europe in the category of those with faster vegetation growth. The delayed reaction of a French provenance was also highlighted in a study based on spring phenology from an international beech provenance in Croatia (Jazbec et al. 2007).

The nonlinear temperature trend was also identified in the case of senescence, and its effect was again highly significant, indicating that senescence advanced as the temperature decreased. It was also observed that, in years when senescence begins more rapidly, sensitivity to temperature is lower, whereas in years when senescence is later, sensitivity is higher. The rate of senescence advancement averaged four days for every -1 °C recorded, with a faster advance in the 10–15 °C temperature range. Studies on the senescence of this species have also highlighted the conditioning of this process by temperature, which is the main factor causing multi-annual delays of up to six days for every -1 °C (Ciocîrlan et al. 2022; Fu et al. 2018; Vitasse et al. 2011).

During the observation period, the average temperature at the third stage of senescence (50% yellowing) was 11 °C, and the thermal requirement to trigger the process was 26 SDD, corresponding to a cooling of the average temperature to 10 °C for approximately five days. The observed delay between the earliest and latest provenance was 10 days, and the cooling requirement amounted to 13 *SDD*, which means that the latest provenance requires 68% more thermal forcing (cooling) than the earliest.

The analyses carried out made it possible to identify provenances with greater sensitivity to temperature decreases. These were 95-Ge-104 and 95-Pl-114, originating from south-eastern Germany and Poland, which showed the fastest onset of senescence. The 95-Ge-104 provenance was identified as the earliest both for the start of vegetation (bud break) and for the end of the growing season (50% yellowing), indicating its high climatic sensitivity. In contrast, the 95-Ge-99 and 95-Ge-72 provenances transferred from southern and central Germany showed a higher need for thermal forcing (cooling), and were thus selected for the latest end of vegetation. After testing senescence in a trial of beech provenances from Poland, Chmura & Rozkowski (2002) observed that provenances from the east and south of the country have a faster onset of senescence than the other provenances tested, and Petkova et al. (2017) identified that a provenance from southern Germany, tested in a comparative trial in Bulgaria, showed the fastest onset of leaf yellowing. These conclusions support selecting the

German and Polish provenances from the Sacele trial for their early response to the end of the vegetation period.

Following the identification of provenances with different reactions to vegetation start and end, increased attention is recommended when using them for artificial regeneration, as they may be affected by late and early frosts (Chmura & Rozkowski 2002; Gömöry & Paule 2011; Robson et al. 2011). Thus, the transfer of forest reproductive material must only be carried out after the correct identification of the provenances that fall within the local thermal regime (Konnert et al. 2015).

The growing season lasted an average of 162 days, with a 12-day difference between the extremes. Similarly, Bigler & Vitasse (2019) identified an average growing season of approximately 149 days with a variation of 12 days during the 26 years analysed. The French provenance 95-Fr-15 recorded the shortest growing season, three days shorter than the average, and was also selected for the latest vegetation start. The German provenances 95-Ge-69 and 95-Ge-99 had a growing season eight days longer than the average and were included in the group of provenances with the longest growing season. These provenances were included in the rank of best-performing provenances for growth traits in the Sacele trial (Besliu et al. 2024c), thus confirming the positive influence of the length of the growing season on the growth performance of beech provenances (Gömöry & Paule 2011; Prislan et al. 2019).

4.6. Anatomical analysis of wood

4.6.1. Evaluation of radial increment

Variations in mean ring width (*MRW*) are influenced to a proportion of over 56% by the effect of year. This mainly indicates the decisive impact of interannual climatic variations on growth. Variations generated by trees within provenances account for approximately 9% of the total variance. Therefore, within the same provenance, there is a certain level of differentiation in terms of growth. However, replication has no effect on growth, indicating a high degree of homogeneity in the microenvironmental conditions in the Fantanele trial. In the case of mean lumen area (*MLA*), the level of variation differs from that observed for *MRW*. This time, the variation at the tree level is much higher, indicating constancy in lumen size between years and suggesting polygenic genetic control of this anatomical wood trait across provenances. Nevertheless, almost 45% of the variation is explained by year, highlighting the dependence of lumen size on climatic variations. Replication does not contribute to lumen variation either, further supporting the homogeneity of site conditions. It should also be noted that the residual variance is lower, indicating a better fit of the model than that applied for *MRW*.

