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Genetic variability of Norway spruce [*Picea abies* (L.) Karst.] in provenance trials in Romania

SUMMARY

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Contents

Introduction

Norway spruce *(Picea abies)* is the most important conifer species in Europe. It occupies an area of approximately 30 million ha in Europe, which represents 38% of the area occupied by conifers. More than 20% of this surface represents its extension outside the natural area [1].

In Europe, according to RCP 8.5 projections, Norway spruce is likely to retreat in the Alps, Carpathians, and Scandinavia above 60° latitude, disappearing entirely from the lowlands of Central Europe [2]. In Romania, according to the RCP 4.5 projection, it is estimated that the area lost until 2100 will be 8%, while the area gained will be only 2% [3]. Changes have already occurred in Romania; areas with climatic conditions suitable for the main forest species have become favourable for other species. Norway spruce will expand to higher altitudes but will be less common and lose its range, especially in the Eastern Carpathians [4].

The global warming limit of 1.5 °C could be reached in the first half of the next decade [5]. As a result, severe and extreme climate events will occur with higher frequency [6], [7], [8], [9], [10] and have greater severity and longer durations [11], [12].

Forests have great potential for mitigating climate change, but drought and other extreme climate events can affect their growth, productivity, genetic diversity, area, as well as the various services they provide [13], [14], [15], [16], [17], [18], [19], [20]. Between 1987 and 2016, drought caused extensive forest drying phenomena for about half a million hectares in Europe [21].

Tree species have different adaptive capacities to mitigate the impact of climate change: adaptation through natural selection, migration to new habitats or phenotypic plasticity [22]. Given that the natural migration of tree species is much slower than climate change, assisted migration is a measure to facilitate the adaptation of tree species [23], [24], [25]. Through this transfer, the productivity and health of forests can be maintained, if not improved in the future [26], [27], [28].

Drought resilience has genetic and environmental components, and different populations of the same species may respond differently to the same climatic conditions [29]. Numerous studies have demonstrated that there is genetic variation in the sensitivity/tolerance of forest species to droughts, both at the inter-population and intra-population level [30], [31], [32], [33]. Using genomic analyses, significant associations were found between single nucleotide polymorphism (SNP) and traits related to drought adaptation in Norway spruce [34], [35].

Beyond the potential negative effects of climate change, there is also a potential to increase productivity due to longer growing seasons and increased photosynthetic activity. Quantitative genetic variability is essential for the adaptability of species to climate change. The use of suitable reproductive material in afforestation works is an important factor in mitigating the negative effects but also taking advantage of the positive ones [36], [37], [38].

Therefore, one way to ensure the genetic adaptation of forest tree species to drought is to select the most resilient provenances [39], [30], [40], [41], [42], [43] and to use them in artificial regeneration works. Maintaining and increasing the resilience of forest ecosystems is the most effective forest management in the face of climate change.

Selection for greater growth, quantity and quality of wood, and adaptability are among the main objectives of tree breeding programs, and comparative trials provide essential information for meeting these objectives. However, stability analysis is often performed for a single feature, especially for tree species.

In this doctoral thesis, the genetic variability of the main traits of economic and adaptive interest were analysed (Subchapter 4.1), the correlations between some analysed traits and between them and the place of origin of the provenances (Subchapter 4.2), as well as the influences of climatic conditions on the biometrical traits of Norway spruce origins (Subchapter 4.3).

Subchapter 4.4 presents the results obtained following the use of two selection indices, not used so far for forest tree species, considering growth and quality traits and survival percentage, to identify and select the most performing and stable provenances of Norway spruce.

Considering the large number of provenances tested, which cover almost the entire area of the species in Europe, as well as the age of the comparative trials, half of the age of the exploitability of the Norway spruce in Romania, it can be stated that the tested populations have "experienced" climate changes. Thus, the results obtained in this doctoral thesis are important and can be used for the selection of valuable seed sources and the conservation of Norway spruce genetic resources both in Romania and in other countries.

1. THE CURRENT STATE OF KNOWLEDGE REGARDING THE VARIABILITY OF NORWAY SPRUCE IN PROVENANCE TRIALS

1.1. Distribution range, ecological requirements, and importance of Norway spruce

1.1.1. Natural and cultivated distribution range

Norway spruce is the most important conifer species in Europe. It occupies an area of approximately 30 million ha in Europe, which represents 38% of the area occupied by conifers. More than 20% of this area represents its extension outside the natural area [1]. The current distribution of the Norway spruce is characterised by three main areas: Nordic, Alpine and Carpathian [44].

Norway spruce has a vast natural range, extending from 41° 27' to 72°15' north latitude and from 5°27' to 154° east longitude. Altitude-wise, it is found from sea level in Northern Europe and rises to over 2300 m in the Italian Alps [45].

In Romania, it occupies a total area of 1.37 million hectares (21% of the total forest area) [46], of which, at the level of 2007, approximately 360 thousand hectares (over 25%) represented plantations created outside the area, in premontane and hill forest sites, down to the oak subzone [47].

1.1.2. Ecological requirements

Norway spruce is a species of wet, cold lands with high cloudiness [47]. It is sensitive to drought, especially in the first 2-3 years. It prefers sandy-loamy, weakly skeletal, loose, slightly moist, moderately acid soils; it also develops on very acidic podzols if they are loose and have sufficient moisture; as for dry soils, Norway spruce development is weak on them [48]. Due to its semi-shade temperament, it can last under the massif for up to 20-30 years. This species' internal phytoclimate characteristic is determined by its litter's slow and partial decomposition [48].

The main destabilising factors for Norway spruce stands are strong winds and storms (causing windfalls and windthrows and snow breaks), periods of excessive/prolonged drought, bark beetle attacks, and root and stem cryptogamic infections [49].

Norway spruce trees in the state forests experienced infestations with bark beetles, on almost 100,000 ha/year in the period 1965-1985, respectively of 220,000 ha/year in the period 1991-2022. The decline has been caused by storms and excessive drought [50], [51]. The decline of Norway spruce outside the natural range was mainly caused by drought and the invasive species *Ips duplicatus* [52].

The vulnerability of Norway spruce to drought has been presented in many studies [53], [54], [55]. It is a very sensitive species to increasing temperatures and water scarcity [45], to decreasing water availability and has a reduced adaptive capacity in central and southern European areas [56], [57].

Even a moderate drought has been observed to alter the total biomass and the distribution of fine roots in the soil depth in Norway spruce [58]. A prolonged drought causes more profound growth of Norway spruce fine roots and fungal hyphae [59]. The stress caused by drought also affects the morphology of the needles, but only in the portions of the canopy exposed to sunlight [60]. In addition, cracks appeared in the tree stem following water stress [61].

Drought causes a decrease in its vitality [62], which leads to lower resistance to the attack by bark beetles, especially *Ips typographus* [63], [64]. It is considered the most important pest of Norway spruce stands in Eurasia. In Europe, for the period 1950-2000, the degradation produced by bark beetles, mainly *Ips typographus*, was between 2 and 9 million m^3 of wood/year [65]. In the last decade, the attack of this pest has become much stronger - the volume harvested because of the attack produced by this bark beetle in the Czech Republic was 13 million m^3 in 2018 and about 23 million m^3 in 2019, compared to 1.5 million m^3 for the period 2003-2015 [66].

Thus, the mortality risk of Norway spruce and other conifer species could be higher with increasing temperatures and decreasing amounts of precipitation, especially for populations outside the natural range [67].

1.1.3. Importance

Wood is used for a wide range of products, such as lumber, furniture, musical instruments, composites, and veneer, with solid wood and paper having the highest economic value [68].

Norway spruce has an important role in climate change and carbon storage [69], [70]. Regarding soil organic carbon content, it was concluded that conifers (Pinus, Tsuga, Larix, Picea), and especially Norway spruce, contain higher soil organic carbon stocks than other species [69]. In Germany, values of 3.3 t/ha/year were reported for European beech stands and 3.2 t/ha/year for Norway spruce stands in terms of carbon stored by biomass; the net exchange was 0.98 t/ha/year for hemlocks and -0.39 t/ha/year for Norway spruces. Exploitation activities can explain the negative value of Norway spruce stands. The carbon stored in the biomass above the ground had values between 101 t/ha - Norway spruce stands and 127 t/ha - beech stands [71].

From an aesthetic and recreational point of view, Norway spruce stands generally scored lower than pine stands in terms of preference and landscape beauty [[72], [73], cited by [74]].

1.2. Norway spruce variability in provenance trials

1.2.1. Common garden experiments

Comparative trials are experiments through which genetic differences at the level of forest species can be evaluated by testing different origins, sexual progenies, and clones under the same environmental conditions.

Through comparative trials, information can be obtained about:

- Genetic variability and heritability of growth characters, wood quality, resistance or tolerance to diseases and pests or abiotic factors (e.g. drought);
- Phenotypic and genetic correlations between traits;
- Juvenile-adult correlations;
- Epigenetic effects;
- Genotype x environment (GxE) interaction [75].

The name of provenance is given by the place where a tree stand is found. It can be of known or unknown origin, made with local material, or introduced from other geographical areas [76].

Provenance trials are established to separate the genetic and seasonal components of phenotypic variability between different geographical sources. The aim is to find out how the respective populations will react to the transfer in different environmental conditions and to select the most valuable and adapted provenances by testing them in homogeneous environmental conditions [77].

They are important for species of high economic or ecological value, as they provide information on plasticity, adaptive or growth potential, and resistance to disease, insect attack, and climatic stress [[78], cited by [79]].

Also, provenance trials provide necessary data for modelling the impact of climate change on forest tree species, identifying the species and provenances that will be best adapted to the new climatic conditions [80], [81], [82], [83]. Moreover, they can be useful in restoring degraded areas where conditions are unfavourable (land prone to drought, unproductive or less fertile soil, etc.) [75].

In some provenance trials, the local provenance performed better than the others. However, there are many examples where local provenance is overcome by provenances from milder environmental conditions (from more southern latitudes or lower altitudes). There are arguments that local provenance is not always the most appropriate for afforestation programs [84], cited by [77]. First, natural selection has led to an adaptation to meet the requirements of an entire life cycle: both vegetative fitness (the ability to survive to reproductive age) and reproductive fitness (the ability to produce seeds and to leave viable offspring) [77]. In an afforestation program, some elements of reproductive fitness are not important in afforestation: because seeds can be produced or collected elsewhere, the ability of trees to flower and reproduce is not essential; the critical phases of germination and establishment of seedlings in natural conditions are skipped, as the seedlings are grown in nurseries; environmental and competitive conditions may be different in plantations due to silvicultural works, fertiliser application, etc. Non-local provenances are not always the best, but local provenance is the safest bet when other data is unavailable. However, if the selection of a provenance is based on traits such as growth and productivity, using a non-local provenance can lead to rapid and inexpensive genetic gains [77].

1.2.2. Genotype x environment interaction

The main objectives of Norway spruce breeding programs, regardless of country, have been to increase wood production, shorten the production cycle, and improve the wood's adaptability and economic value [85].

However, most traits with high economic value and important in breeding programs show polygenic variation, influenced by both genotype and environmental factors. Climatic, soil and relief conditions are often responsible for the different responses of populations of various origins. Campbell and Jones [86] define GxE interaction as the different responses of a group of genotypes for a given trait in different environments. In recent years, the GxE interaction has gained importance for forest trees because natural migration cannot keep up with seasonal changes when environmental conditions change rapidly, as is predicted to happen due to climate change [87], [88]. For this reason, studies of GxE interaction and phenotypic plasticity to select stable and high-performing populations under many seasonal conditions have become of significant importance in breeding programs. Also, the study of this interaction allows the identification of unstable genotypes; their removal from breeding populations is a strategy to reduce GxE interaction [89]. There are numerous studies for almost all commercially important forest species that have reported a significant GxE interaction, such as: Scots pine [90], Eucalyptus [91], Douglas fir [92], Norway spruce [93], [94], [95], [96], [97], poplar [98].

Heinrich et al. [99] defined the stability of a trait as the ability of a genotype not to fluctuate over a wide range of environmental conditions. Laing [100] distinguished between spatial stability, defined as the relative response of a genotype to environmental changes in a specific location, and temporal stability, which varies from year to year. According to Becker and Leon [101], stability has two contrasting concepts: "static" and "dynamic". The concept of static means that the provenance is stable when it maintains its performance across different environments. Dynamic stability is when there is no GxE interaction, and provenance performance across multiple trials parallels the average of tested provenances.

Therefore, provenance trials provide essential information for selecting the most adapted and valuable provenances [77]. However, a superior genotype in one trial may be inferior in another trial [102]. For tree breeding, GxE interaction can be addressed in two ways: selecting stable genotypes, which are not sensitive to environmental changes, or selecting genotypes suitable for specific environments [103]. At the same time, the evaluation of the GxE interaction at the adult stage, close to or over half of the rotation cycle, is more relevant from the perspective of commercial forestry [104], [105].

1.2.3. Norway spruce provenance trials installed worldwide

At the international level, most of the Norway spruce provenance trials were established under the coordination of the I.U.F.R.O. (International Union of Forest Research Organizations) in the 1940s [106] and have mainly contributed to the worldwide identification of trends in variation for economically and adaptively important traits [45].

The first international series to study genetic variability in Norway spruce provenances was initiated within I.U.F.R.O. in 1938 and 1939. It contained 36 seed sources planted in 26 trials in Europe and the USA [106]. A trial was also installed in Romania, in the Râșnoavei Valley [107].

The second series, IUFRO 1964/1968, inspired by the results of the first, included 1100 seed sources. In this experiment, 20 trials were installed in 13 countries, including eastern Canada [106]. No comparative trial was installed in Romania, but our country participated with 36 provenances [107].

The third series began in 1972, with 43 test sites in 10 countries. A comparative trial was not established in Romania. In this series, 20 Polish provenances were compared with local seed sources [45].

Provenances tested in **Hungary** from the Eastern Carpathians (Dorna Candrenilor, Jasina) and the Bihor Mountains (Turda and Câmpeni) were among those that maintained their high productivity at the age of 44 [108].

In **Latvia**, in the only provenance trial from the 1972-1974 series, analysed at the age of 32, in which measurements and observations could still be made before a storm destroyed it, some local provenances (Remte) and Carpathians (Dorna Candrenilor, Hripelev, Lazehchyna) maintained their superiority in terms of growth for more than a third of the production cycle [109].

In **Poland**, Chmura et al. [104] show that the ranking of provenances undergoes changes over time, some provenances can rise in the ranking by up to 15 positions, and others lose up to 16 between the previous analysis and the current one. Therefore, the comparison with previously obtained results for the same tests shows that the identification of good provenances should be postponed for older ages.

In **Austria**, climate response functions were analysed for height at 15 years of 379 populations in 29 provenance trials [36]. An increase in height at 15 years of up to 45% has been predicted by 2080. The authors highlight that the right choice of seed sources can increase productivity by up to 11%.

In **Canada**, based on studies carried out in four trials of Norway spruce provenances, it was concluded that vigorous tree growth does not have the effect of depleting basic cations in the soil, being correlated with biological mechanisms that return more nutrients to the ecosystem [110].

Significant differences between provenances in terms of flowering earliness and number of cones were revealed in a comparative trial from **Lithuania**. 120 provenances from the Baltic States, Russia, Poland, Finland, and Sweden were tested. Thus, southern provenances showed a higher number of flowering trees and cones per tree [111].

A series of 5 comparative trials with 16 provenances from Sweden, the Czech Republic, Denmark, Germany, and France and a local provenance was installed in the **UK** in 2021 to identify provenances suited to climatic conditions over 50 years [112].

Romanian provenances achieved higher growth at low altitudes in eastern Norway than local provenances [113].

In **Sweden**, eastern European Norway spruce provenances were selected and vegetatively multiplied (grafted) from a comparative trial and planted alongside local provenances. Progenies of Eastern European provenances started later the vegetation season and were less affected by early frosts [114].

1.2.4. Norway spruce provenance trials in Romania

The first comparative trial of Romanian Norway spruce provenances was installed by Iuliu Moldovan in the Asăului Valley, in 1935. Obvious differences between the provenances were found and the Norway spruce from the north of the country is superior to that from the Southern Carpathians [115].

Norway spruce breeding programs have been initiated in many European countries, but the breeding objectives have been diverse, depending on how the genetic material is used. Thus, in Romania, the improvement program began in the 1960s by selecting seed source stands and plus trees, establishing 78 ha of plantations and 15 provenance trials in which 50 native and 71 allochthonous provenances [116], [95].

The first series of Norway spruce provenance trials was installed in 1968 by Cornelia Nițu. The results obtained after the first year showed that seedling height decreases with latitude [117]. According to the results obtained at the age of 40 for two trials from this series, in terms of average volume/tree, the Wessterhoff and Dorna Candrenilor provenances are in the first place in the Sinaia comparative trial, and for Toplița, the most productive provenances are Toplița and Dorna Candrenilor [95].

For the comparative trials installed in 1972, which are the subject of study of this thesis, the superiority of the Romanian Norway spruce is demonstrated by the results obtained at 20 years [118], at 25 years [119] and 35 years [95].

Between 1977 and 1983, under the coordination of Valeriu Enescu, 20 Norway spruce trials were established to test progenies and seed sources. Six comparative trials, where 33 provenances from the whole natural area of the Romanian Norway spruce were tested, were installed in the spring of 1980. Thus, three of these experiments (Avrig, Târgu Lăpuș and Câmpina) were installed outside the natural area, and the other three (Brețcu, Nehoiu and Gurghiu), in the ecological optimum of the species [120].

Two series of comparative trials, in which 24 Romanian provenances and one German (used as standard) were tested in the first series, and in the second, 9 Romanian provenances, were installed in 1984. The provenances from the north of the Eastern Carpathians achieved performances above average 20 years after planting [95].

2. AIM AND OBJECTIVES

The aim was to characterize the genetic variability of the Norway spruce (*Picea abies*) - the most important softwood species in Romania from an ecological and economic point of view - to improve the national breeding strategy and conservation measures of the Norway spruce genetic resources in Romania in the context of climate change.

Specific objectives:

- Evaluation of genetic variability of the main economic and adaptive traits in provenance trials installed in Romania;
- Evaluation of the genotype x environment interaction;
- Analysis of the phenotypic correlations between economic and adaptive traits and between them and the geographic gradients of origin of the provenances;
- Analysis of the influence of climatic conditions on the biometric traits of Norway spruce provenances;
- Selection of the best Norway spruce provenances based on selection indices.

3. MATERIAL AND METHODS

3.1. Description of the Norway spruce provenance trials

The study material consists of 81 Norway spruce provenances, of which ten are Romanian and 71 from 12 other European countries: Austria (11), Finland (13), France (10), Switzerland (8), Germany (4), Sweden (6), Norway (5), Bulgaria (2), Italy (3), Poland (3), Hungary (3) and the Czech Republic (3).

The data were obtained from three provenance trials: Dorna Candrenilor, Zărnești, and Turda, installed in 1972 by Nițu and Gruescu [121]. Initially, there were four such trials, but in 1998, the Novaci comparative area was decommissioned due to windfall. Data about these trials are shown in Table 1, and their location in Fig. 1.

The provenances cover the natural and artificial range of the species in Europe, from 41.6° to 63.28° North latitude and from 6.03° to 34.62° East longitude. Also, from an altitudinal point of view, the provenances tested are from 20 m (some provenances from Germany, Sweden, and Finland) to 2000 m (provenance 98-Rodopi Smolian, from Bulgaria). Regarding the climatic conditions for the period 1901-1970, the provenances are from places where the average annual temperature is between 1.7 and 10 °C, and the amount of annual precipitation is between 450 and 2400 mm (Fig. 2).

Depending on the geographical regions of origin, they were divided into 11 groups: 1. Northern Europe, 2. North-East Germany, 3. North-East Poland, 4. Bohemian Plateau, 5. French (Jura and Vosges Mountains), 6. Western Alps, 7. Central Alps, 8. Eastern Alps, 9. Western Carpathians, 10. Eastern Carpathians and 11. Bulgarian (Rila and Rhodope Mountains). The grouping of provenances is represented in Fig. 1, and details about the provenances are shown in Table 2.

Table 1. Comparative trials with Norway spruce provenances installed in 1972

Trial	Dorna Candrenilor	Zărnești	Turda
Provenance region	A210 – Eastern Oriental Carpathians, Norway spruce forests	C120 - Northern Meridional Carpathians, Beech and conifers mixed forests	E310 – Eastern Apuseni Mountains, Norway spruce forests
Altitudinal vegetation layer	FM2 – Montane layer of beech and conifers mix	FM2 - Montane layer of beech and conifers mix	FM3 - Montane layer of Norway spruce forests
Forest site type	3333 – Mountain of mixes, Bs, big brown edaphic with *Asperula - Dentaria*	3322 – Mountain of mixes, Bm(i), brown podzolised or cryptopodzolic, medium edaphic with *Festuca + Calamagrostis*	2332 – Montane of Norway spruce forests Bm, brown edaphic acid sub medium with *Oxalis-Dentaria* + acidophiles
Soil type	3301 – Districambosoil	4101 – Prepodzol	3201 – Districambosoil
Slope	20° - 30°	25°- 30°	20°- 30°
Exposition	V	SV	NV
Area (ha)	3,40	2,67	3,43
Lat. N	47,20	45,50	46,50
Long. E	25,33	25,33	23,75
Altitude (m)	940-1040	1050-1250	1230-1340
Mean Annual Temperature (°C) 1972-2020	5,4	5,4	4,6
Sum of annual precipitations (mm) 1972-2020	749	927	757

Fig. 1. Geographic location of Norway spruce provenances and trials

Dots and numbers represent the provenances, and the triangles represent the trials.

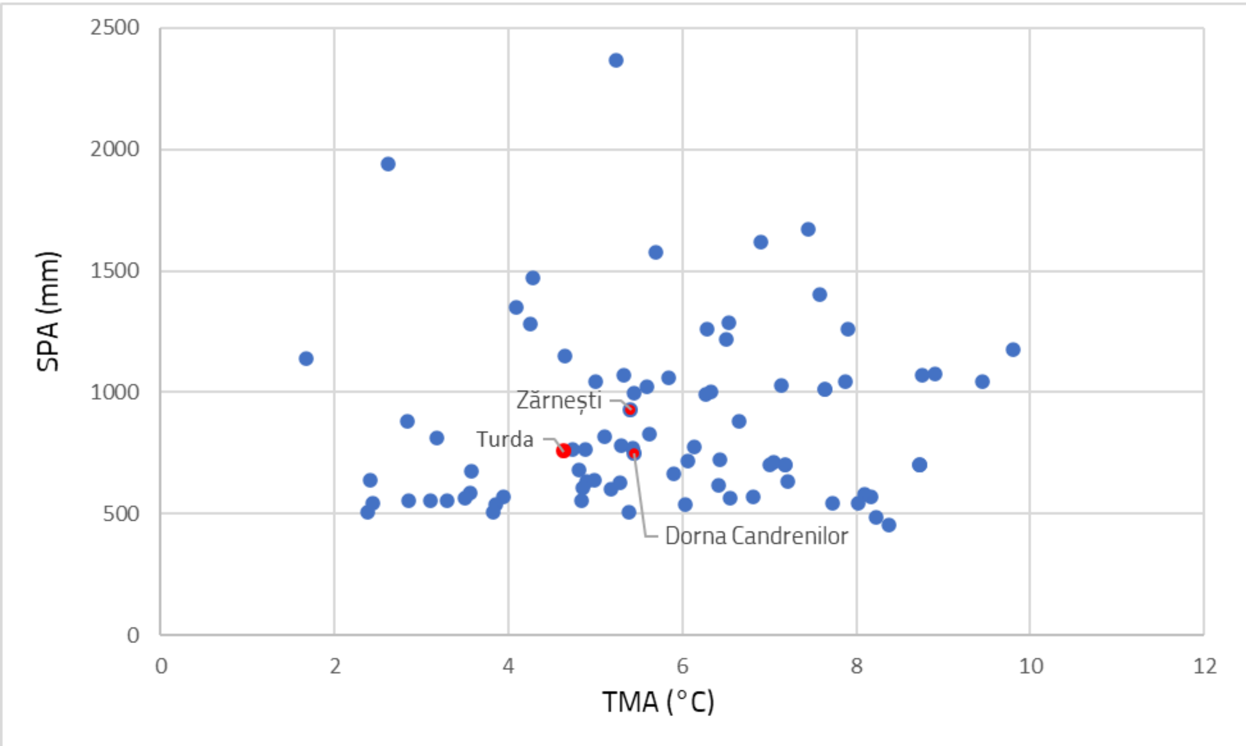


Fig. 2. Mean annual temperature (TMA) and the sum of annual precipitation (SPA) from the sites of origin of the provenances for the period 1901-1970 (blue dots) and from the test sites for the period 1972-2020 (red dots)

Table 2. Norway spruce provenances tested in the three trials

Number of provenance	Name of provenance	Country	Group	Lat. N	Long. E	Altit.
1	Senum	Norway	Northern	58.67	7.75	390
2	Branstad	Norway	Northern	58.47	8.70	45
3	Sandar	Norway	Northern	59.20	10.18	50
4	Bagstad	Norway	Northern	59.97	10.63	160
5	Seljord	Norway	Northern	59.45	8.73	120
6	Straiture I	France	French	48.12	6.93	650
7	Straiture II	France	French	48.12	6.93	650
8	La Ganne	France	Western Alps	45.73	6.33	900
9	Mignovillard III	France	French	46.75	6.20	1000
10	Plan de Cosaques	France	French	46.48	6.10	1170
11	Morzine	France	Western Alps	46.20	6.80	1750
12	Lantosque	France	Western Alps	43.95	7.40	1500
13	Saint Laurent II	France	French	46.57	6.03	960
14	Plan Bois	France	Western Alps	46.32	6.45	500
15	Gerardmer I	France	French	48.18	6.90	650
18	Eptingen	Switzerland	Central Alps	46.78	8.58	1040
19	Kerns	Switzerland	Central Alps	46.42	8.67	1460
20	Le Brassus	Switzerland	Central Alps	46.50	9.17	1310
21	Lukmenier	Switzerland	Central Alps	46.33	9.33	1500
23	Stampa	Switzerland	Central Alps	46.25	7.67	1600
24	Tagevillen	Switzerland	Central Alps	47.50	8.83	520
25	Wassen	Switzerland	Central Alps	46.70	8.58	1160
26	Winterthur	Switzerland	Central Alps	47.50	8.75	545
27	Bodenseichen	Germany	NE Germany	52.78	14.00	80
30	Kiekindermarx	Germany	NE Germany	53.42	11.75	86
31	Brmenhagen	Germany	NE Germany	54.33	12.58	20
32	Gandenitz	Germany	NE Germany	53.17	13.42	25
33	Wigry	Poland	NE Poland	53.92	23.00	130
34	Borki	Poland	NE Poland	54.08	22.08	160
35	Bialowieza	Poland	NE Poland	52.67	23.83	150
36	Brajes	Italy	Eastern Alps	46.25	12.00	1425
37	Latemar	Italy	Central Alps	46.17	11.00	1700
38	Val Di Fiemme	Italy	Central Alps	46.03	10.00	1350
39	Klaunz Bannwald	Austria	Eastern Alps	47.00	12.57	1750
40	Wietersdf	Austria	Eastern Alps	47.25	14.53	800
41	Eppenstein	Austria	Eastern Alps	47.15	14.73	965
42	Rotlgut Liezen	Austria	Eastern Alps	47.53	14.25	800

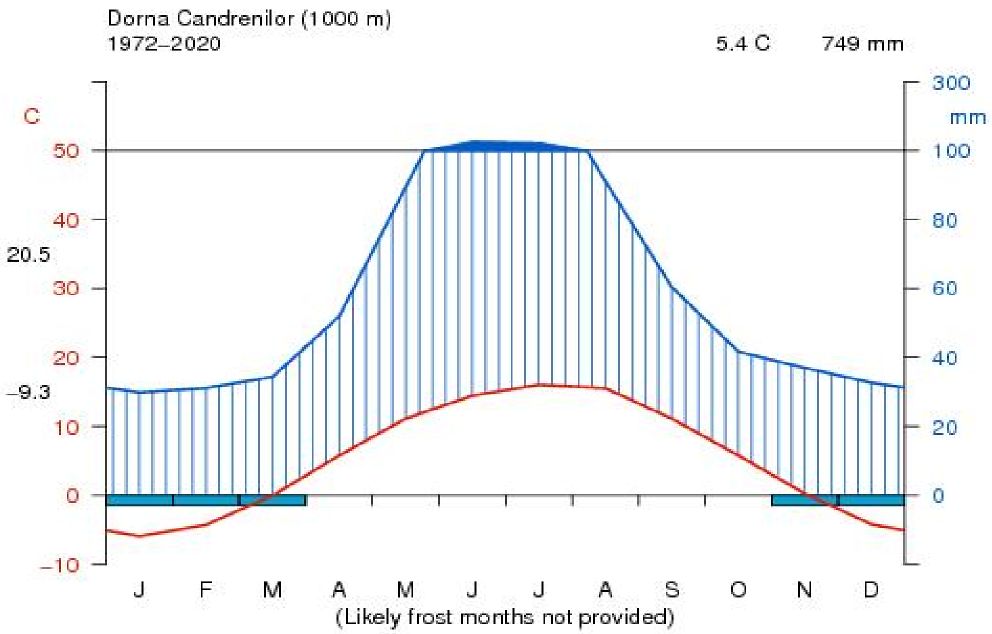
45	Hollenburg	Austria	Eastern Alps	46.32	14.13	1125
48	Strabwalchen	Austria	Eastern Alps	47.63	13.25	650
49	Redl-Zipf-Fuchsberg	Austria	Eastern Alps	48.02	13.45	550
50	Hoyos-Ernest-reith	Austria	Eastern Alps	46.67	15.65	530
51	Herfenberg	Austria	Bohemian	48.53	14.18	750
52	Sandl-bei-Freistadt	Austria	Bohemian	48.53	14.67	975
53	Neustift	Austria	Eastern Alps	47.63	16.45	620
54	Kolarp	Sweden	Northern	57.55	13.12	160
55	Munkahus	Sweden	Northern	58.20	11.88	20
56	Anfasterod	Sweden	Northern	58.20	11.88	50
57	Mossebo	Sweden	Northern	57.45	13.45	260
58	Aspas	Sweden	Northern	58.27	13.45	170
59	Nytthan	Sweden	Northern	59.68	15.08	115
60	Keletbukki Allami	Hungary	Western Carpathians	48.50	20.37	300
61	Nyugatbukki Allami	Hungary	Western Carpathians	48.50	20.37	300
63	Nyugatbukki Allami	Hungary	Western Carpathians	48.50	20.37	300
64	Gheorghieni	Romania	Eastern (Romanian) Carpathians	46.62	25.75	1000
66	Marginea	Romania	Eastern (Romanian) Carpathians	47.77	25.83	670
67	Frasin	Romania	Eastern (Romanian) Carpathians	47.47	25.80	760
68	Breaza	Romania	Eastern (Romanian) Carpathians	47.53	25.33	1250
70	Coşna	Romania	Eastern (Romanian) Carpathians	47.30	25.17	1025
71	Moldovi a	Romania	Eastern (Romanian) Carpathians	47.37	25.57	980
72	Dorna Candrenilor	Romania	Eastern (Romanian) Carpathians	47.28	25.25	1000
73	Stulpicani	Romania	Eastern (Romanian) Carpathians	47.42	25.75	980
74	Galu	Romania	Eastern (Romanian) Carpathians	47.25	25.42	650
75	Broşteni	Romania	Eastern (Romanian) Carpathians	47.15	25.72	940
82	Sund	Finland	Northern	60.00	20.50	20
83	Bramarv	Finland	Northern	60.22	23.33	20
84	Pihtipudas	Finland	Northern	63.28	25.45	165
85	Heinola	Finland	Northern	63.15	26.00	275
87	Kourevesi	Finland	Northern	61.17	24.83	100
88	Pualanka	Finland	Northern	62.00	28.17	140
89	Pielisjarvi	Finland	Northern	60.42	22.83	50
90	Mantta	Finland	Northern	62.02	24.67	120
91	Jokioinen	Finland	Northern	62.00	23.33	190

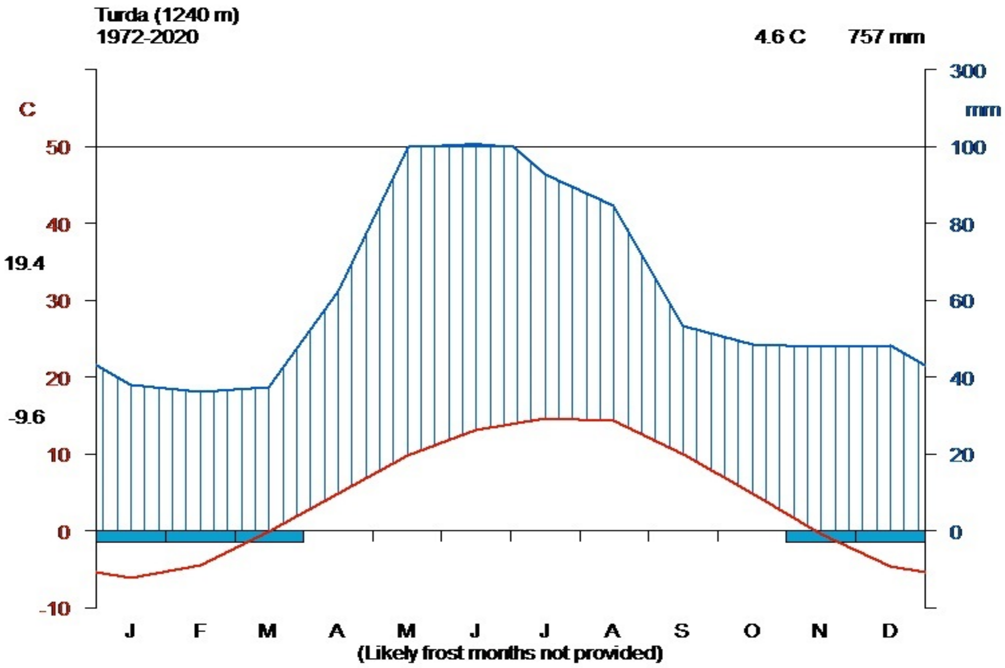
92	Padasjoki	Finland	Northern	60.85	25.33	85
93	Urjala	Finland	Northern	60.92	23.50	130
94	Janakkala	Finland	Northern	61.33	24.67	100
95	Tuusula	Finland	Northern	61.03	24.90	120
96	Rila	Bulgaria	Bulgarian	42.20	23.63	1300
98	Rodopi Smolian	Bulgaria	Bulgarian	41.60	24.62	2000
99	Zelesna Ruda	Czech Republic	Bohemian	49.17	13.25	850
100	Kasperske Hory	Czech Republic	Bohemian	49.63	13.58	650
101	Valke Karlovice	Czech Republic	Western Carpathians	49.35	18.32	780

The comparative trials analysed were established in three Forestry Inspectorates (Directorates), located in the Western, Southern and North-Eastern Carpathians of Romania, in the montane layer of beech and resinous mixtures (Dorna Candrenilor and Zărnești), and the montane layer of Norway spruce trees (Turda).

There are differences regarding the climatic conditions of the comparative trials: continental climate with Scandinavian-Baltic influences in the North (Dorna Candrenilor) and temperate continental with oceanic influences in the West (Turda) and the central part of the country (Zărnești) [122], [123].

The climate diagrams of the comparative trials for the period 1972-2020 were made with the help of the *climatol* package in R [124], according to the model proposed by Walter and Lieth [125] (Fig. 3).