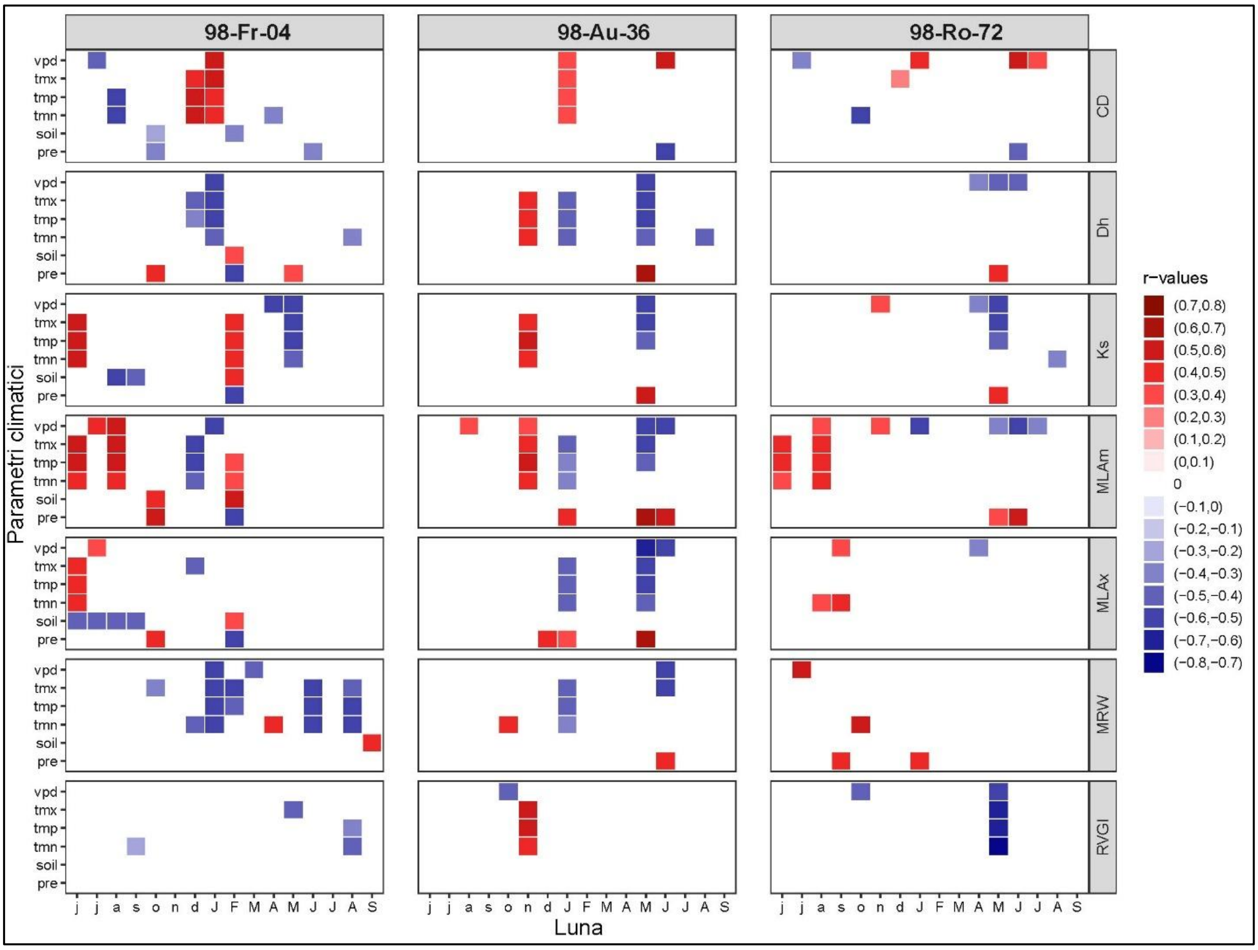
The analysis of *MRW* for the testing period indicates a similar response of the three provenances. The provenances were grouped together, indicating that the differences are not statistically significant. Regarding *MLA*, the results are similar to those obtained for *MRW*. However, the differentiation between provenances 98-Ro-72 and 98-Fr-04 approaches the significance threshold (p = 0.057), indicating a different response in terms of lumen size.

4.6.2. Relationship between climate and wood anatomical parameters

From the analysis of correlations between climate and anatomical parameters (Figure 4.28), a diverse response of the provenances was identified, indicating different response strategies, while growth (*MRW*) proved to be less sensitive to climatic variation than the other parameters. The vessel grouping index (*RVGI*) also did not show a clear relationship with climate. Provenance 98-Fr-04 is mainly influenced by the climate of the previous growing season (June–October), but also by the beginning of the growing season of the current year (March–May). Overall, the strong correlations with *vpd* and temperatures from the previous year (both negative and positive) indicate sensitivity to hydric and atmospheric stress from the previous year. Thus, in the case of a dry previous year, the anatomical activity of the current year is negatively affected, regardless of the conditions of the current year. This is due to a conservative, memory-based strategy, which involves a sudden reduction in vessel size and hydraulic conductivity.

In the case of the alpine provenance (98-Au-36), the relationship between climate and anatomical parameters did not show a response influenced by the climate of the previous year. The response of this provenance is determined exclusively by the climate of the current year, for which correlations with precipitation (*pre*), *vpd*, and temperature were identified. Therefore, the strategy is based on relatively constant growth and vessel size over time, without control generated by climatic extremes, which ensures continuity of performance regardless of climatic conditions.

The local provenance (98-Ro-72) is characterised by climate influences from both the previous and current years. The climate of the previous growing season (June–October) influences the anatomical parameters (*MLAm*, *MLAx*) and therefore conditions xylem formation, but it does not clearly affect growth (*MRW*). This influence is controlled by temperature and *vpd*, which set the response for the following year. In addition, correlations with anatomical parameters were also identified for *vpd*, temperature, and precipitation (*pre*) during the current year. Thus, a warmer previous growing season (without hydric limitation) leads to the formation of larger vessels in the current year. Consequently, this provenance uses previously accumulated resources to develop a more efficient hydraulic system in the current year. However, its response does not depend only on memory, but also on a regulation of physiological activity determined by the climatic conditions of the current year.