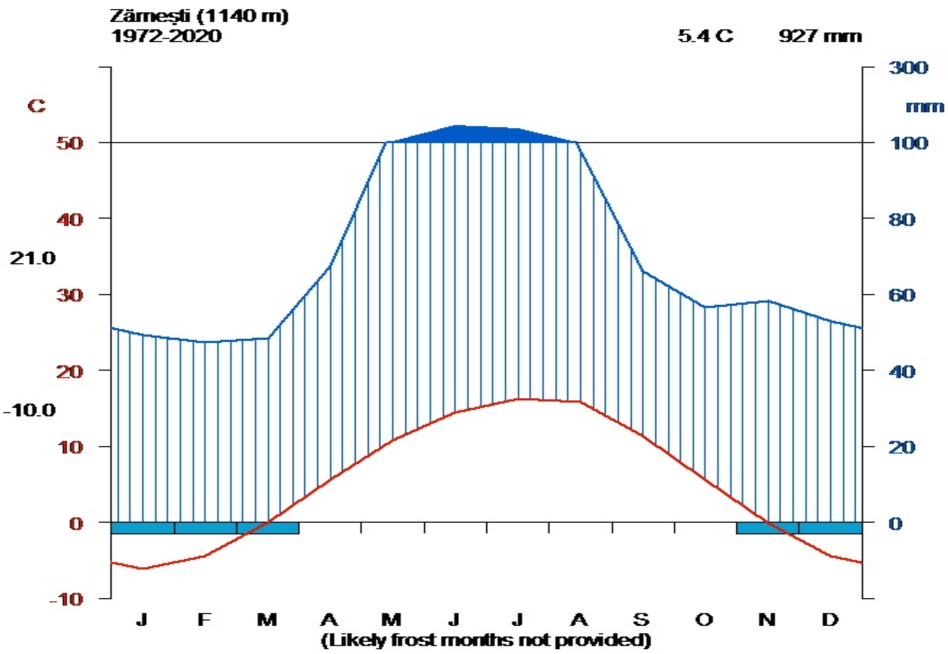


Fig. 3. Climate diagrams for the three comparative trials for the interval 1972-2020

J-D – calendar months

The provenances were planted in a balanced square lattice statistical device with 9 x 9 provenances and three replicates. The grid is a layout obtained by grouping variants into overlapping incomplete blocks (short lines). Balancing requires each variant/provenance to encounter each of the others in the same repetition, thus requiring a certain number of repetitions [126]. The size of the unit plots is 16 individuals (4 x 4), with a planting scheme of 2 x 2 m.

The distribution of provenances within the repetitions allows the elimination of soil differences between the repetitions, and the double arrangement of the variants in blocks and columns eliminates site differences within the repetitions.

3.2. Measurements and observations

The measurements and observations were carried out in the fall of 2020, 49 years after planting, representing approximately half of the age of exploitation of the Norway spruce in Romania. The traits analysed to assess adaptive variation were total height (HT), height to the first green branch (pruned height) (HE), diameter at breast height (D1.30), survival percentage (Suprav), trunk shape, branching, annual radial growth– ring width (CA), latewood (LTA) and earlywood (LTI); latewood percentage (LTP) and conventional wood density (DCL).

HT and HE were measured with Vertex IV, with an accuracy of 0.1 m, and D1.30m with a Haglöf calliper, with an accuracy of 0.1 cm. Survival percentage was calculated by relating the number of trees remaining at age 49 to the number of trees planted in each unit plot.

The number of remaining trees measured varied between 4 and 13 per plot (in repetition), and the number of trees per provenance varied between 12 and 31 per trial, which ensured the results were precise.

The shape of the trunk was evaluated using three indices: 1 – rectilinear, without curves; 2 – with slight defects (curves in the same plane, looseness at the base); 3 – sinuous.

Stem forking was assessed using a forking index established with the help of two parameters. The first refers to the location of the branching on the tree trunk: 4 – unbranched, 3 – branched in the upper third, 2 – ~ half of the trunk and 1 – in the lower third. This parameter was multiplied by 10 and the obtained value was divided by the number of stems [127].

The conventional wood density, expressed in g/cm^3, was calculated for each core using the formula proposed by Dumitriu-Tătăranu et al [128]:

$\rho c = 1/[(Mmax/Mo) - 1 + 1/\rho ml]$,

where: ρc = conventional density (g/cm^3),

Mmax = mass of the saturated sample (g),

Mo = dry sample mass (g),

ρml = wood density (1.53 g/cm3).

To extract cores, four trees were selected based on the mean diameter from each provenance in each replicate. Using the Haglöf growth drill, one core was extracted at breast height from each tree on the slope line to avoid compression and tension wood.

The cores were then left to dry and progressively sanded. The Epson Expression 12000XL scanner was used to obtain high-resolution images of the cores (1200 dpi). Radial growths were measured with the *CooRecorder* software [129].

For each comparative trial, annual growth series were checked and inter-dated using the *dplR* package [130] in the free software environment R [131]. Annual growth series with intercorrelation values (average correlation coefficient between different cores) below 0.328 ($p>0.05$) were excluded from the analysis. The final number of annual growth series was 2709: 947 for Dorna Candrenilor, 906 for Zărnești and 856 for the comparative trials Turda.

The standardisation was done with the help of the *detrendeR* package [132]. Through standardisation, the influence of natural biological growth of trees, the influence of age, is estimated and removed to obtain stationary index series with mean one and relatively constant variance [133].

The spline function was used, with a length of the oscillation period equal to two-thirds of the series length (number of years of the series). Standardised increments were abbreviated as annual increment (iCA), late wood (iLTA) and early wood (iLTI).

Climate data for the period 1972–2020 were obtained using the Climate Downscaling Tool (*ClimateDT*) [134]. Except for minimum and maximum monthly temperatures, all other climate variables were used to assess the link between climate and annual increases in diameter.

The altitude-corrected latitude (Lat_c) was calculated using the formula [135]:

Lat_c = latitude + altitude/100,

where: latitude is expressed in centesimal degrees and altitude in meters.

To determine years in which meteorological droughts occurred, the Standardized Precipitation Evaporation Index (SPEI) [136] was calculated based on precipitation and potential evapotranspiration (PET) from 1972-2020, using the *SPEI* package [137]. The equation proposed by Thornthwaite [138] was used to calculate the PET, using the temperature data.

SPEI was evaluated at three months, SPEI-3, and the years in which values lower than -1 were obtained for this index were classified as follows: between -1.00 and -1.49 – moderate drought; between -1.50 and -1.99 – severe drought; and for values below -2.00 – extreme drought.

To verify that the extreme years identified based on SPEI-3 were indeed years in which trees were affected, the analysis of pointer years in the *dplR* work package was used based on the algorithm of Becker et al. [139]. The term " pointer year" defines the years in which a good part of the trees shows very small annual growth (negative pointer year) or very high (positive pointer year) [133], [140]. A threshold of at least 60% of the affected trees was set to determine whether a year is a pointer.

3.3. Statistical analyses

Genetic variability for each trait was analysed for each provenance trial and across trials.

For the analysis of genetic variability in each trial, a linear mixed model was used, adapted from the model proposed by Nanson [141] where provenance was considered as a random factor, and group and repetition as fixed factors:

$Y_{ijk} = \mu + G_i + P_j + R_k + P_j \times R_k + e_{ijkl}$, (1)

where:

μ is the overall mean,

G_i is the effect of group i,

P_j is the effect of provenance j,

R_k is the effect of repetition k,

$P_j \times R_k$ is the provenance x repetition interaction, and eijkl is the error term associated with the ijkl tree.

A factor is considered fixed if the interest is centred on concrete/specific levels of the factor included in the experiment, repetition, group, and locality in our case. A factor is considered to be random if the levels included in the experiment represent a sample of a larger population and the implications of the study follow the entire population or the future performance of the levels [77].

The provenance x repetition interaction was not statistically significant, so it was dropped from the model. The *lmerTest* package was used to calculate and test the linear mixed models [142].

The analysis of genetic variability across all trials was based on the following linear mixed model, where provenance and the provenance x trial interaction were considered random factors and trials as a fixed factor [141]:

$Yijk = \mu + Ci + Pj + Rk + Ci \times Pj + eijkl$

where: μ is the overall mean,

Ci it is the effect of trial i,

Pj is the effect of provenance j,

Rk is the effect of repetition k,

Ci x Pj is the provenance x trial interaction,

and eijkl is the error term associated with the ijkl tree.

Analysis of the genetic variability of tree resilience parameters was performed only at the level of each comparative trial, not at the level of all, considering that the effects of droughts and those after droughts vary between regions [143].

The analysis of performance stability, by calculating the correlation coefficients between the values of the same trait obtained in the provenance trials, represents another possibility to determine the influence of the provenance x trial interaction. Correlation coefficient values close to 1 indicate reduced interaction and higher stability.

The drought response of the provenances was evaluated by tree resilience parameters: resistance (Resist), recovery (Recup), resilience (Rezil) and relative resilience (Rel. rezil) [144].

Resistance is the ratio of growth in the year with extreme drought to growth in the previous period (extreme year CA / previous CA). Values above 1 indicate high tolerance, and values below 1 indicate low tolerance.

Recovery reflects the ability to revitalise after an episode of drought. It is the ratio of CA after drought to CA during drought (CA after extreme year / CA extreme year).

Resilience expresses the ability to return to pre-drought CA values. It is the ratio of CA after drought to CA before drought (CA after extreme year / CA before). Subunit values indicate reductions in growth with long-term effects.

Relative resilience is resilience considering the impact of the drought year ((CA after extreme year - CA extreme year) / CA before).

After and before drought growths were calculated as averages of the three-year growths before and after the year in which the extreme drought occurred.

Pearson correlation coefficients were used to analyse the correlations between the geographical gradients of the provenances tested, the wood traits, and the resilience parameters of the trees, to examine the extent to which the variation of the traits is influenced by the local adaptation to the climatic conditions of the place of origin.

The *treeclim* package [145] was used for moving window correlation analysis in each comparative trial. Mobility has been defined as a change in the magnitude or direction of the association between variables over time [146]. The climate variables used for this analysis were the monthly values of each year from March to September (growing season) for the interval 1981–2020. 25-year sub-periods were analysed, each starting one year later, resulting in 16 sub-periods.

Climatic response functions describe the correlation between a tree population's quantitative trait and the planting sites' different climatic conditions. The specific objective of using response functions is determining the climatic conditions under which the maximum value for the trait of interest can be obtained (or minimum, depending on the trait) [147]. The function was of the quadratic type:

$z = a + b*x^2 + c*y$,

where: z is the trait,

a, b and c are the regression coefficients,

x and y are the temperature/precipitation variables.

Response functions were constructed for latewood percentage, using annual climate data for each comparative trial, to analyse the impact of climate in each comparative trial on provenance performance. The response functions for total height and diameter at breast height were performed at the level of the three trials and the mean values of the climatic variables from the comparative trials for the period 1972-2020 were used.

Given the assumption that tree populations are adapted to local climatic conditions, transfer functions analyse correlations between quantitative traits and climatic differences between the planting site and the site of origin [147].

Transfer functions were performed for total height and survival percentage in each comparative trial, using the differences between the climatic variables of the planting site and those of the place of origin.

Using the *caret* package [148], a model with a single constant term was first defined for both the response and transfer functions. Then, the step-by-step regression method was carried out. After identifying the most significant variables, several quadratic models were made because they are considered more appropriate [149], [150], [151]. The final models were selected according to the adjusted R^2 coefficient.

3D plots of response and transfer functions were made using SigmaPlot 12.5 [152]

The selection of Norway spruce origins was made with the help of the indices:

- MGIDI (Multitrait Genotype-Ideotype Distance Index) [153] in each comparative trial; and

- MTSI (Multi-Trait Stability Index) [154], at the level of all trials in the *metan* package [155].

The analysis of a linear mixed model was necessary to estimate the variance parameters based on the Restricted Maximum Likelihood (REML) method and to obtain the BLUP (best linear unbiased prediction) index values of each provenance, which is then used to calculate the indices MGIDI and MTSI.

The group effect in model (1) was discarded in calculating the MGIDI index. The ideotype was proposed to have its values for D1.30m, HE, HT, and Suprav as high as possible [156]. The selection intensity was 15%; that is, 12 of the 81 provenances were selected.

The MGIDI index is calculated based on the following equation [153]:

$$MGIDI_i = \left[\sum_{j=1}^{f}(y_{ij} - y_j)^2\right]^{0.5},$$

Where MGIDIi is the multi-trait genotype-phenotype distance index for provenance i, yij is the score of provenance i in factor j, and yj is the ideotype score.

The lower the MGIDI value of a provenance, the closer it is to the proposed ideotype and has trait values close to the intended goal.

MTSI estimation was performed using the equation [154]:

$$MTSI_i = \left[\sum_{j=1}^{f}(F_{ij} - F_j)^2\right]^{0.5},$$

where:

MTSIi = the multi-trait stability index for provenance i;

Fij = score of provenance i;

Fj=ideotype score.

The lower the value of the MTSI index for a provenance, the closer it is to the ideotype and has high stability and performance for the analysed traits. The calculation of indices based on the selection of several traits simultaneously was carried out with the help of the *metan* package [155] in the free R software environment.

After the model for MTSI was established, different scenarios for stability and performance weights (from 100/0 to 0/100) were run and plotted. The origins were grouped into four categories:

1. Performant and stable

2. Performant, but unstable

3. Underperforming, but stable

4. Underperforming and unstable.

4. RESULTS AND DISCUSSION

4.1. Genetic variability of the main economic and adaptive traits

The results of the linear mixed model for the traits analysed in each comparative Norway spruce trial 49 years after planting are presented in Table 3.

Table 3. Results of the linear model for the traits analysed in each Norway spruce provenance trial at 49 years

	Trait	LRTp	Vp	Vr	MS g	MS b	Mean ± SD
Dorna Candrenilor	D1,30m	5.07*	0.56	28.87	264.06***	15.19ns	23.75 ± 5.58
	HT	55.39***	0.07	8.14	108.68***	62.44***	25.90 ± 3.24
	HE	152.53***	0.62	3.44	33.74***	104.27***	16.74 ± 2.21
	Suprav	12.31***	34.31	104.5	680.76***	533.53**	49.97 ± 13.73
Zărnești	D1,30m	0.44ns	0.14	22.24	49.73*	82.91*	21.14 ± 4.76
	HT	21.55***	0.6	11.12	50.90***	206.67***	21.43 ± 3.53
	HE	98.84***	1.16	6.31	44.59***	322.91***	10.96 ± 2.95
	Suprav	0ns	0	178.2	365.38*	504.92ns	40.66 ± 13.71
Turda	D1,30m	0ns	0	30.12	151.61***	25.25ns	21.57 ± 5.57
	HT	14.35***	0.49	9.45	64.60***	58.99**	21.48 ± 3.28
	HE	55.53***	0.94	7.04	18.22*	24.78*	11.21 ± 2.86
	Suprav	0.16ns	4.5	160.27	880.02***	888.61**	36.78 ± 14.22

*, **, ***: Significant at 5%, 1% and 0.1%, respectively; ns: not statistically significant, p>0.05; LRTp – likelihood ratio test for provenance effect; Vp – variance for provenance random effect; Vr – residual variance; MS – mean squares for group (g) and block (b); D1,30 – diameter at breast height; HT – total height; HE -prunned height; Suprav – survival rate

Differences between groups were significant for all traits in all three comparative trials. The differences between provenances were significant for all traits in the trial Dorna Candrenilor. In the other two trials, differences between provenances were not significant for diameter at breast height and survival percentage.

Given the extensive areas occupied by the comparative trials, there was heterogeneity within each trial. The effect of repetition was significant for almost all traits in all trials. The exceptions were the survival percentage in the Zărnești trials and the diameter at breast height in the Dorna Candrenilor and Turda trials. A substantial effect of repetition was also obtained in the study of two comparative Norway spruce trials from Romania [157].

4.1.1. Diameter at breast height

The highest value of average D1.30m, in the comparative trial Dorna Candrenilor, was obtained by provenance 51-Herfenberg, from the Bohemian Plateau (28.24 ± 1.12 cm), followed by provenances from the Eastern Carpathians (of Romania): 74-Galu, 66-Marginea and 72-Dorna Candrenilor; and provenance 49-Redl-Zipf-Fuchsberg, from the Western Alps. The provenances from Northern Europe – 83-Bramarv, 84-Pihtipudas, 2-Branstad and 87-Kourevesi and from the Western Alps – 11-

Morzine, were the ones with the lowest performances, in terms of D1.30 m, with values between 18.16 ± 0.88 and 20.09 ± 1.33 cm (Fig 4).

In the Zărnești trial, the Northern Europe provenance 83-Bramarv had the highest average D1.30m, followed by the provenances 50-Hoyos-Ernest-reith and 53-Neustift, from the Eastern Alps, 60-Keletbukki Allami, from the Western Carpathians, and 25-Wassen, from the Central Alps. The lowest values of D1.30 m were obtained by provenances 11-Morzine, from the Western Alps, 33-Wigry, from NE Poland, 4-Bagstad, 94-Janakkala and 90-Mantta, from Northern Europe, the values being included between 17.32 ± 0.92 and 19.03 ± 1.24 cm.

The provenances 70-Coșna and 67-Frasin, from the Eastern Carpathians, had the highest mean D1.30m in the comparative trial Turda. They were followed by the provenances 60-Keletbukki Allami, from the Western Carpathians, 25-Wassen and 19-Kerns, from the Central Alps. The lowest values were obtained by the provenances from Northern Europe - 93-Urjala, 94-Janakkala, 83-Bramarv, 58-Aspas and 95-Tuusula, between 15.84 ± 1.13 and 18.80 ± 1.09 cm.

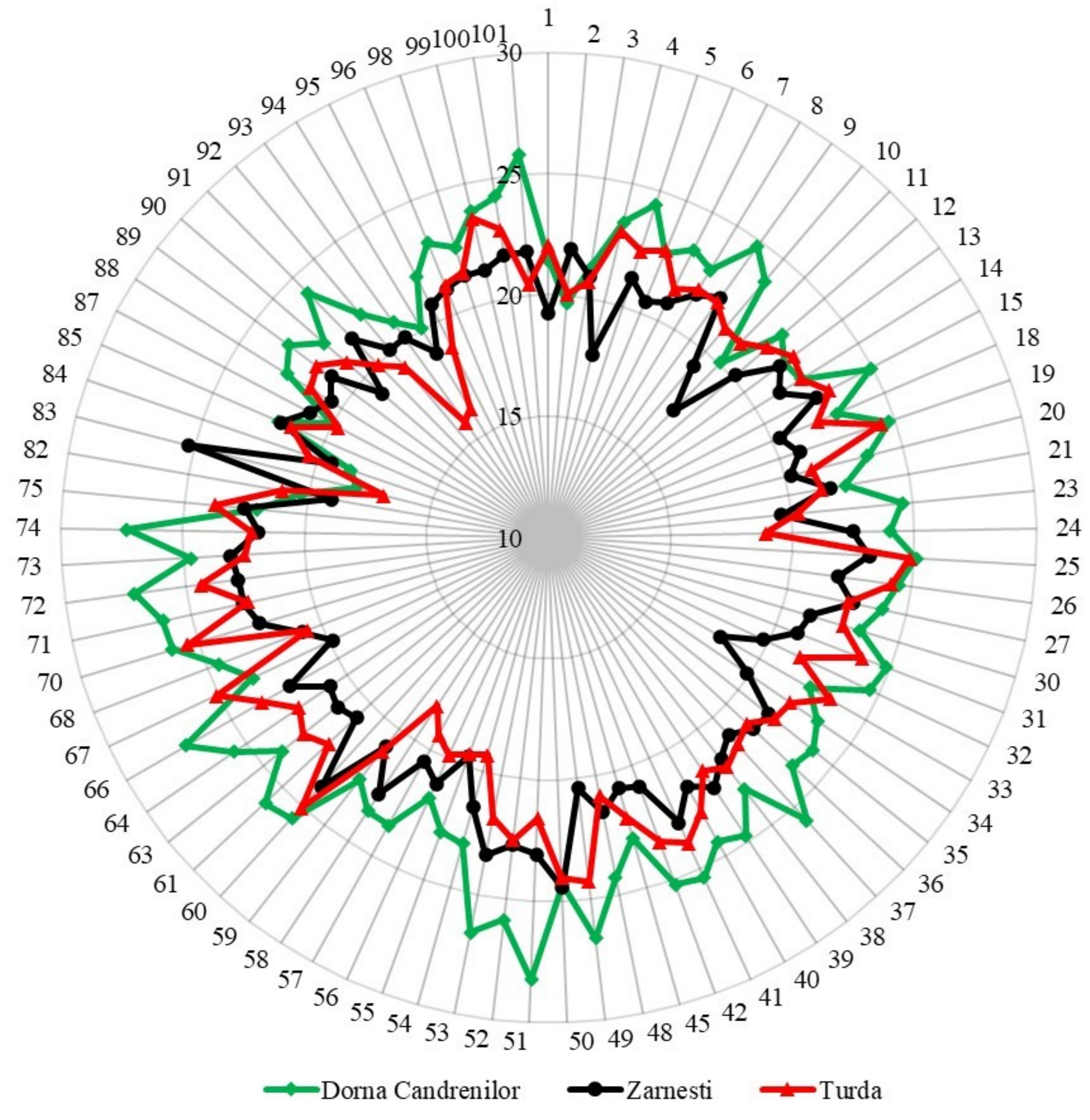


Fig. 4. Variation of diameter at breast height of Norway spruce provenances in each comparative trials at the age of 49 years

4.1.2. Total height

In the Dorna Candrenilor comparative trial, the Romanian provenances 72-Dorna Candrenilor, 66-Marginea, 64-Gheorghieni, 74-Galu, 70-Coșna and 71-Moldoivița obtained the highest total height values, between 29.48 ± 0.36 and 28.31 ± 0.47 m. Provenances from Northern Europe, 84-Pihtipudas, 83-Bramarv, 93-Urjala and 94-Janakkala, as well as 14-Plan Bois, from the Western Alps, had the lowest total heights (Fig. 5).

The provenance 75-Broşteni, from the Eastern Carpathians, had the highest total height value in the comparative Zărnești trial. The next good performing provenances were: 60-Keletbukki Allami from the Western Carpathians, 51-Herfenberg from the Bohemian Plateau, 39-Klaunz Bannwald from the Eastern Alps and 26-Winterthur from the Central Alps, with values between 23.72 ± 0.62 and 23.46 ± 0.51 m. The lowest values were obtained by provenances 33-Wigry from NE Poland, 11-Morzine from the Western Alps, provenances 82-Sund and 4-Bagstad from Northern Europe, and 18-Eptingen, from the Central Alps, the total heights being between 18.16 ± 0.89 and 18.93 ± 0.66 m.

With a total height of 24.46± 0.51 m, the 25-Wassen provenance from the Central Alps was the best in the Turda trial. It was followed by 66-Marginea and 70-Coșna from the Eastern Carpathians, 60-Keletbukki Allami from the Western Carpathians, and 99-Zelesna Ruda from the Bohemian Plateau. The Northern European provenances 83-Bramarv, 94-Janakkala and 93-Urjala had the lowest total height values.

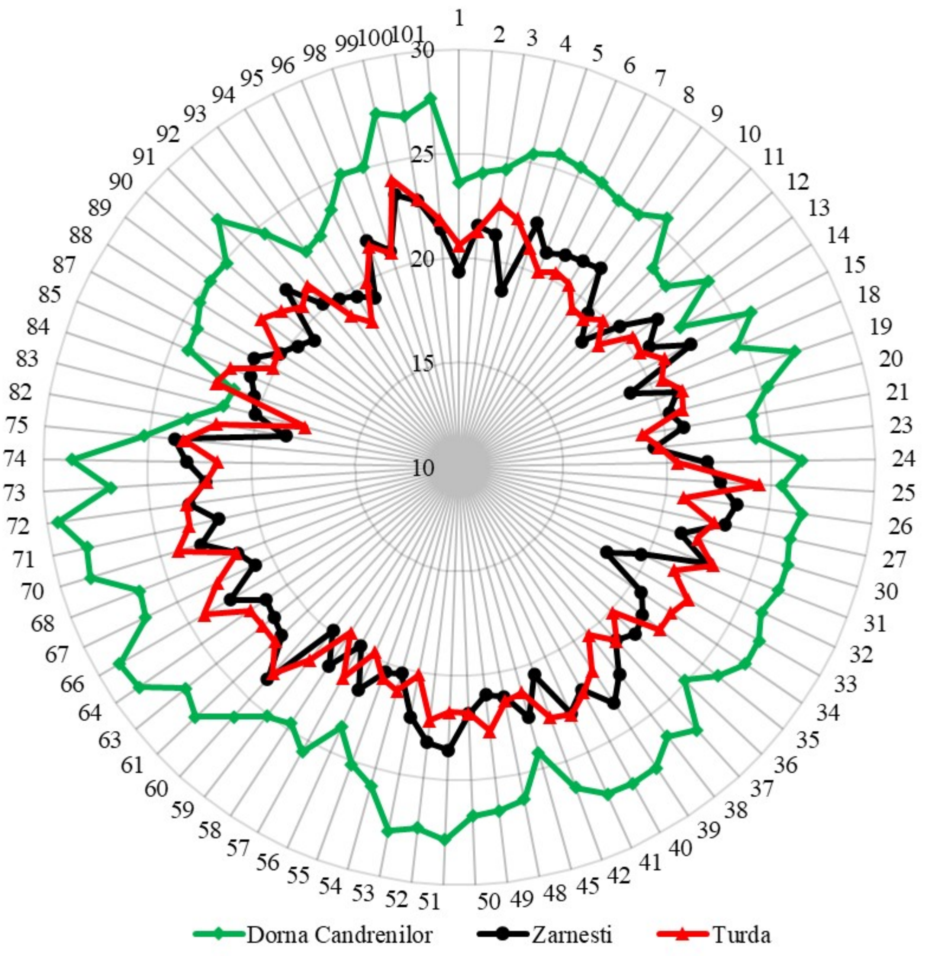


Fig. 5. Variation of the total height of the Norway spruce provenances in each comparative trials at the age of 49 years

4.1.3. Pruned height

The highest average value of the pruned height in the comparative trial Dorna Candrenilor, was 18.74 ± 0.30 m, obtained by provenance 39-Klaunz Bannwald, from the Eastern Alps. Provenance 40-Wietersdf, from the same group and three other provenances from the Eastern Carpathians, were the following, with values ranging between 18.59 ± 0.46 and 18.34 ± 0.41 m. Provenances from Northern Europe, 88-Pualanka, 93-Urjala, 95-Tuusula, 83-Bramarv and 82-Sund had the lowest values, between 13.33 ± 0.58 and 14.17 ± 0.65 m (Fig. 6).

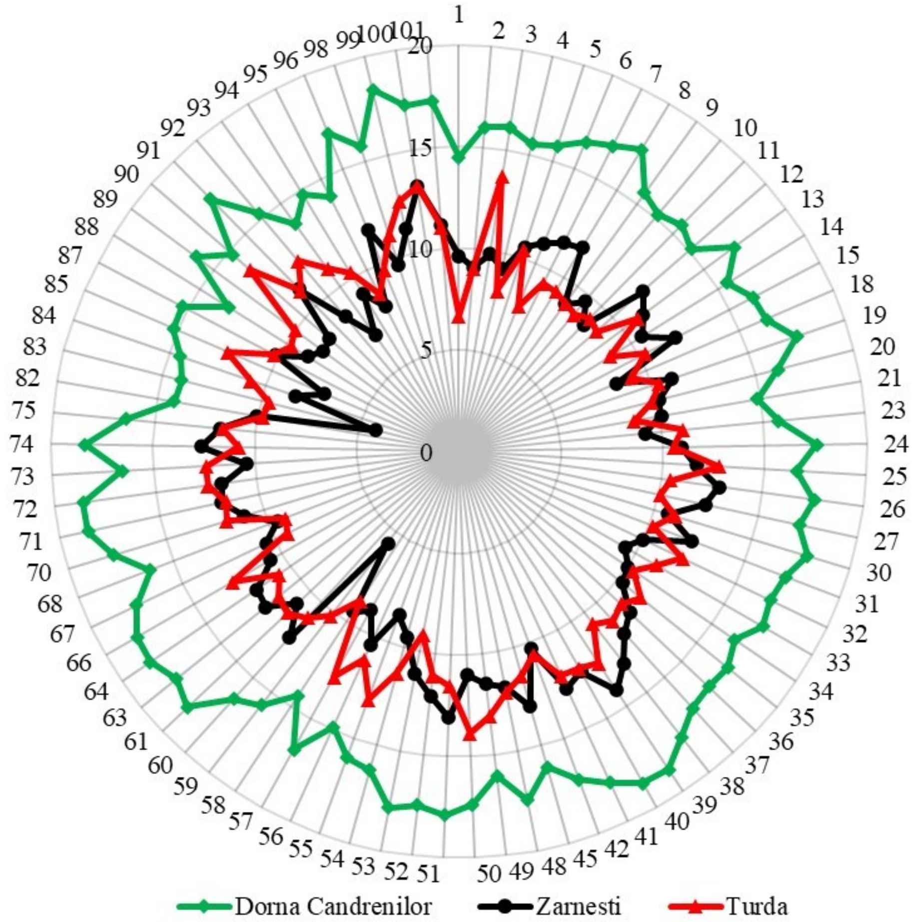


Fig. 6. The variation of the pruned height of the Norway spruce provenances in the comparative trials at the age of 49 years

In the Zărnești comparative trials, only five provenances had values above 13 m: 39- Klaunz Bannwald and 45- Hollenburg, from the Eastern Alps, 100-Kasperske Hory and 51-Herfenberg, from the Bohemian Plateau, and 38-Val Di Fiemme, from the Alps Central, with values between 14.06 ± 0.35 and 13.03 ± 0.36 m. Northern European provenances had the lowest values, below 8 m: 59-Nytthan, 93-Urjala, 85-Heinola, 95-Tuusula, and provenance 83-Bramarv had the lowest value, 4.22 ± 1.33 m.

In the Turda comparative trial, the provenances 50-Hoyos-Ernest-reith and 49-Redl-Zipf-Fuchsberg, from the Eastern Alps, 3-Sandar and 90-Mantta, from Northern Europe, as well as 100-Kasperske Hory, from the Bohemian Plateau, had pruned heights of over 13 m, between 13.87 ± 0.36 and 13.08 ± 0.65 m. Provenances that had small pruned heights were: 1-Senum, 4-Bagstad, and 95-Tuusula , from Northern Europe, 6-Straiture I, French and 21-Lukmenier, from the Central Alps, with values between 6.66 m ± 0.92 and 8.73 ± 0.70 m.

4.1.4. Survival percentage

In the comparative Dorna Candrenilor trial, the provenances 64-Gheorghieni and 70-Coșna, from the Eastern Carpathian group, had a survival percentage of 62.5%. Another 15 provenances had a percentage of 60.42%. The lowest values were recorded by provenances from the Northern Europe group: 88- Pualanka – 14.58%, 1-Senum - 20.83%, 5-Seljord - 25% and 90-Mantta - 27.08% (Fig. 7).

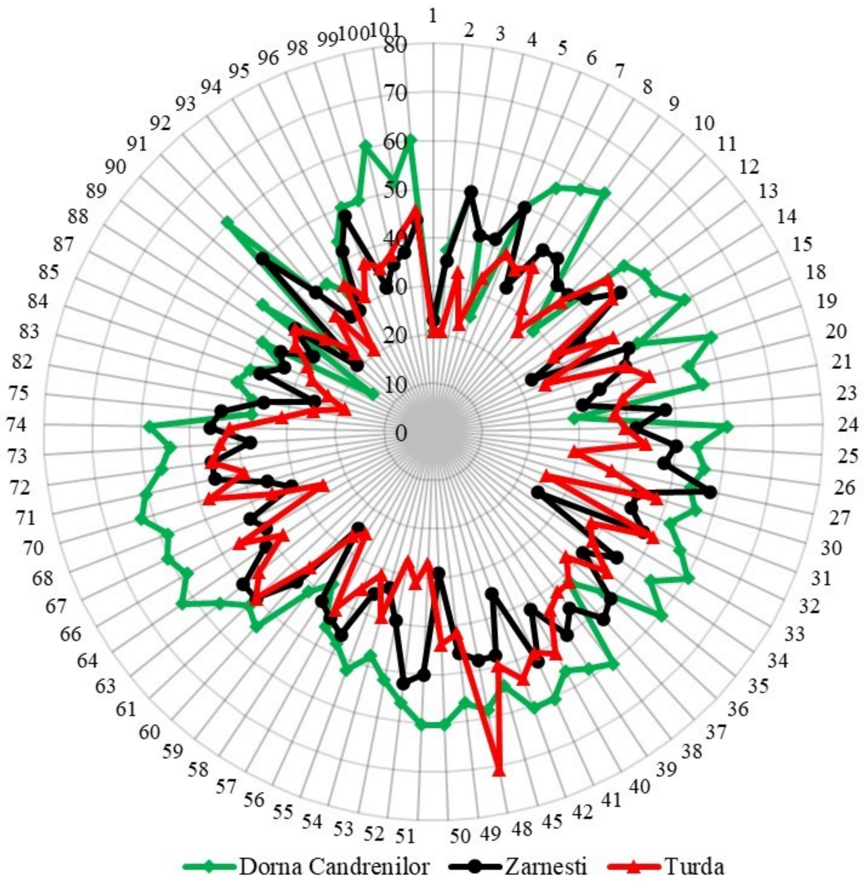


Fig. 7. Variation of survival percentage of Norway spruce provenances in each comparative trial at the age of 49 years

The 27-Bodenseichen provenance, from the NE Germany group, had a survival percentage of 58.33% in the Zărnești comparative trials. The provenances 52-Sandl-bei-Freistadt, from the Bohemian Plateau, 41- Eppenstein and 37-Latemar, from the Eastern Alps group, had a survival percentage of 52.08%. Another nine provenances had a 50% survival rate. The provenances 90-Mantta and 1-Senum, from the Northern Europe group, as well as the provenance 15-Gerardmer I, from the French group, had the lowest survival percentages, of 20.83% (provenance 90) and 22.92% (provenances 1 and 15). Only 25% was obtained by the provenance of 33-Wigry from NE Poland, 59-Nytthan and 83-Bramarv from the Northern Europe group.

The best survival percentage in the Turda trial, 70.83%, was obtained by provenance 48-Strabwalchen, from the Eastern Alps. Two other provenances from the same group, 42-Rotlgut Liezen and 40-Wietersdf, had survival percentages of 54.17% and 52.08%. Four provenances had a survival rate of 50%. Provenances from the Northern Europe group had the lowest survival percentages in this trial: 83-Bramarv - 18.75%, 1-Senum, 2-Branstad and 93-Urjala - 20.83%, and 84-Pihtipudas, 4-Bagstad and 91-Jokioinen - 22.92%.

4.1.7. Annual radial growths

Within each trial, there were significant differences between provenances and between years in terms of annual radial growths and latewood percentage (Table 4). The effect of repetitions was significant for all traits except CA in the Turda trial.

The interaction year x provenance was significant for CA and LTI in the Zărnești comparative trial and for CA, LTI, and LTP in the Dorna Candrenilor trial.

Variations in standardised annual radial growths and latewood percentage can be seen in Fig. 8.