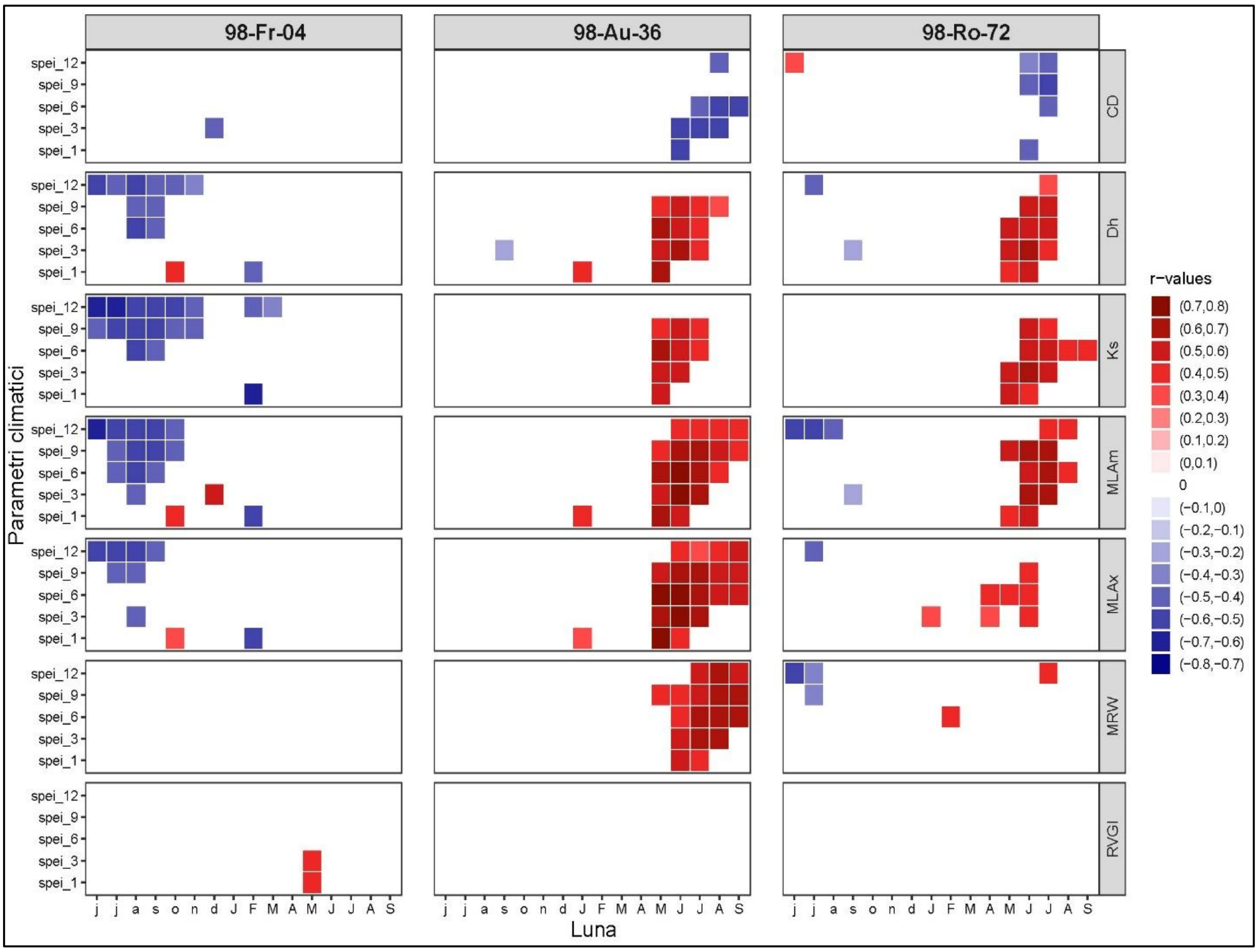


r – correlation value between anatomical parameters: CD – cell density; Dh – mean hydraulic diameter; Ks – hydraulic conductivity; MLAm – minimum mean lumen area; MLAx – maximum mean lumen area; MRW – mean ring width; RVGI – vessel grouping index; and climatic parameters: vpd – vapour pressure deficit; tmx – maximum temperature; tmp – mean temperature; tmin – minimum temperature; soil – soil moisture index; pre – mean precipitation. Months of the year are indicated by lowercase letters for the previous year and uppercase letters for the current year.

Figure 4.28. Correlations between climate and anatomical parameters.

The analysis of the relationship between *SPEI* and anatomical parameters (Figure 4.29) highlights more clearly the behaviour of the provenances under drought conditions or during years with higher precipitation. The provenance originating from France (98-Fr-04) shows negative correlations, particularly between *SPEI 6–12* and the main xylem parameters (*Dh*, *Ks*, *MLA*), only for the previous year. Therefore, the strategy of this provenance to respond to hydric stress from the previous year by a sudden reduction in vessel size and hydraulic conductivity is confirmed. For the current year, the absence of correlations indicates the avoidance of a real-time response, meaning that the reaction is driven by the signal recorded in the previous year. In the case of provenance 98-Au-36, the absence of correlations with the previous year indicates the lack of a climatic memory effect on the response of the current year. Therefore, the reaction of this provenance is determined exclusively by the current year, for which strong positive correlations were identified for the xylem parameters (*Dh*, *Ks*, *MLAm*, *MLAx*), as well as for growth (*MRW*), this being the only provenance that shows correlations at the level of growth.