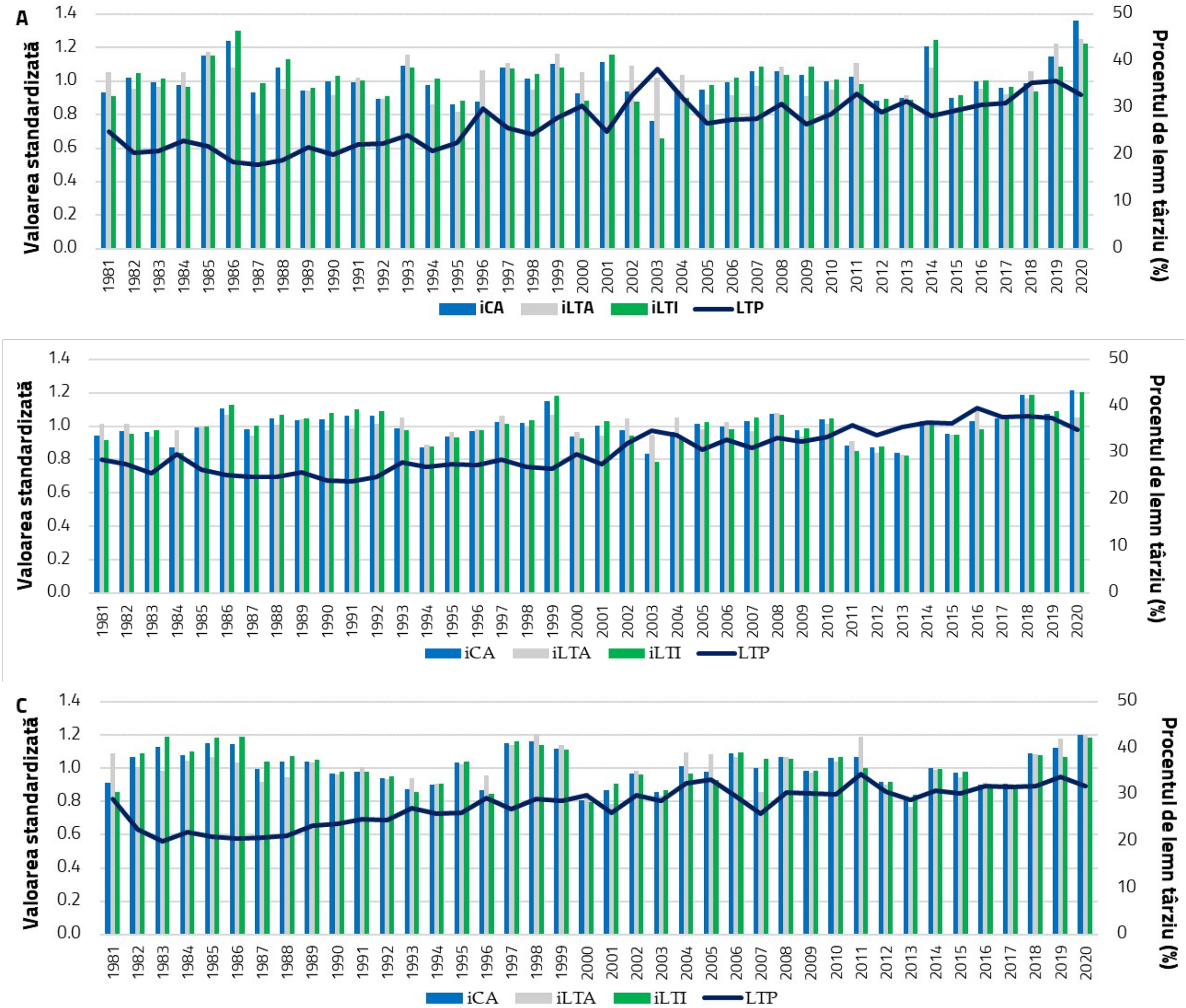


Fig. 8. The variation of the standardised annual radial growth and the average LTP per year in the Norway spruce provenance trials for the period 1981-2020; A - Dorna Candrenilor, B - Turda, C - Zărnești

For the analysed period, the CA average per trial was between 2.55 ± 0.19 mm, in the Zărnești trial and 2.81 ± 0.29 mm, in the Turda trial.

Table 4. Linear model results for annual increases in diameter and latewood percentage in each Norway spruce trial at 49 years

		LRTp	LRT an x prov	Vp	V an x prov	Vr	MS rep	MS an	Mean ± SD
Zărnești	CA	711,55***	66,98***	0,027	0,016	0,689	91,56***	1116,66***	2,55 ± 0,19 mm
	LTI	677,85***	84,63***	0,021	0,014	0,542	38,94***	739,12***	1,90 ± 0,17 mm
	LTA	376,41***	0,00 ns	0,002	0,000	0,115	11,12***	46,88***	0,65 ± 0,05 mm
	LTP	510,66***	0,00 ns	2,462	0,000	110,742	4583,10***	13944,90***	27,78 ± 1,65 %
Dorna Candrenilor	CA	712,85***	12,42***	0,027	0,007	0,798	47,88***	1996,86***	2,73 ± 0,18 mm
	LTI	579,62***	30,60***	0,018	0,009	0,624	12,07***	1310,91***	2,08 ± 0,14 mm
	LTA	639,68***	1,29 ns	0,003	0,000	0,093	16,98***	65,86***	0,66 ± 0,07 mm
	LTP	491,92***	26,37***	1,696	0,900	69,428	3207,50***	20586,80***	27,06 ± 1,54 %
Turda	CA	1259,9***	0,00 ns	0,064	0,000	1,074	2,09 ns	1315,16***	2,81 ± 0,29 mm
	LTI	1003,0***	0,00 ns	0,038	0,000	0,755	2,28*	835,49***	2,03 ± 0,22 mm
	LTA	996,03***	0,00 ns	0,005	0,000	0,120	0,66**	56,16***	0,78 ± 0,08 mm
	LTP	326,70***	0,00 ns	1,766	0,000	99,852	1389,3***	15916,00***	30,76 ± 1,62 %

, **, * – Significant for 5%, 1% and 0.1% probability of transgression; ns – insignificant, p > 0.05; LRTp, year x prov – likelihood ratio test for the effect of provenances and the interaction year x provenance; LTI – earlywood; LTA – latewood; LTP –latewood percentage; CA – annual growth; Vp, year x prov – the variance of the random effect of provenances and the interaction year x provenance; Vr – residual variance; MS rep – average of squares of sums for repetition; MS year – the average of the squares of the amounts for the year; SD – standard deviation.*

4.1.7.1. Ring width

The average CA value in the Dorna Candrenilor trial was 2.73 mm, with provenance values between 2.15 mm, provenance 83-Bramarv, and 3.11 mm, provenance 25-Wassen (Fig. 9).

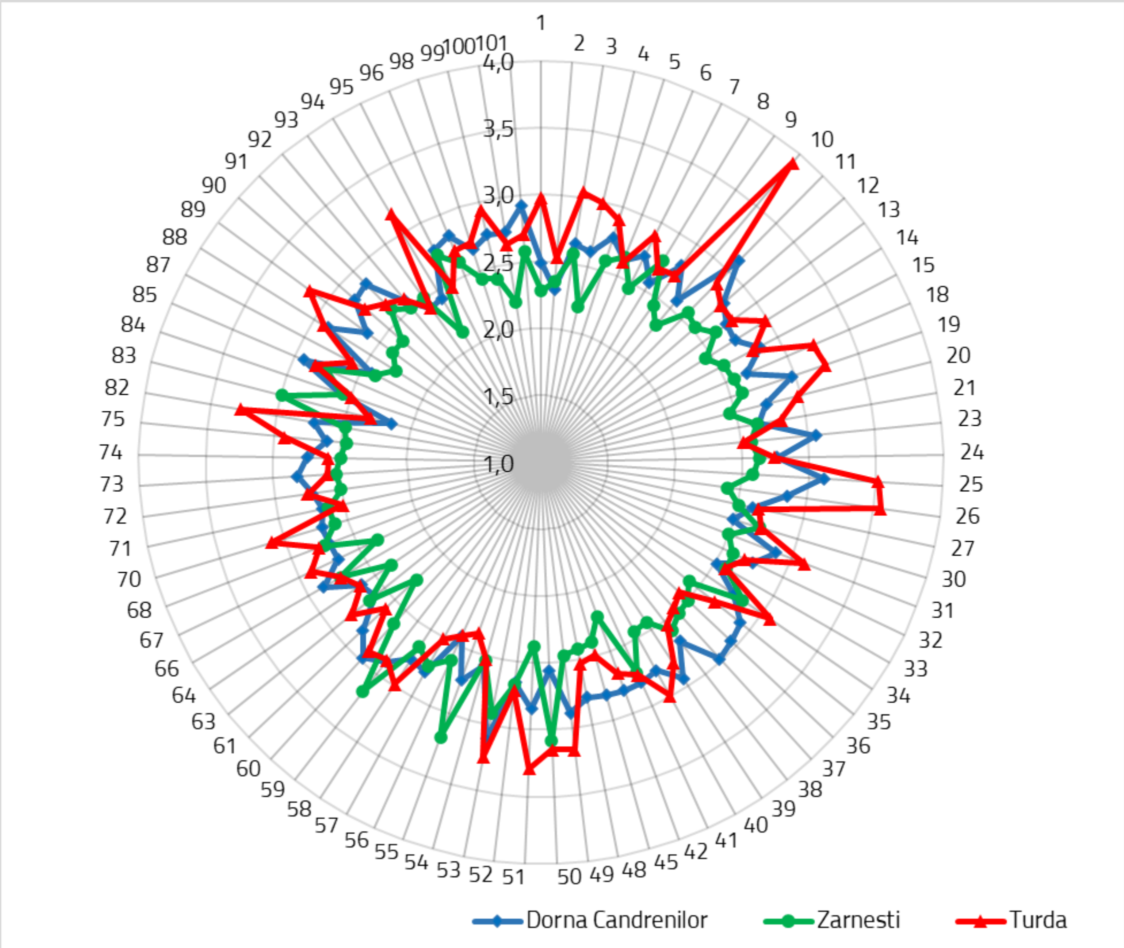


Fig. 9. Variation of the average ring width of Norway spruce provenances for the period 1981-2020

The Zărnești trial recorded the lowest average CA value among the three trials, 2.55 mm. The provenance mean values were between 2.13 mm, provenance 94-Janakkala, and 3.18 mm, provenance 55-Munkahus.

In the comparative trial Turda, the Norway spruce provenances had average annual increases between 2.31 mm, provenance 83-Bramarv, and 3.92 mm, provenance 10-Plan de Cosaques.

4.1.7.2. Earlywood

In the Dorna Candrenilor comparative trial, the provenances with large earlywood for the period 1981-2020 were 25-Wassen, 53-Neustift and 60-Keletbukki Allami, and at the opposite pole were the provenances 83-Bramarv, 2-Branstad and 1-Senum (Fig. 10).

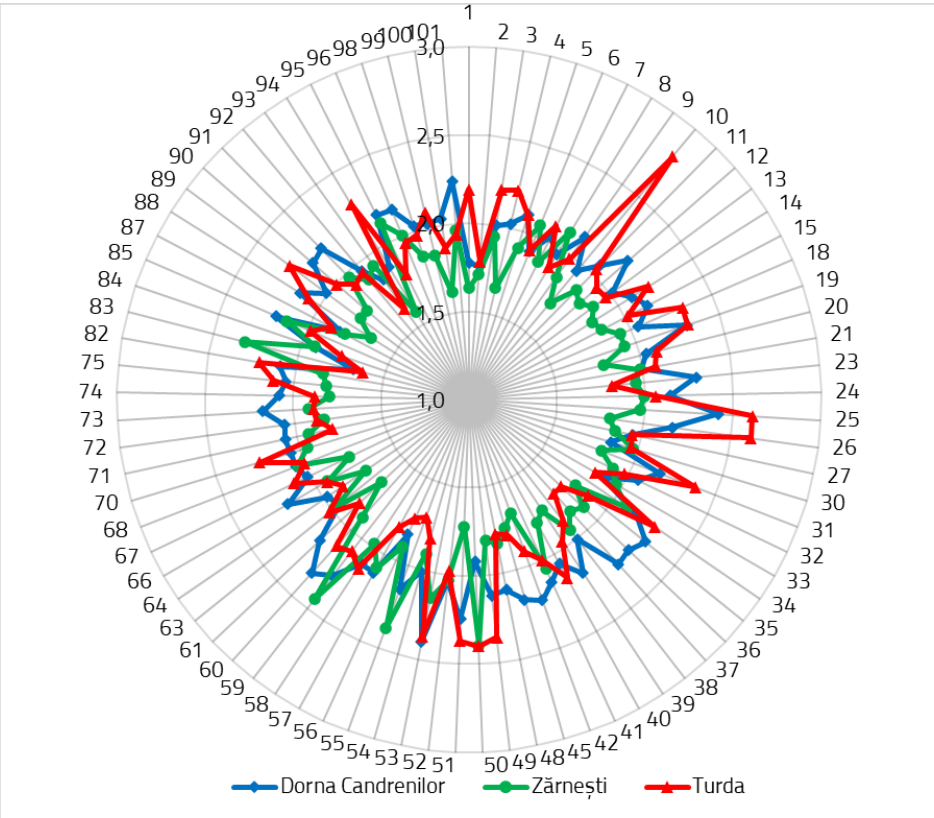


Fig. 10. Variation of early wood growth of Norway spruce provenances for the period 1981-2020

The average LTI of the Norway spruce provenances in the Zărneşti trials was between 1.58 mm, provenance 94-Janakkala, and 2.43 mm, provenance 59-Nytthan.

In the comparative trial Turda, the provenances obtained average LTI values between 1.62 mm, provenance 83-Bramarv, and 2.80 mm, provenance 10-Plan de Cosaques.

4.1.7.3. Latewood

In the comparative Dorna Candrenilor trial, the average LTA value for 1981-2020 was 0.66 ± 0.07 mm. The average values of the provenances were between 0.47 mm, provenance 83- Bramarv, from Northern Europe, and 1.04 mm, provenance 11- Morzine, from the Western Alps. Other provenances with a low average value (below 0.57 mm) of LTA were: 54-Kolarp, 75-Broşteni, 94-Janakkala and 2-Branstad (Fig. 11).

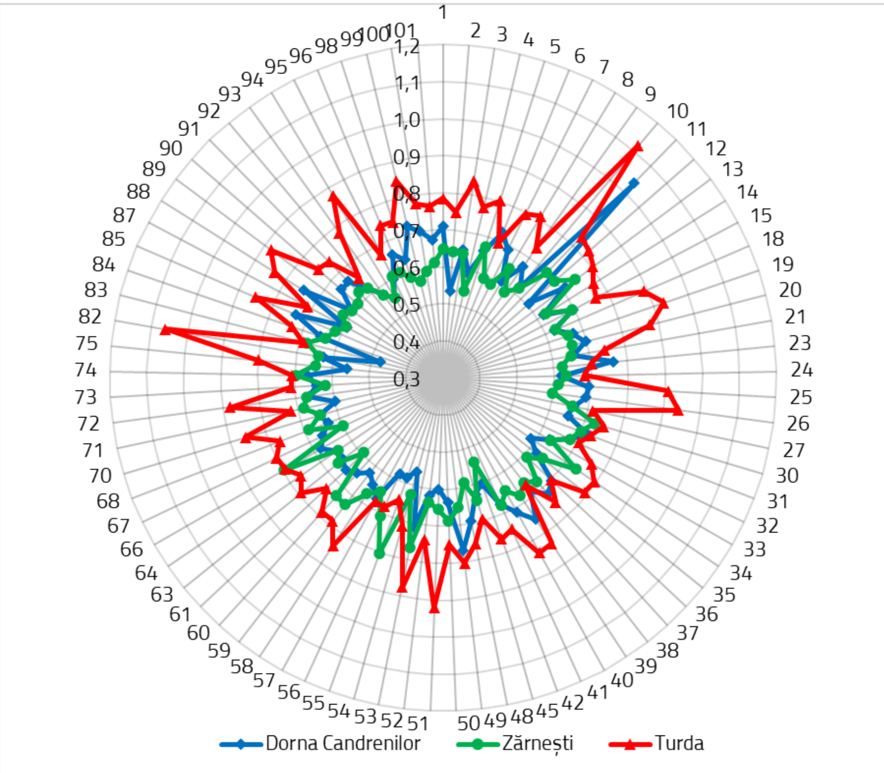


Fig. 11. Variation of late wood growth of Norway spruce provenances for the period 1981-2020

The average value of LTA in the comparative trial Zărnești was close to that of the trial Dorna Candrenilor, 0.65 ± 0.05 mm. The average values of the provenances were between 0.54 mm, provenances 4-Bagstad, from Northern Europe, and 42-Rotlgut Liezen, from the Eastern Alps, and 0.81 mm, provenance 55-Munkahus, from Northern Europe. Other provenances with high average values of LTA, over 0.74 mm were 66-Marginea, 53-Neustift, 13-Saint Laurent II, 34-Borki, Provenance 94-Janakkala, from Northern Europe had in this comparative trial a low value of the average LTA, of 0.55 mm as well.

In the comparative trial Turda, the highest value of average LTA was obtained,0.78 ± 0.008 mm. Along with the provenance 92-Padasjoki, 55-Munkahus, from Northern Europe, which was the best in the comparative trial Zărnești, had the lowest average LTA values in this comparative trial, 0.65 mm. The maximum value of average LTA was obtained by provenance 10-Plan de Cosaques, from France, 1.12 mm, followed by 82-Sund, 26-Winterthur, 19-Kerns, 51-Herfenberg and 25-Wassen, all with values of over 0.90 mm.

4.1.7.4. Latewood percentage

The average value of LTP in the comparative Dorna Candrenilor trial was 27.06 ± 1.54%, and the average values of the provenances ranged between 23.98%, the 95-Tuusula provenance from Northern Europe, and 32.72%, the 11-Morzine provenance from the Western Alps (Fig. 12).

The average LTP in the Zărnești comparative trial was 27.78 ± 1.65%. The average values of the provenances were between 24.09%, provenance 50-Hoyos-Ernest-reith, and 32.06%, provenance 66-Marginea. Provenances 83-Bramarv, 93-Urjala, 6-Straiture I, 85-Heinola and 95-Tuusula had average LTP below 25%.