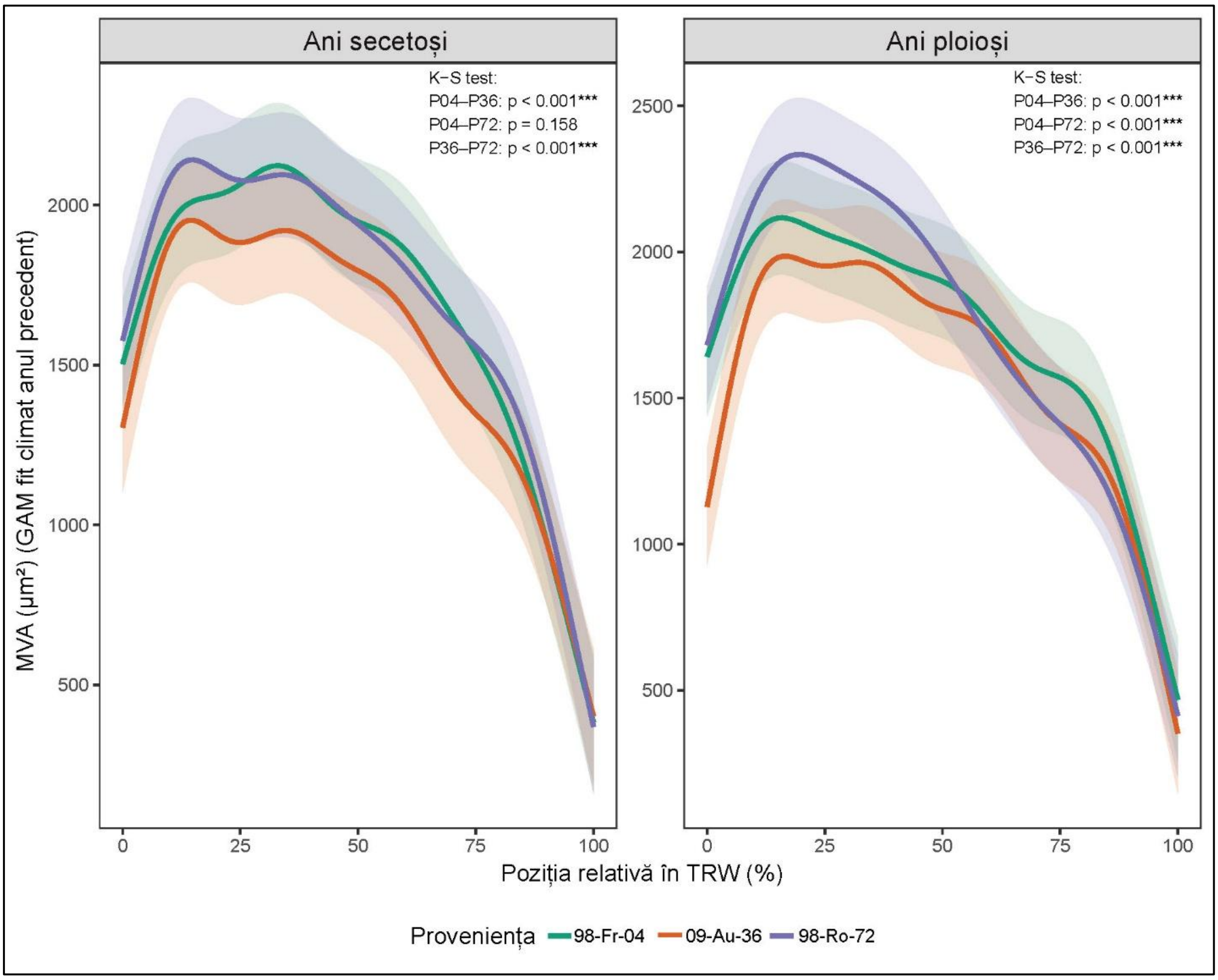
For provenance 98-Ro-72, the analysis of correlations with the *SPEI* index indicates a climatic signal from both the previous and current years. Negative correlations from the previous year indicate a reduction in vessel size and growth, associated with a cautious start in the following year. In contrast, positive correlations in the current year indicate that when the climatic signal is favourable, the provenance responds by increasing physiological activity.



r – correlation value between anatomical parameters: CD – cell density; Dh – mean hydraulic diameter; Ks – hydraulic conductivity; MLAm – minimum mean lumen area; MLAx – maximum mean lumen area; MRW – mean ring width; RVGI – vessel grouping index; and climatic parameters: SPEI 1–12 – standardised precipitation–evapotranspiration index. Months of the year are indicated by lowercase letters for the previous year and uppercase letters for the current year.

Figure 4.29. Correlations between SPEI and anatomical parameters.

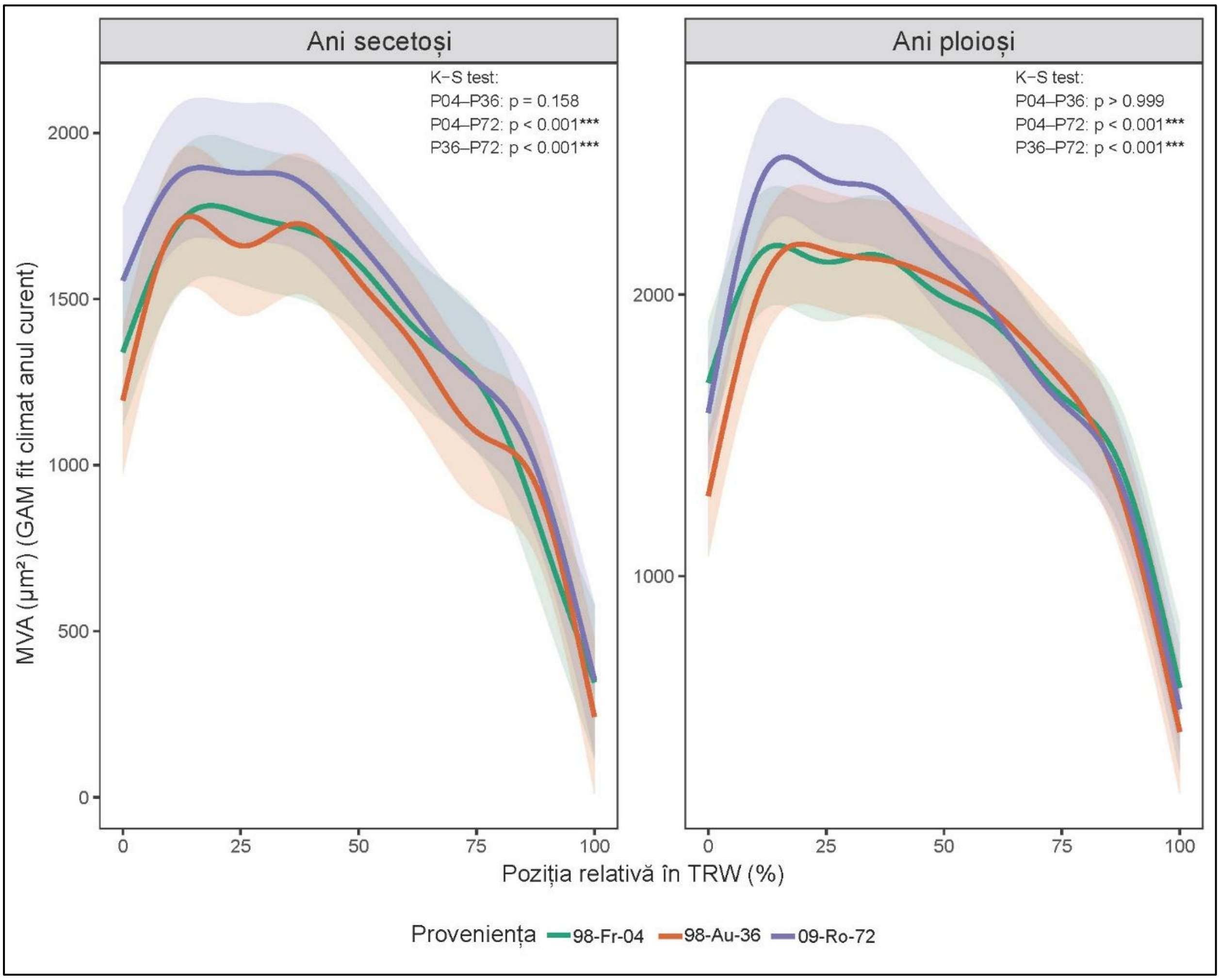
The evaluation of previous years, analysed separately for the years identified as drought years (2003, 2007, 2015) and for those with abundant precipitation (2005, 2010, 2014), indicates the response pattern of the provenances under these conditions and how the climatic signal from the previous year influences the mean vessel area (*MVA*). Wet previous years lead to an increase in vessel size at the beginning of the following growing season, in the sectors corresponding to earlywood within the rings, while drought years reduce the potential for vessel formation (Figure 4.30). The provenances show different responses, especially in wet years, confirming once again the genetically determined response pattern. After a drought year, provenance 98-Fr-04 maintains a high *MVA* level, even showing a higher peak in earlywood growth than in wet years. Therefore, the climatic sensitivity of this provenance is low, displaying an inert behaviour in relation to climatic conditions. Provenance 98-Au-36 adopts the previously identified strategy, characterised by a constancy of growth regardless of climatic conditions. Thus, after dry previous years, it slightly reduces vessel size in earlywood, while after wet years, it moderately increases vessel size; however, the onset of growth remains more cautious compared with the other provenances, regardless of the climate of the previous year. The local provenance shows the highest *MVA* values in the sectors corresponding to earlywood, both after wet previous years and after drought years. Following a previous year with higher precipitation, it forms larger vessels by using the accumulated resources, whereas after a drought year, it slightly reduces vessel size but does not substantially reduce physiological activity.