The highest average LTP value of 30.76 ± 1.62% was obtained in the comparative trial Turda. The provenances obtained average values between 26.89%, provenance 92-Padasjoki, and 35.57%, provenance 93-Urjala, both from Northern Europe.

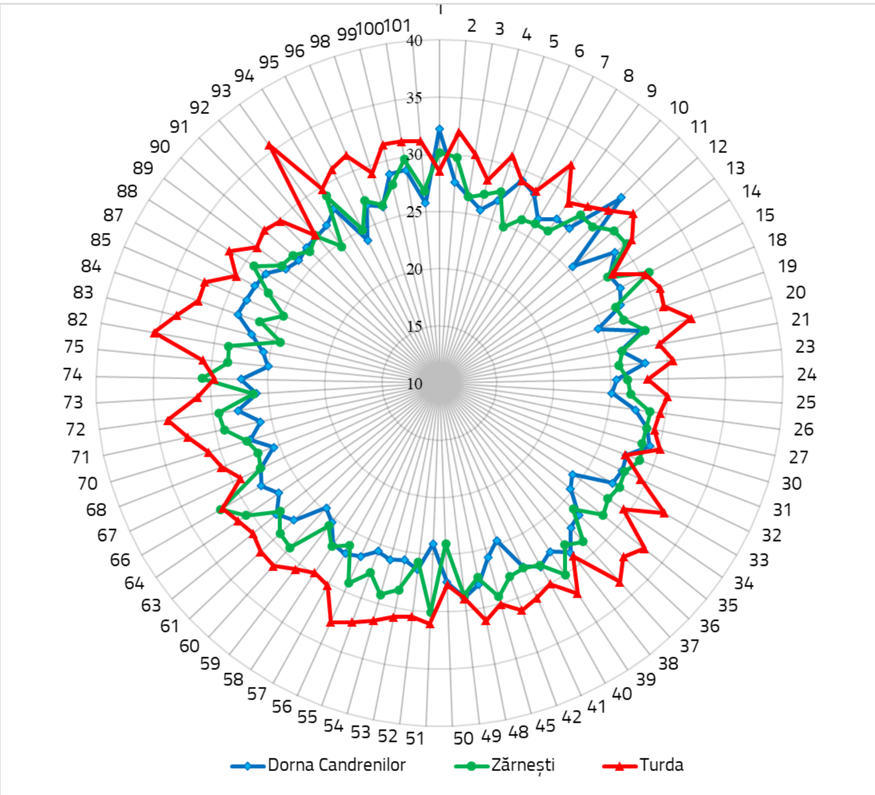


Fig. 12. Variation of latewood percentage of Norway spruce provenances for the period 1981-2020

4.1.8. Conventional wood density

Significant differences between Norway spruce provenances in terms of wood density were observed only in the comparative trial Dorna Candrenilor (Table 5). In this provenance trial, the mean DCL values of the provenances were between 0.311 g/cm^3, provenance 89-Pielisjarvi, and 0.356 g/cm^3, provenance 56-Anfasterod, both from Northern Europe (Fig. 13).

Table 5. Analysis of variability of conventional wood density in each Norway spruce provenance trial at 49 years

	Dorna Candrenilor	Zărnești	Turda
LRTp	7.821 **	0.065 ns	1.577 ns
Vp	0.000	0.000	0.000
Vr	0.006	0.001	0.001
MS r	0.001 ns	0.003*	0.000 ns
Media ± SD g/cm^3	0.331 ± 0.026	0.341 ± 0.027	0.337 ± 0.031

, **, * – Significant for 5%, 1% and 0.1% probability of transgression; ns – insignificant, p > 0.05; LRTp – likelihood ratio test for the effect of provenance; Vp – variance of the random effect of provenance; Vr – residual variance; MS r – average of squares of sums for repetition; SD – standard deviation.*

In Turda trial, the average wood density per provenance was between 0.309 ± 0.044 g/cm^3, provenance 93-Urjala, from Northern Europe, and 0.360 ± 0.051 g/cm^3, provenance 26-Winterthur, from the Central Alps.

The average density of the provenances in the Zărnești trial was between 0.320 ± 0.018 g/cm3, provenance 58-Aspas, from Northern Europe, and 0.365 ± 0.026 g/cm3, provenance 68-Breaza, from the Eastern Carpathians.

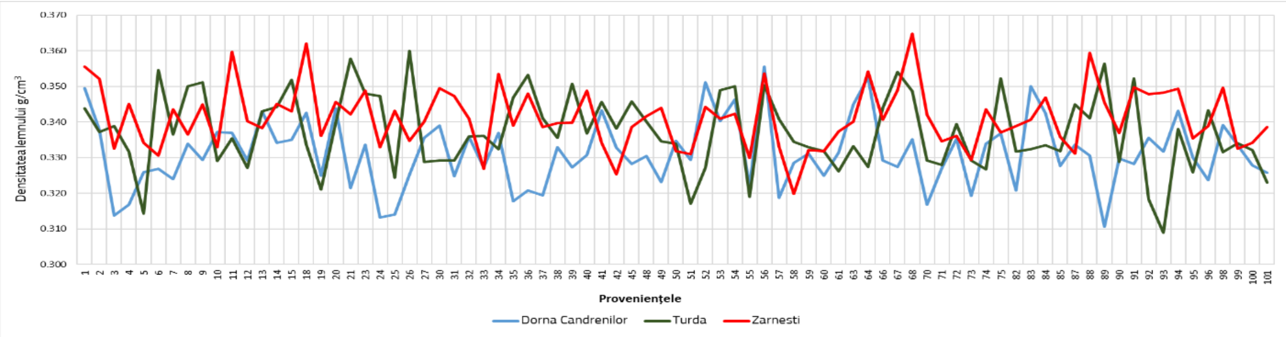
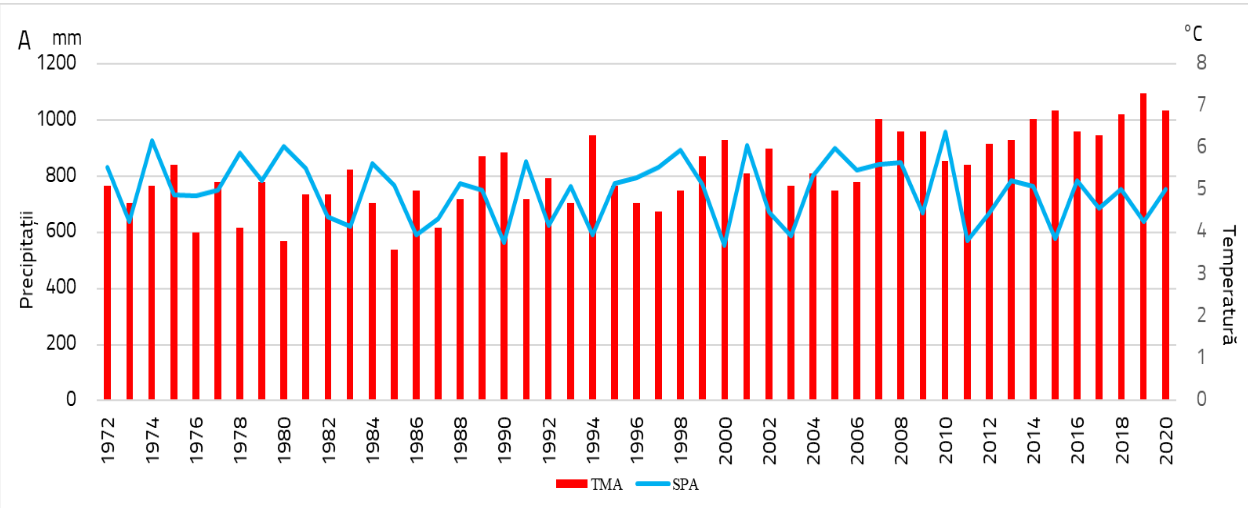


Fig. 13. Variation of conventional wood density of Norway spruce provenances in the three trials at the age of 49 years

4.1.9. Resilience parameters

4.1.9.1. Determining extreme drought years

Large variations in mean annual temperature and annual precipitation were observed in each comparative trial (Fig. 14). The year 2000 recorded the lowest value of the amount of annual precipitation for the analysed period in all three comparative trials, with values between 511 mm in the comparative trial Turda, and 646 mm in the comparative trial Zărnești. The highest value of the average annual temperature was recorded for the year 2019 in all trials, with values between 6.6 °C in the comparative trial Turda and 7.3 °C in the other two comparative trials.



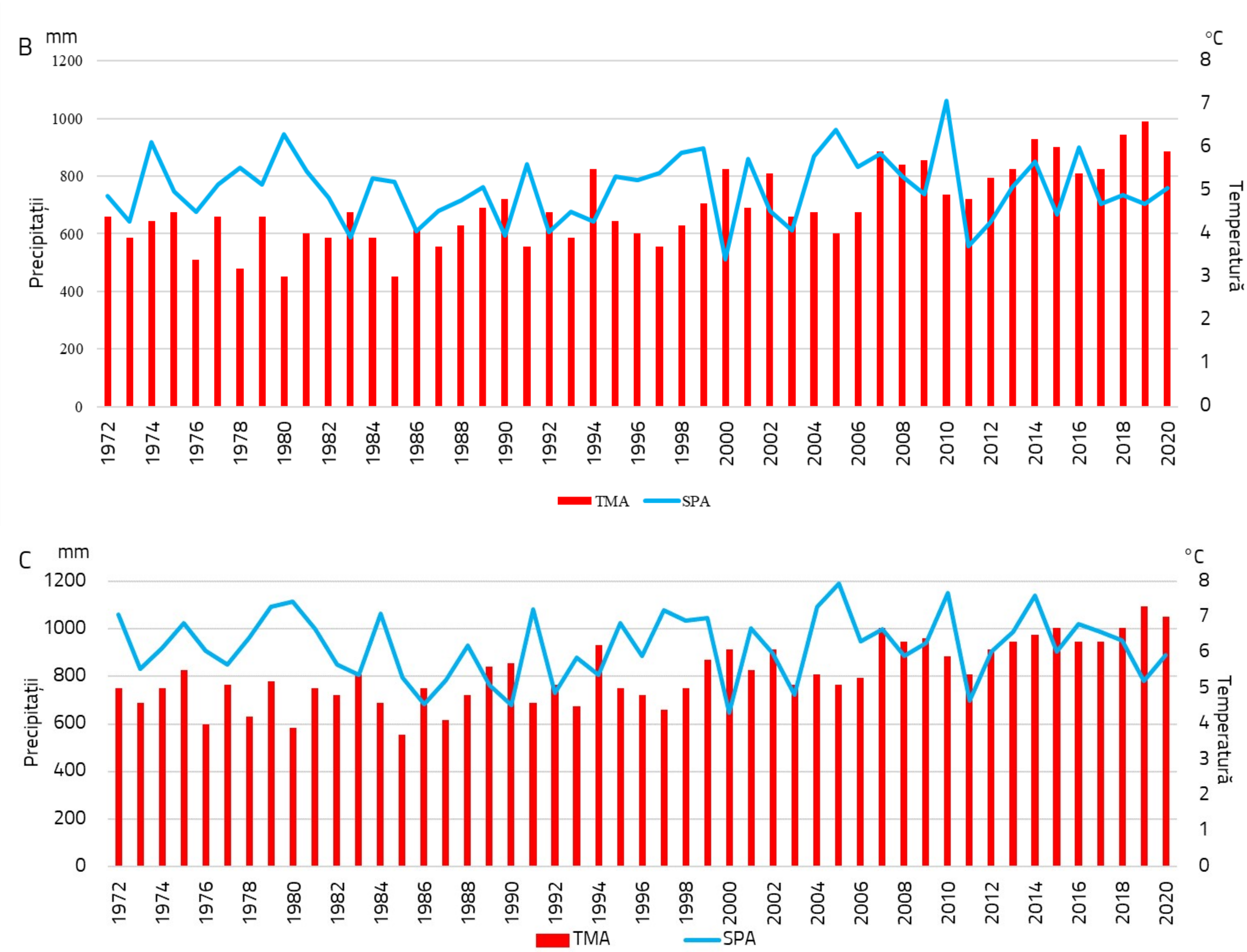


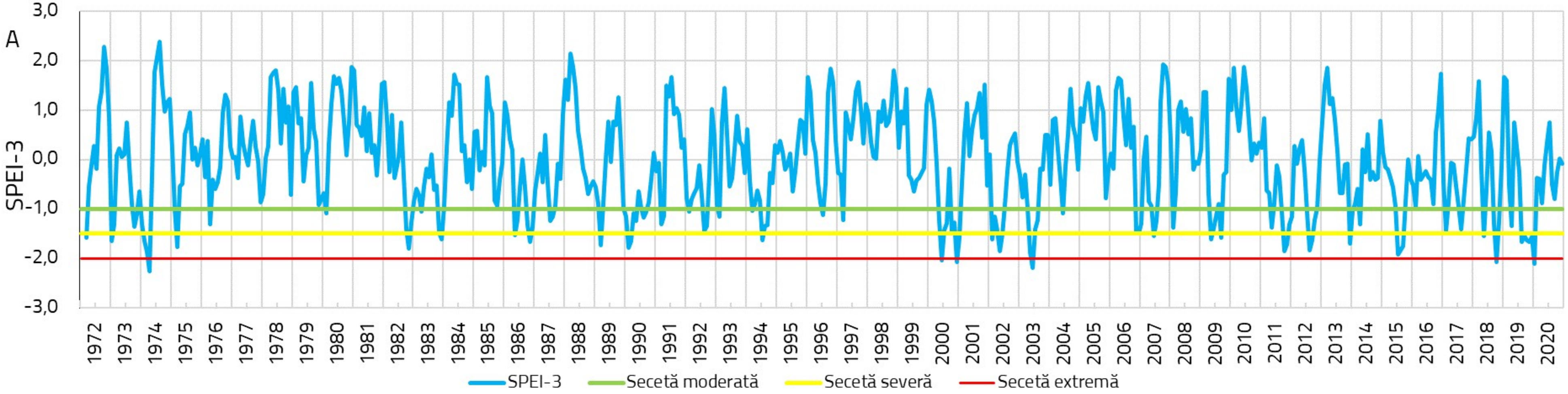
Fig. 14. Variation of the mean annual temperature (TMA) and the sum of annual precipitation (SPA) for the period 1972-2020; A – Dorna Candrenilor, B – Turda, C – Zărnești

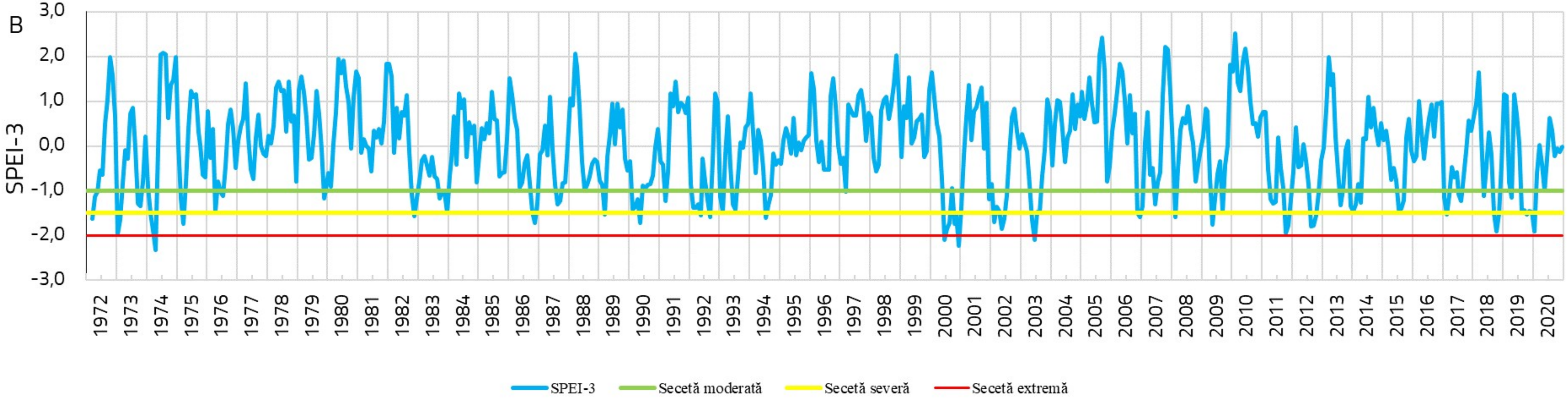
For the period 1972-2020, moderate, severe, and extreme drought years were identified based on SPEI-3 (Fig. 15). Twenty-three years with severe and extreme droughts were identified for the Dorna Candrenilor and Turda trials, and twenty-four were identified for the comparative Zărnești trial (Table 6).

The number of years with extreme droughts varied between trials, being between three in the comparative Turda trial, and five in the Dorna Candrenilor trial. The years with extreme drought, common to the three comparative trials, were 2000 and 2003. In the year 2000, the lowest values of the amount of annual precipitation were recorded in all three trials: 511 mm in Turda, 553 mm in Dorna Candrenilor and 646 mm in Zărnești.