MVA – mean vessel area; TRW – tree-ring width; KS – Kolmogorov–Smirnov test (for p < 0.05; ** for p < 0.01; *** for p < 0.001).*

Figure 4.30. Model results for the influence of previous-year climate on mean vessel area across ring sectors.

The real-time responses of the provenances to climatic variations can be observed during the current year (Figure 4.31). The effect of a dry year is reflected in a reduction of *MVA* in earlywood and in a relatively sharper transition to latewood, whereas in years with abundant precipitation, vessel sizes are larger, particularly in the sectors corresponding to earlywood. At the provenance level, differences occur between the local provenance and the international ones, which follow a similar trend. The French and the Alpine provenances show a reduction in *MVA* in drought years, more pronounced in the Alpine provenance. In wet years, both increase *MVA* growth, although the Alpine provenance shows slightly higher values. In contrast, the Romanian provenance shows a different response compared with the two international provenances, displaying significantly higher values in both drought and wet years. The trend observed at the annual ring level indicates intense growth in the earlywood zone during the first part of the growing season, followed by a gradual reduction in vessel size as climatic constraints increase. In drought years, this provenance reduces vessel size in earlywood, but not to a very low level, thus maintaining functionality. In favourable years, it benefits from the available resources and produces larger vessels, thereby increasing hydraulic conductivity.



MVA – mean vessel area; TRW – tree-ring width; KS – Kolmogorov–Smirnov test (for $p < 0.05$; ** for $p < 0.01$; *** for $p < 0.001$).*

Figure 4.31. Model results for the influence of current-year climate on mean vessel area across ring sectors.

4.6.3. Discussions

Wood anatomical analysis provides the possibility to observe in detail the adaptive potential of tree species by accurately identifying the mechanisms that determine tree growth and the relationship between growth and site conditions (von Arx et al. 2016). Anatomical characteristics are mainly influenced by climate (Gennaretti et al. 2022), but also by genotype (Nabais et al. 2018), thus highlighting the possibility of identifying populations with more efficient adaptation mechanisms (Hajek et al. 2016) and, more importantly, explaining the performance of different populations and the physiological mechanisms used for survival (Fontes et al. 2022).

In this study, three provenances tested in the Fantanele trial were analysed at the anatomical level. The experiment is located at the limit of the natural distribution range of beech, which provides the opportunity to observe the response of provenances to limiting growing conditions, since in these areas forest species are considered to be more sensitive to environmental changes (Gennaretti et al. 2022).

The analysed provenances showed a similar level of radial growth, as well as close values for lumen area, with no significant differentiation between them. Similar results were also identified in a study conducted by Stojnic et al. (2013) on a comparative trial established in Serbia under site conditions similar to those of the Fantanele trial. The authors noted that the provenances showed a similar response regardless of whether the site from which they were transferred was wetter, highlighting their potential to adapt to drought conditions as well. This result was also confirmed in the present study, where the alpine provenance (98-Au-36) showed growth levels that did not differ from those of the other provenances. Similar growth trends at the level of the testing sites were also observed by Unterholzner et al. (2024), who concluded that local environmental conditions have a stronger influence on growth than the genetic background of beech provenances. This conclusion was also highlighted in another study conducted in a comparative trial in the Netherlands (Eilmann et al. 2014). Therefore, under the site conditions at the eastern limit of the natural distribution range of beech, the growth of the provenances tends to be similar, without notable differences. This phenomenon is determined by the climatic constraints of the testing site, which influence growth and override genotype effects.

In marginal areas, where radial growth is dictated by environmental conditions (Unterholzner et al. 2024), the study of wood at the anatomical level can reveal more effectively the physiological response of provenances, since anatomical traits are much more sensitive to environmental fluctuations and can clearly explain the relationship between climate and tree performance (Choat et al. 2012; Rita et al. 2022). Consequently, the study of the relationship between climate and anatomical parameters is necessary for identifying the adaptive strategies adopted by different populations to ensure their survival and growth even under limiting conditions (Fontes et al. 2022; Johnson et al. 2018).

The anatomical parameters analyzed for the three provenances did not show a clear differentiation at the level of the raw data, a pattern that has also been observed in beech under marginal conditions (Arnič et al. 2021; Gričar et al. 2024), but the analysis of the relationship with climate, using the effective method of dividing the annual ring into segments (Huang et al. 2025), revealed different strategies adopted by the provenances to reduce the negative effects of the environment (Oladi et al. 2014), strategies are influenced by genotype and allow a differentiation between provenances.

The French provenance (98-Fr-04), transferred from the western part of the species' range, from an area influenced by Atlantic climatic conditions, which recorded the lowest performance in the Fantanele trial but was identified as having a plastic reaction in the two trials established in series 98, proved to have a physiological response based on climatic memory, lacking an adaptive potential expressed in real time. The behaviour of this provenance is largely dictated by climatic memory (Kannenberg et al. 2020), thus being inert to environmental fluctuations during the growing season. It functions mainly based on the climatic signal received in the previous year and on the imprint left by earlier droughts, which creates a carry-over effect for the following years (Rukh et al. 2023), while the responses to environmental fluctuations in the current year are weak and fragmented. The response of this population is reflected in a sudden reduction in vessel size and, consequently, in hydraulic conductivity following a drought year (Gleason et al. 2016), which becomes even more pronounced during drought conditions in the current year, leading to the occurrence of cavitation, the main determinant of mortality (Choat et al. 2012). Therefore, this provenance has a low adaptive potential and a pronounced sensitivity to the high climatic variability characteristic of edge areas of the species' range (Klisz et al. 2019), which makes it vulnerable during prolonged unfavourable periods and especially under the projected climate changes (Aitken et al. 2008; Lee et al. 2023). In addition, the plasticity identified in the biometric characteristics proved to be, in fact, a non-adaptive plasticity at the anatomical level (Ghalambor et al. 2007), due to environmental pressure that exceeds the adaptive potential of this provenance (Chevin et al. 2010), thus, it does not represent an adaptive plasticity, which would involve a reduction in growth in response to environmental constraints as a first step in the process of adaptation (Bradshaw 1965; Bradshaw 2006; Bussotti et al. 2015).

The provenance transferred from the Austrian Alps (98-Au-36), from the altitudinal limit of beech distribution, which showed the highest performance in terms of survival and height, exhibited a balanced and stable anatomical response over time. The response of this population is determined exclusively by the climatic variations of the current year, avoiding reactions to extremes. In drought years, it slightly reduces its physiological activity, but does not block it, while in favourable years, it does not strongly intensify growth, thus maintaining hydraulic stability. This behaviour was also identified by Miranda et al. (2022) in a study conducted on beech populations along an altitudinal gradient in the Apennine Mountains. The authors noted that high-altitude populations showed lower plasticity in anatomical characteristics and a more cautious hydraulic activity, which did not differ markedly between years and was therefore influenced only by the climate of the current growing season, without clear responses to climatic extremes. In addition, vessel size was found to be influenced by both temperature and precipitation, a pattern also observed in the present study. This stability in xylem activity ensures high long-term performance and efficient adaptation to harsh site conditions. The strategy of the Alpine population indicates an adaptation to the conditions of its origin, where the growing season is short, and winter desiccation occurs, similar to drought, limiting water movement from the roots to the stem (Charrier et al. 2021). This behaviour of reducing the negative effects of extreme climate through efficient hydraulic management was also observed in Alpine provenances in a study conducted in a comparative trial established under optimal conditions for beech in Slovenia

(Mrak et al. 2024). The adaptive response of beech provenances transferred from the Alpine region to restrictive environmental conditions at the limit of the species' range has also been reported in other studies (Gömöry 2009; Mátyás et al. 2009a; Mátyás et al. 2009b). Thus, these populations possess a high adaptive potential that allows them to grow even under drought conditions and, especially, under the restrictive conditions characteristic of high altitudes. These findings confirm the projections obtained in this study and in others, according to which beech is expected to expand in high mountain areas (Fuchs et al. 2025; Noce et al. 2023), as well as the potential of forest tree species to grow beyond the limits of their current distribution range (Griesbauer et al. 2025).

The local provenance, transferred from western Romania, which did not show the highest performance but was close to being included among the best-performing provenances in the Fantanele trial, exhibited a plastic response through active anatomical adjustment according to the environmental signal. Its response to variations in site conditions proved to be a combined one, using the climatic signal from the previous year to regulate the intensity of growth initiation in the current year. However, during the growing season, the anatomical adjustment is determined in real time by the seasonal climate, which exerts the strongest influence. This provenance displayed significantly larger vessels than the other two provenances, and the most pronounced growth occurred during spring, while hydraulic activity decreased during summer. This pattern indicates the presence of an anatomical regulation mechanism used to avoid the negative effects of drought, which has also been identified at the southern limit of the beech distribution range (Prigoliti et al. 2023). After a favourable previous year, the provenance forms larger vessels in earlywood, whereas after a dry year, it slightly reduces vessel size without strongly decreasing hydraulic activity, indicating an active hydraulic regulation (Arnič et al. 2021; Olano et al. 2022). Thus, the strategy of this provenance, which involves the use of both types of climatic signals, proves to be effective for the area at the eastern limit of the species' range, where the greatest problems occur during summer due to atmospheric stress (Roibu et al. 2022), and where the growth of beech stands is directly influenced by drought (Budeanu et al. 2016). However, despite this, the strategy adopted by this provenance has not ensured the highest phenotypic performance up to the age of approximately 30 years. This ranking may change among provenances as age increases (Colangelo et al. 2017; Krajnc et al. 2023), but it effectively supports the persistence of the species under these growing conditions (Roibu et al. 2017). An efficient adaptive response to drought conditions in beech provenances transferred from Romania was also reported by Unterholzner et al. (2025), in a study conducted in three trials belonging to the same series as those analysed in the present research. Two of the three Romanian provenances tested were identified as effectively withstanding hydric stress through reductions in vessel size and hydraulic regulation. Similarly, a provenance from Bulgaria, tested in an international beech trial in the Netherlands, stood out for having the most efficient hydraulic system. It adopts a strategy similar to that of the local provenance in the present study, namely, not to drastically reduce vessel size and to continue anatomical activity (Eilmann et al. 2014).