Table 6. Years and months in which severe and extreme droughts (bold) were identified based on SPEI-3 in each Norway spruce provenance trial

Year	Months with severe and extreme droughts		
	Dorna Candrenilor	Turda	Zarnesti
1972	March	March	March, April
1973	Jan	January, February	-
1974	Febr. - **April**	Febr. - **April**	Febr. - April
1975	March	March	March
1977	-	-	December
1978	-	-	January
1982	November	November	November
1983	December	December	April
1986	May, November	November	May, October
1989	March	March	March
1990	Febr., March	May	March
1992	-	May, September	September
1994	July	July	-
1996	-	-	July
2000	**June, December**	**June**-August, October-**December**	June, July, August, **December**
2001	January	-	January
2002	Febr., May, June	Febr., May, June	Febr., May, June
2003	May, **June**	May, **June**	May, **June, July**, August
2006	-	December	December
2007	June	-	June, **July**
2008	-	February	-
2009	May, September	May	-
2011	Oct., November	October, November	October, November
2012	Aug, September	August-October	August, September
2013	December	-	-
2015	July, August, September	-	July
2017	-	February	-
2018	May, **October**	September-November	May, **October**
2019	August-December	October	August, September, November, December
2020	**January**	January	January


A
SPEI-3
3,0
2,0
1,0
0,0
-1,0
-2,0
-3,0
1972 1973 1974 1975 1976 1977 1978 1979 1980 1981 1982 1983 1984 1985 1986 1987 1988 1989 1990 1991 1992 1993 1994 1995 1996 1997 1998 1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015 2016 2017 2018 2019 2020
SPEI-3
Secetă moderată
Secetă severă
Secetă extremă


B
SPEI-3
3,0
2,0
1,0
0,0
-1,0
-2,0
-3,0
1972 1973 1974 1975 1976 1977 1978 1979 1980 1981 1982 1983 1984 1985 1986 1987 1988 1989 1990 1991 1992 1993 1994 1995 1996 1997 1998 1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015 2016 2017 2018 2019 2020
SPEI-3
Secetă moderată
Secetă severă
Secetă extremă

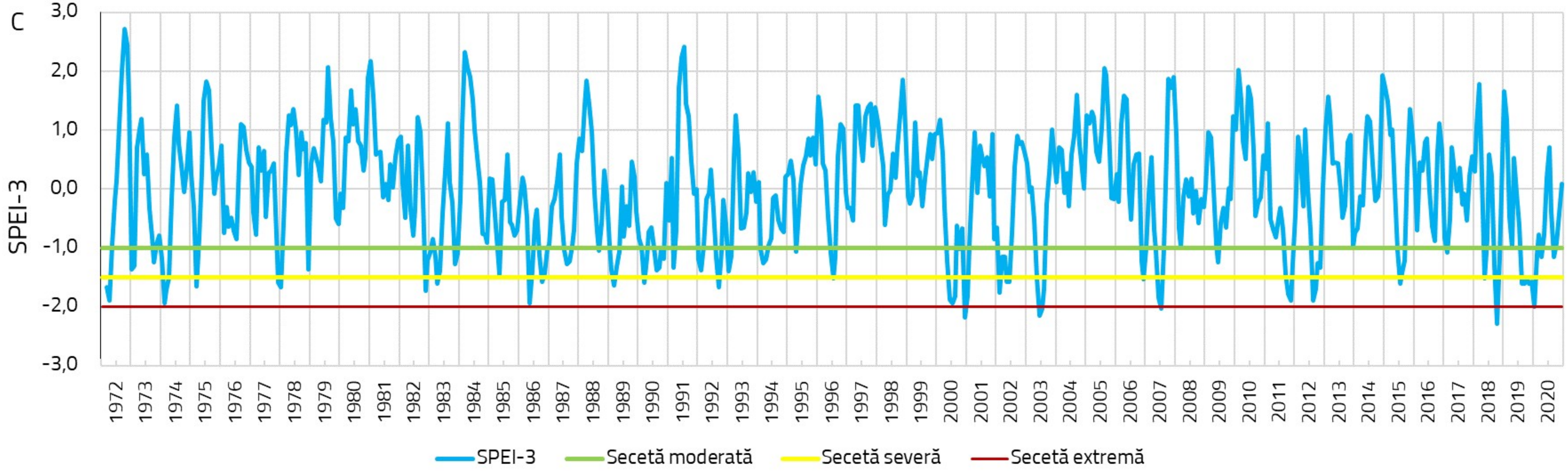


Fig. 15. The variation of the standardised precipitation and evapotranspiration index, calculated for 3 months (SPEI-3) for the Norway spruce trials, for the period 1972-2020; A - Dorna Candrenilor, B - Turda, C - Zărnești

The variation of pointer years is shown in Fig. 16.

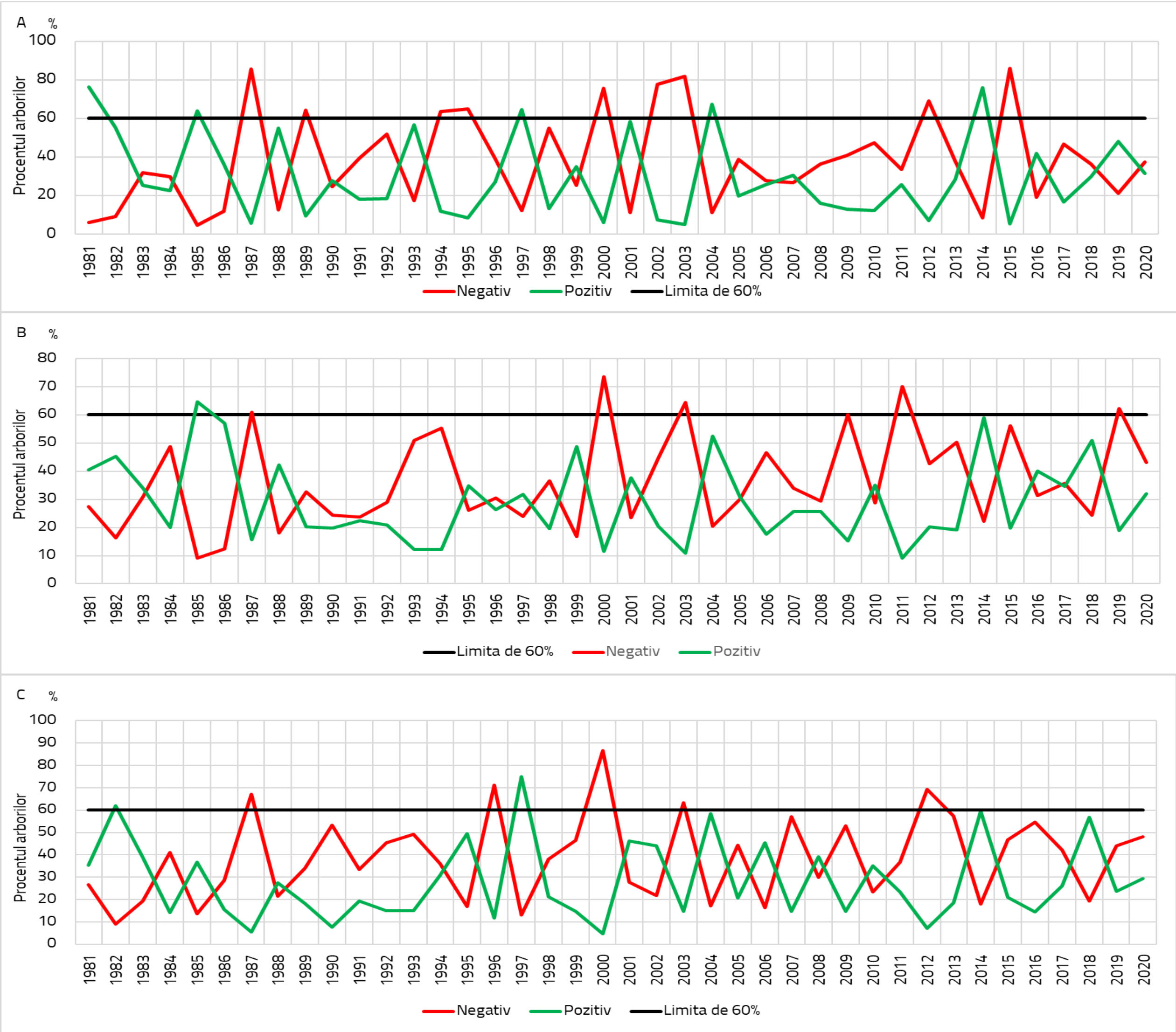


Fig. 16. The variation of the pointer years for the period 1981-2020 in the Norway spruce provenance trials; A - Dorna Candrenilor, B - Turda, C - Zărnești

The number of negative years, in which more than 60% of the trees were affected, varied between five in the comparative trials Zărnești and Turda and nine in the comparative trial Dorna Candrenilor. This analysis confirmed the extreme drought events of 2000 and 2003, based on SPEI-3, common to the three comparative trials.

The year 2000 was when the highest percentage of trees affected by drought was recorded in the comparative trials Turda and Zărnești. In the Dorna Candrenilor trial, there were four years in which the percentage of affected trees was higher than in 2000: 1987, 2002, 2003 and 2015.

4.1.9.2. Resilience indices of provenances for the extreme droughts of 2000 and 2003

Analysing the different responses of provenances to the drought of 2000, significant differences were observed between provenances for all tree resilience parameters in the Zărnești comparative trial. In the Turda comparative trial, differences between provenances were significant for all indices except resilience. In contrast, in the Dorna Candrenilor trial, resilience was the only index for which the differences between provenances were significant.

The drought episode of 2000 had a different impact on the three Norway spruce provenance trials. The most substantial impact occurred in the Zărnești comparative trial, where no provenance had an average Resist greater than 1; in other words, all provenances were affected. The best resistance values (Fig. 17) were obtained in the Turda and Dorna Candrenilor trials, the average per trial being 0.89 and 0.88, higher by 21.92% and 20.55% than the average value in the Zărnești trial.

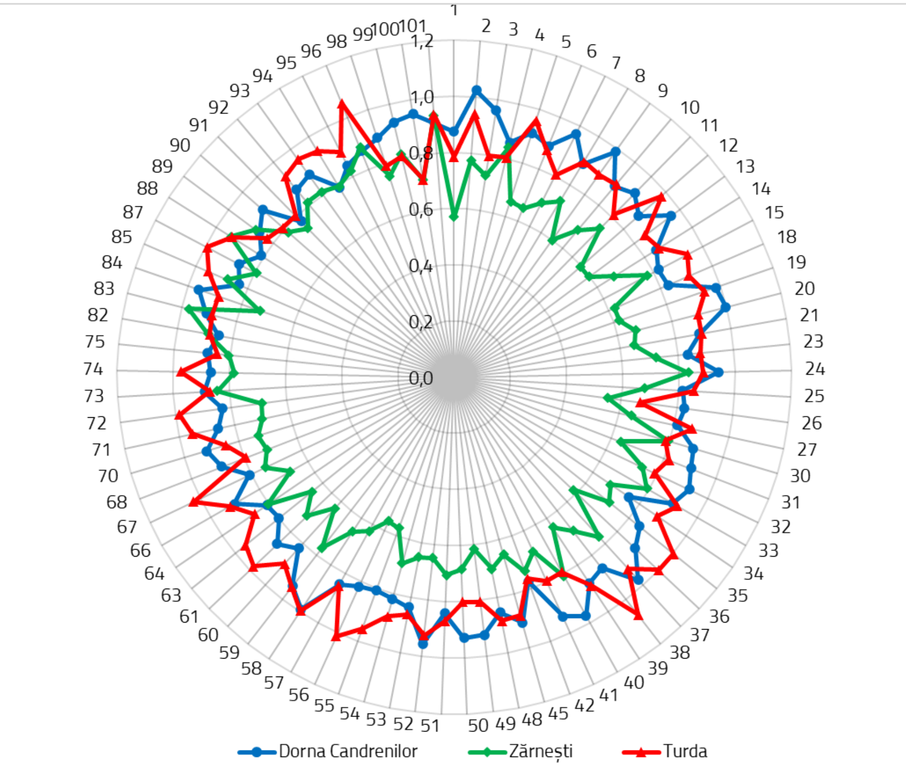


Fig. 17. The variation of the resistance to the extreme drought from 2000 of the Norway spruce provenances

The highest amplitude of the average resistance of the provenances was in the comparative trial Zărnești, the values being between 0.55, provenance 26-Winterthur, and 0.97, provenance 83-Bramarv. The mean resistance of this trial was 0.72, the lowest of the three.

In the Turda comparative trial, the provenances obtained an average resistance between 0.67, provenance 26-Winterthur, and 1.07, achieved by provenance 38-Val Di Fiemme.

In the comparative trial Dorna Candrenilor, the average resistance values of the provenances were between 0.75, provenance 34- Borki, and 1.02, provenance 2- Branstad.

The average values of the recovery corresponding to the extreme drought of the year 2000 are shown in Fig. 18.

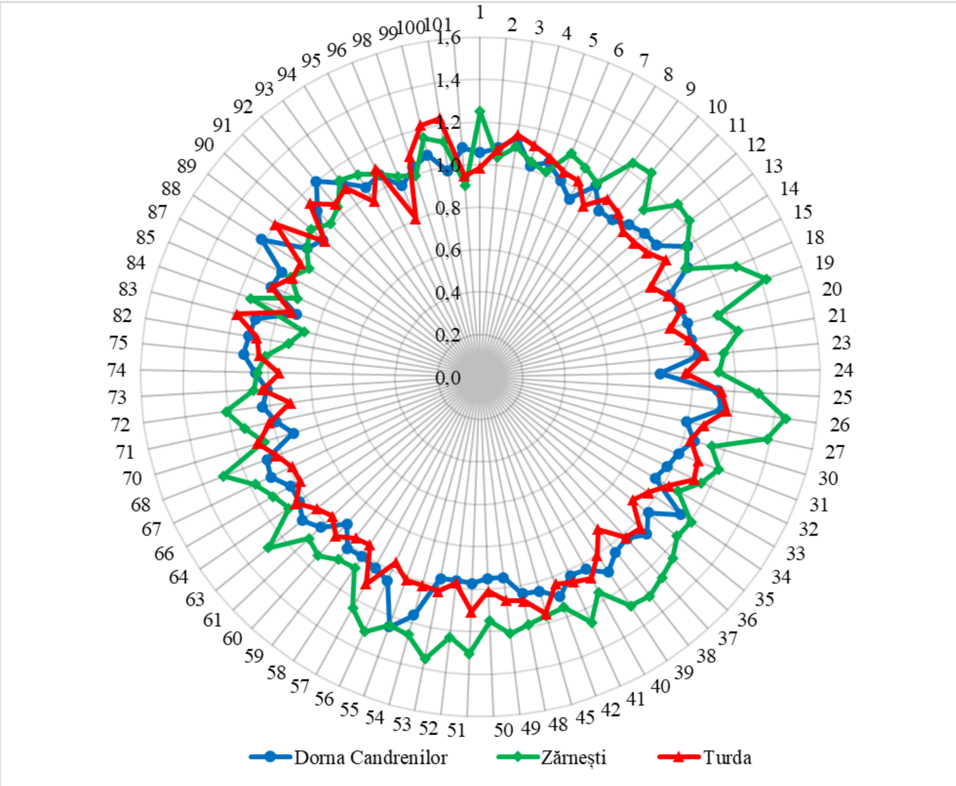


Fig. 18. Variation in the recovery of Norway spruce provenances after the extreme drought of 2000

Regarding the average value of the recovery of Norway spruce provenances from the year 2000 from the comparative trial Zărnești, only five provenances obtained values lower than one: 88-Pualanka, 85-Heinola, 82-Sund, 101-Valke Karlovice and 83-Bramarv. The maximum was achieved by provenance 26-Winterthur, 1.45.

In the Dorna Candrenilor trial, the number of provenances with average recovery values below one was 20, the values being between 0.85, provenance 24-Tagevillen and 1.25, provenance 55-Munkahus.

In the comparative trial Turda it was registered the largest number of provenances that did not achieve an average recovery of more than one, more precisely 28. The average recovery values in this trial were between 0.81, provenance 96-Rila, and 1.23, provenance 100-Kasperske Hory.

Regarding the average recovery per trial, the highest value was obtained in the comparative trial Zărnești (1.15). In the Dorna Candrenilor and Turda trials, it was 1.04 and 1.03, respectively.

No provenance obtained an average value of resilience from the year 2000 higher than one in the comparative trial Zărnești, the values being between 0.65, provenance 5-Seljord, and 0.95, provenance 37-Latemar (Fig. 19).

The provenances from Northern Europe: 2-Branstad, 3-Sandar, 92-Padasjoki, and 55-Munkahus, were the ones that had a greater resilience than one in the comparative Dorna Candrenil trial, for the extreme drought of 2000. The rest of the provenances had values between 0.76, provenance 60-Keletbukki Allami, and 0.99, provenance 20-Le Brassus.

In the comparative trial Turda, mean resilience values greater than one were obtained by the provenances 83-Bramarv (1.06) and 5-Seljord (1.05). The provenances 93-Urjala and 85-Heinola had an average resilience equal to one, and the lowest value was 0.75, obtained by the provenance 1-

Senum. The Romanian provenance 67-Frasin and provenance 45-Hollenburg had an average resilience of 0.99.

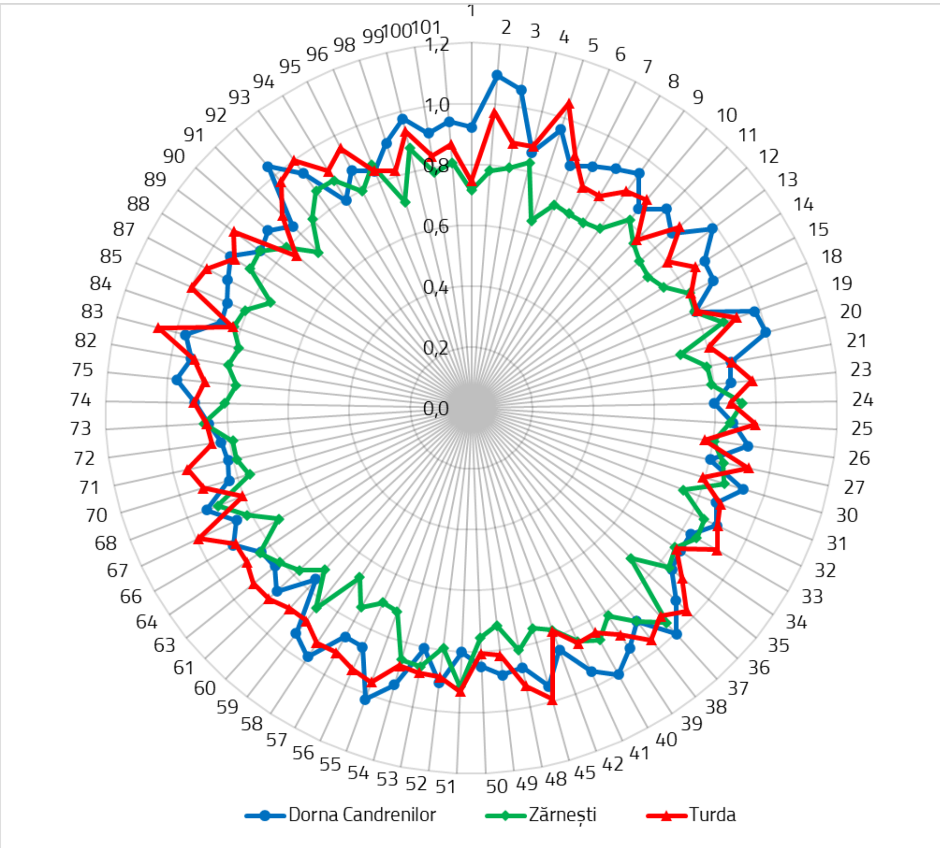


Fig. 19. The variation of the resilience to the extreme drought from 2000 of the Norway spruce provenances

The highest average value of resilience in the year 2000 was obtained in the Dorna Candrenilor trial (0.90), followed by Turda (0.89) and Zărnești (0.80).