CHAPTER 5: CONCLUSIONS. ORIGINAL CONTRIBUTIONS. RESULTS DISSEMINATIONS. FUTURE PERSPECTIVES

5.1. Conclusions

5.1.1. Conclusions of the analysis of survival and biometric characteristics

- The analysis based on survival and biometric characteristics showed that international beech provenances generally exhibited a positive adaptation response to the testing conditions in Romania after 24 years (1998 series) and 27 years (1995 series) of testing. International provenances proved to be more efficient than native ones.
- The differences between the environmental conditions of the testing sites significantly influenced the adaptive potential of the provenances. Thus, the site with the lower average annual temperature and the one installed at the species' range limit negatively influenced the provenances, which responded by reducing their performance and, implicitly, narrowing their adaptive potential.
- The variations identified in the response of provenances indicate the existence of genetically controlled adaptive potential, thus highlighting the possibility of applying assisted transfer. However, in this process, priority must be given to the relationship between provenance performance and site conditions, thereby ensuring the success of the transfer.

5.1.2. Conclusions of the analysis of phenotypic plasticity

- The plasticity value was higher for survival than for the other traits analysed (height and diameter), indicating a greater sensitivity of the plasticity index to survival and a stronger link between survival and adaptability.
- The tested provenances showed a plastic response to interaction with the test sites in Romania, but their phenotypic performance was reduced in the limiting areas, which indicates the action of phenotypic plasticity, which causes a reduction of performance in order to adapt to the level of environmental favourability.
- Considering the complexity of the tree species adaptation process, more complex studies are needed to distinguish between provenances in terms of plasticity, including parameters corresponding to internal tree processes, so the overall level of plasticity may be separated into two categories of plasticity: adaptive and non-adaptive.

5.1.3. Conclusion of the analysis of provenance transfer

- The transfer functions applied at the 95 series level highlighted the sensitivity of provenances to temperature increase, which positively influenced survival and diameter growth, while at the 98 series level, it was noted that the adaptation of provenances is conditioned more by criteria related to the ecology of the species than by the geographical origin of the provenance.

- Some of the provenances transferred from similar environments to those of the test sites performed very well, but the similar reaction of provenances transferred from totally opposite sites, as well as the large differences between provenances with very similar climatic origins, indicate the existence of high variation in climatic sensitivity among beech populations in Europe. Therefore, the need for large-scale testing of beech provenances and their transfer only to sites similar to those in which they performed is reconfirmed.

5.1.4. Conclusion of height growth modelling at the level of Romania

- The current distribution of height growth of beech in Romania, following the application of the *Universal Response Function* model, assimilates the highest growth potential with the mountainous, Subcarpathian, and hilly areas, corresponding to most of the species' current natural range, while moderate and low growth has been identified in the extra-Carpathian regions, in areas at the edge of the range, as well as in high mountain areas that are less favourable to the species in the current climate.
- The maximum growth potential, estimated at approximately 70% of current growth, which could be achieved in future beech stands up to the age of 20, in the context of maintaining current climatic conditions (2011-2020), indicates a decline in beech growth over time due to the impact of climate change, which influences the decline in site favourability.
- The low growth rates outside the Carpathian chain, predicted for both climate scenarios, but with a significantly higher intensity in the case of RCP 8.5, follow the same direction as studies indicating a high sensitivity of beech, which will contribute to a gradual elimination or fragmentation of populations growing at the lower limit of the species' range. In parallel with this phenomenon, the model suggests a future migration process of the species to higher-altitude areas in the Carpathian Mountains.

5.1.5. Conclusions of phenology analysis

- Phenological processes highlighted the existence of high annual variations among the provenances tested in the Sacele trial, mainly generated by air temperature fluctuations. Provenance played a significant role in the early stages, indicating the existence of genetic control over these processes. However, the effect of provenance was lower than that of the year of observation or repetition, suggesting that test-site conditions exert a more decisive influence on phenological processes than genetic pattern.
- The nonlinear effect of temperature on leafing stages explains why phenological onset is faster at higher temperatures, but at the same time, the duration of the entire process can be slowed down, thus becoming constant between years with early or late phenological start. Also, the rate of leafing progress was 2.6 days for every +1 °C. Variations in the phases corresponding to the definition of the final leaf shape could not be explained by temperature.
- Senescence was explained by the nonlinear effect of temperature, which indicates that senescence advances as the temperature decreases. It was also observed that in years when

senescence begins more rapidly, sensitivity to temperature is lower, whereas it is higher in years when senescence is later. The rate of senescence advancement averaged four days for every -1 °C recorded.

- The growing season registered an average of 162 days, with a difference of 12 days between the extremes. The provenances with the longest growing season were among the best-performing for growth traits in the Sacele trial, confirming the positive influence of growing season length on beech provenance growth performance.
- Due to differences in the thermal requirements (heating and cooling) of the provenances, it is recommended that special attention be paid when using them for artificial regeneration, as their performance may be affected by late and early frosts.

5.1.6. Conclusions of anatomical wood analysis

- Anatomical analysis of wood has proven to be a highly effective tool for quantifying in detail the adaptive potential of beech provenances.
- The pressure of the limiting environment, in the marginal area of the beech range, induces the homogenization of the radial growth of the provenances, and their adaptive response can be underestimated without analysing the hydraulic capacity.
- The physiological strategies adopted by provenances again indicate the need for detailed studies prior to their transfer. However, the high adaptive and productive potential of the Alpine provenance indicates the possibility of introducing it in Romania. Nevertheless, the use of Romanian beech genetic resources, supported by the anatomical plasticity of the native provenance, remains the most feasible solution for maintaining the stability of forests in the current climate.

5.2. Original contributions

- Multidirectional testing of the adaptive potential for numerous international beech provenances to the environmental conditions in Romania, upon reaching a representative point in the testing process, namely, half of the cycle proposed at installation;
- Use of quantitative and qualitative phenotypic traits to determine the adaptive potential of international beech provenances tested in Romania;
- Use of the phenotypic plasticity index in the analysis of the behaviour of international beech provenances tested in Romania;
- Testing the reaction of international beech provenances using the ecological transfer distance method under various environmental conditions representative of Romanian beech forests;
- Evaluation of beech provenance performance based on the ratio between survival and height;
- Exploratory modelling of height growth for beech provenances in Romania using the *Universal Response Function* Model;

- Predicting the distribution of beech in Romania based on the reaction of tested provenances in different climate scenarios;
- Determining the phenological behaviour of beech provenances by monitoring and modelling phenological processes;
- Assessment of the adaptability of beech provenances based on anatomical analysis of wood;
- Reintroducing into the sphere of international forest research of the beech provenance trials conducted in Romania.

5.3. Results diseminations

The dissemination of the research results obtained from this study was carried out through publications in ISI-rated journals and BDI, as well as through participation in national and international conferences and symposiums. In total, three WoS articles and two BDI articles were published, and four contributions were recorded in terms of participation in scientific events.

Articles published in Web of Science-indexed journals (WoS):

- **Besliu, E.**; Curtu, A.L.; Apostol, E.N.; Budeanu, M. Using Adapted and Productive European Beech (Fagus sylvatica L.) Provenances as Future Solutions for Sustainable Forest Management in Romania. Land 2024, 13, 183. https://doi.org/10.3390/land13020183. Nr. citări: 18.
- **Besliu, E.**, Curtu, A. L., Budeanu, M., Apostol, E. N., & Ciocîrlan, M. I. (2024). Exploring the effects of the assisted transfer of European beech (Fagus sylvatica L.) provenances in the Romanian Carpathians. Notulae Botanicae Horti Agrobotanici Cluj-Napoca, 52(3), 13968. https://doi.org/10.15835/nbha52313968. Nr. citări: 3.
- Ciocîrlan, M.I.C.; Ciocîrlan, E.; Chira, D.; Radu, G.R.; Păcurar, V.D.; **Beșliu, E.**; Zormpa, O.G.; Gailing, O.; Curtu, A.L. Large Differences in Bud Burst and Senescence between Low- and High-Altitude European Beech Populations along an Altitudinal Transect in the South-Eastern Carpathians. Forests 2024, 15, 468. https://doi.org/10.3390/f15030468. Nr. citări: 4.

Articles published in journals indexed in international databases (BDI):

- **Beșliu, E.**, Curtu, A. L., Apostol, E. N., & Budeanu, M. (2022). Fagus sylvatica L. genetic resources in Romania: a review. Revista de Silvicultură şi Cinegetică, 27(51).
- **Besliu, E.**, Budeanu, M., & Curtu, A. L. (2024). Analyzing the Adaptive Reaction of European Beech Provenances from the Perspective of Quality Traits. Bulletin of the Transilvania University of Brasov. Series II: Forestry Wood Industry Agricultural Food Engineering, 1-20.

Scientific papers presented at national and international conferences:

- **Besliu, E.** (2022). Testarea variabilității genetice a fagului în culturi comparative de proveniențe internaționale. Sesiunea națională a doctoranzilor în silvicultură, 7 Decembrie 2022, Suceava, România.

- **Besliu, E.**; Curtu, A.L.; Apostol, E.N.; Budeanu, M. (2023). Phenotypic variability and plasticity of European beech (*Fagus sylvatica*) provenances tested in Romania. ''Forest science for people and societal challenges''. The 90th ''Marin Drăcea'' INCDS Anniversary, 2-5 Octombrie 2023, București, România.
- **Besliu, E**., Curtu, A. L., Apostol, E. N., Budeanu, M. (2023). Growth performances and transfer analyses of European beech (*Fagus sylvatica*) in two common garden experiments from Romania. Second EVOLTREE Conference 2023 – ''Resilient forest for the future'', 12-15 Septembrie 2023, Brașov, România.
- **Besliu, E**., Curtu, A. L., Budeanu, M. (2024). Analysing the adaptive reaction of European beech provenances from the perspective of quality traits. 11TH INTERNATIONAL SYMPOSIUM FOREST AND SUSTAINABLE DEVELOPMENT, 17-18 Octombrie 2024, Brașov, România.

5.4. Future perspectives

Future research will prioritise a detailed investigation into the adaptability of the species F. sylvatica in Romania. To achieve this, the following objectives will be pursued:

- Expanding the beech testing network in provenance trials across Romania;
- Establishing a seed orchard for the beech species;
- Replicating the anatomical analysis of wood in other beech provenance trials in Romania;
- Improvement of the *Universal Response Function* model at the country level by including data from other beech provenance trials;
- Testing assisted migration practices in the case of European beech.

In addition, efforts will be made to extend the analyses to other tree species, to initiate new methods for modelling the adaptability of tree species, and to integrate new technologies into provenance trials studies.

CHAPTER 6: REFERENCES

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