The variation of the relative resilience of Norway spruce provenances to the extreme drought of the year 2000 is represented in Fig. 20.

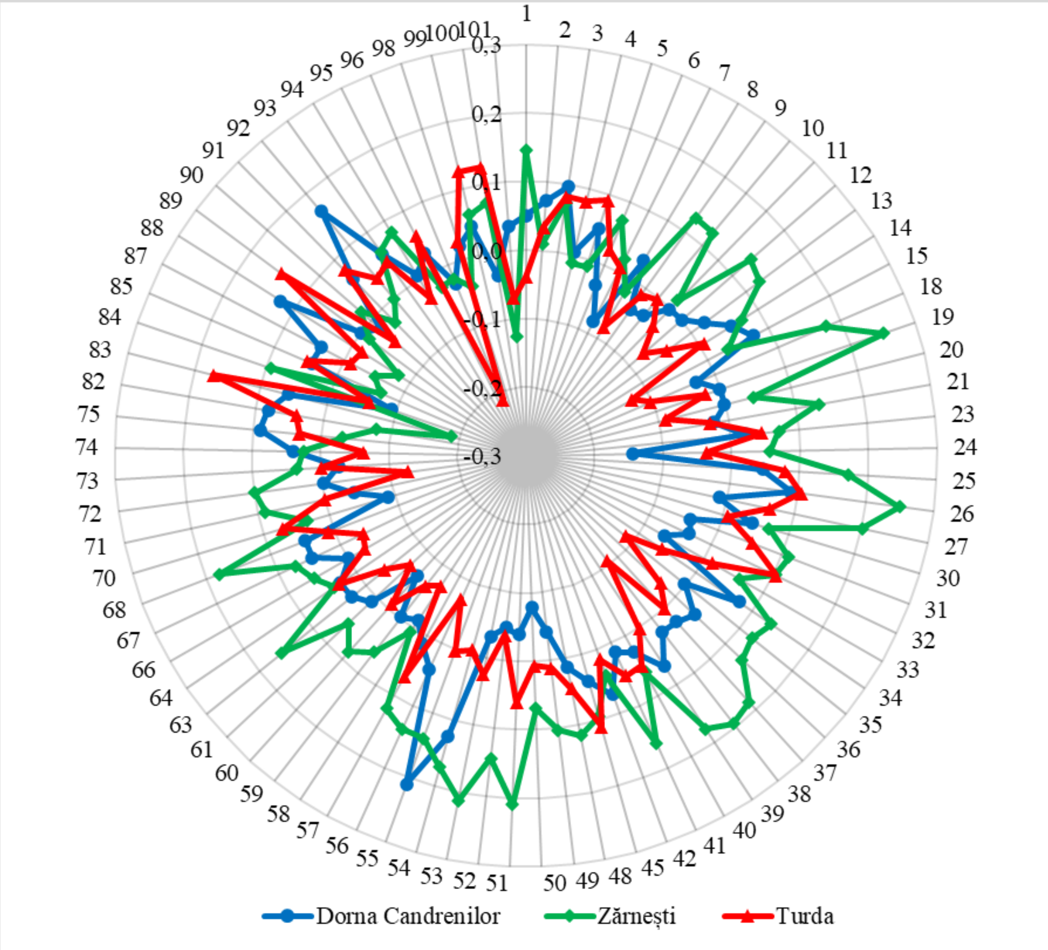


Fig. 20. The variation of the relative resilience of Norway spruce provenances to the extreme drought of the year 2000

In the comparative trial Zărnești, the highest value of average relative resilience was obtained, and the lowest was obtained in the Turda trial.

For the extreme drought of 2003, significant differences were observed between provenances in the comparative trial Zărnești for all resilience parameters (Fig. 21). The differences between provenances were not statistically significant in the other two trials.

Norway spruce provenances had a good revitalisation capacity after the drought episode of 2003 in the Zărnești trial. Except for provenances 93-Urjala and 83-Bramarv, which obtained a recovery of 0.99, all other provenances had values above 1, the maximum obtained by provenance 8-La Ganne.

Regarding the resilience to the drought episode of 2003, Norway spruce provenances obtained values between 1, provenance 15- Gerardmer I, and 1.43, provenance 39-Klaunz Bannwald.

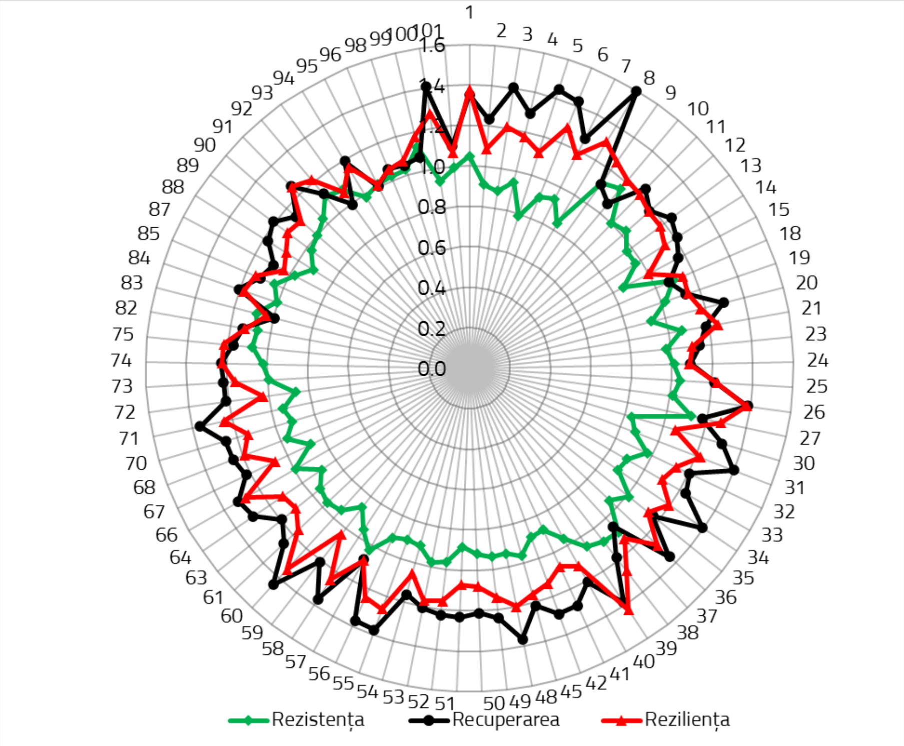


Fig. 21. The variation of resistance, recovery, and resilience of Norway spruce provenances to the extreme drought of 2003 in the Zărnești trial

A valuable provenance is 25-Wassen, from the Central Alps, with an average of CA between 3.11 and 3.52 mm, made in the comparative trials Dorna Candrenilor, respectively Turda, ranking first and third, respectively. In the comparative trial Zărnești, it had a CA of 2.58 mm, being ranked above average, in the 32nd place. The drought of the year 2000 led to reductions in its annual growth of 15% in the Turda trial and 34% in the trial Zărnești, the Resist values being 0.85 and 0.66 respectively in the two trials. The average values of Recup from the three comparative trials were good, greater than 1, between 1.12 in Dorna Candrenilor and 1.38 in Zărnești. The average rezil of this provenance was slightly better than that of provenance 53, with values ranging from 0.86 to 0.93.

The provenance 19-Kerns, also from the Central Alps, had good growth in all three comparative trials and an average recovery – values between 0.99 in Dorna Candrenilor and 1.42 in Zărnești. The average resistance in Dorna Candrenilor was 0.98, and 0.86 in Turda. In the Zărnești comparative trial, it was more strongly affected by the drought of 2000 than in the other comparative trials, CA being reduced by 38% compared to the three years before, the resistance value being only 0.62.

Among the Romanian provenances, 75-Broșteni had a ring width above the average in the comparative trials of Dorna Candrenilor and Turda (2.92 mm) and below average in Zărnești (2.42 mm). It was less affected by the drought of 2000, the average annual growth being reduced by 12% in Dorna Candrenilor and by 19% in Zărnești, the average resistance being 0.88 and 0.81, respectively. Average recovery values were above 1 in all three comparative trials, and average resilience was 0.97 in Dorna Candrenilor, 0.88 in Turda and 0.77 in Zărnești.

The provenance 70-Coșna, also Romanian, performed well in terms of CA in the three comparative trials. In the comparative trial Dorna Candrenilor was affected only 8% by the drought of 2000, having a resistance of 0.92. It was more strongly affected in Zărnești than provenance 75, with a percentage of 27%, its resistance for the year 2000 being 0.73, but it had a great recovery in this trial. Resilience was close to average in all three comparative trials.

4.1.10. Discussion

The high genetic variability between populations is due to the vast area of provenances tested, which includes the three regions of post-glacial recolonisation in Europe: Scandinavian, Hercino-Carpathian and Alpine. Seasonal conditions with different climates (continental in the North, temperate-continental in the South and continental with oceanic influences in the West) also had an important role in the high level of variation obtained.

In the comparative trial of Dorna Candrenilor, the best performances were obtained. Between the comparative trials Zărnești and Turda there were no differences from a statistical point of view, in terms of diameter at breast height and total height.

The high performance obtained in the Dorna Candrenilor trials is also due to its type of forest site, which is of superior quality (Table 1). The quality of the forest site from the Turda trial is average, and that from the Zărnești trial is average-inferior.

The average values per trial of the diameter at breast height were between 21.14 ± 4.76 and 23.75 ± 5.58 cm, in the Zărnești and Dorna Candrenilor trials, respectively. Regarding the total height, it had average values per trial between 21.43 ± 3.53 and 25.90 ± 3.24 m, in the Zărnești and Dorna Candrenilor trials, respectively.

In a comparative trial in Eastern Latvia, where 20 Norway spruce clones and two planting schemes were tested, the percentage of survival at 50 years was 30.3%, for the 1 x 3 m planting scheme, respectively of 69.5%, for the planting scheme of 5 x 5 m [158]. For the 1 x 3 m planting scheme, the mean values of diameter and total height at 50 years were 24.3 ± 0.6 cm and 21.5 ± 0.3 m, respectively. For the 5 x 5 m planting scheme, the average values were 36.5 ± 0.7 cm and 25.1 ± 0.3 m, for the diameter at breast height and total height, respectively [158]. The average values of the clones in the 5 x 5 m planting scheme were between 31.9 ± 5.6 – 43.9 ± 5.4 cm, for the diameter at breast height, respectively 20.9 ± 6.6 – 28.1 ± 1.1 m for the total height [159].

A low wood density is found in species such as fir and Norway spruce, with values of 0.358-0.378 g/cm^3 [160], [161]. In the trials studied in this thesis, the average values of the comparative trials for wood density were somewhat lower, the highest value being recorded in the comparative trial Zărnești, 0.341 ± 0.027 g/cm^3. The lowest value was obtained in the Dorna Candrenilor trial, 0.331 ± 0.026 g/cm^3, 2.85% lower than that obtained in the Zărnești comparative trial. Close values were also obtained in two other Norway spruce trials in Romania, 0.348 and 0.329 g/cm^3 [162].

Conventional wood density has an important role in the mechanical stability of trees, wood strength, energy content, as well as carbon storage [163], [164], [165]. Selecting provenances with the highest conventional wood density can improve these properties.

The extreme drought episode of 2000 had different impacts in the three comparative trials. The highest was in the Zărneşti comparative trial, where all provenances were affected, had average values of resistance that were lower than 1. Only in this trial significant differences were observed between provenances in terms of resilience parameters for the 2003 drought episode. A 10-35%

decrease in annual Norway spruce diameter growth caused by the 2000 and 2003 droughts was also observed in the study by Bosela et al. [166].

It should be noted that the recovery, resilience, and relative resilience calculated for the year 2000 were influenced by the severe drought of 2002 as well as the severe drought of 2003, which occurred in all three comparative trials. In addition, there was also a severe drought in January 2001, in the comparative trials Dorna Candrenilor and Zărnești. Obviously, the resistance calculated for the year 2003 was affected by these events. Future studies should follow extreme events that are more distant in time, something that is becoming more and more difficult, considering the recent events in Europe, from the period 2018-2022 [167], or the climate projections for Romania [168].

In Romania, since 1901, each decade had between 1 and 4 years with extreme drought or extreme precipitations events. The number of identified droughts has increased since 1981 [169]. A reduction in annual precipitation is expected, especially in the southeastern part of the country [170].

A high proportion of affected trees in terms of annual radial growth was recorded in 1987 in all three comparative trials. According to Meteo Romania, in this year was recorded the lowest average value of the March temperature from the period 1961-2022, of -2 °C. The trial Dorna Candrenilor, where the percentage of affected trees exceeded 80% in 1987, is located approximately 10 km from the town of Poiana Stampei, where a weather station recorded an absolute minimum temperature of -30.0 °C for the period of 3- 5 March 1987 [171]. Thus, it is possible that the trees were affected by frost that year.

Significant differences only between resistance and resilience of larch provenances were also evidenced in a comparative trial from northeastern Austria at 50 years [172].

4.2. The correlations between traits and between them and the place of origin of the provenances

4.2.1. Correlations between growth traits, survival percentage and conventional wood density and the geographic gradients of provenances' origin

The diameter at breast height was significantly and positively correlated with the altitude of origin of provenances in the Dorna Candrenilor and Turda trials. The correlation between diameter and latitude, whether true or corrected, were negative in all three trials.

Total height was negatively correlated with the corrected latitude of provenances in all three trials and with the latitude of origin of provenances in the Dorna Candrenilor and Zărnești trials. In the Turda trial, total height was positively correlated with provenance's longitude.

Pruned height was significantly and positively correlated with the altitude of origin of the provenances and negatively with the latitude of origin of the provenances in the Dorna Candrenilor and Zărnești trials. In the Turda trial, pruned height was positively correlated with provenance's longitude.

Survival percentage was significantly and negatively correlated with the corrected latitude and latitude of origin of provenances, and positively with their altitude of origin, in all three comparative trials.

In the Dorna Candrenilor trial, latewood was significantly and positively correlated with the origin altitude of the provenances and negatively with the latitude and longitude of the provenances. In the other two trials, there were no statistically significant correlations.

In the Dorna Candrenilor trial, earlywood was significantly correlated with altitude and negatively with the latitude of origin of provenances. In the Turda trial, earlywood was negatively correlated with provenance longitude.

The latewood percentage was significantly and negatively correlated with the longitude of origin of provenances in the Dorna Candrenilor trial; and the same with the corrected latitude of provenances in the Zărnești trial. In the Turda trial, latewood percentage was significantly correlated with corrected latitude and longitude of provenances.

4.2.2. Correlations between resilience parameters and geographic gradients of provenances' origin

In the comparative Dorna Candrenilor trial, the altitude of origin of provenances was not significantly correlated with any resilience parameter from the year 2000. It was negatively correlated with resilience and relative resilience in the Turda trial and positively with recovery and relative resilience in the Zărnești trial.

The corrected latitude of provenance was significantly and positively correlated with recovery, resilience, and relative resilience in the Dorna Candrenilor trial, with resilience in the Turda trial and with resistance in the Zărnești trial. This was negatively correlated with the relative recovery and resilience of Zărnești trial provenances.

The latitude of origin of the provenances was significantly and positively correlated with the recovery and relative resilience of the provenances in the Dorna Candrenilor trial. In the Turda trials, correlations between latitude and recovery, resilience and relative resilience of provenances were all positive. In the Zărnești trial, the latitude of the provenances was negatively correlated with the relative recovery and resilience of the provenances and positively with their resistance.

The origin longitude of the provenances was negatively correlated with their resistance in the Dorna Candrenilor trial and positively with their resilience in the Turda trial. In the Zărnești trial, the longitude of the provenances was negatively correlated with their recovery and relative resilience and positively with their resilience and resistance.

4.2.5. Discussion

Regarding the correlations between late and earlywood, and the altitude of origin of the provenances, they were significant only in the Dorna Candrenilor trial, with provenances from higher altitudes achieving greater values than those from lower altitudes.

Provenances from high altitudes presented a higher survival percentage, with correlation coefficients between 0.234 in the Zărnești trial and 0.332 in the Turda trial.

Provenances originating from high latitudes showed reduced values of diameter at breast height, total height, and survival percentage in the three trials. Total height was not significantly correlated with latitude in the Turda trial, but with corrected latitude, the correlation was positive.

No significant correlations were obtained between conventional wood density and geographic gradients of provenances. Between conventional wood density and the other analysed traits, correlations were negative, weak, or very weak. Similar results have been published [173], [174], [175], [176], [177], [178], [179], [180]. In the study by Skrøppa et al. [181] in Norway, the correlation between wood density and height growth was moderately to strongly negative at the juvenile stage. In two comparative *half-sib* trials of Norway spruce from Romania at 25 years of age, correlations between conventional wood density and height and diameter at breast height were also negative [182]. In a study in which 250 trees from 25 plantations in the Romanian Carpathians, were analysed between 1 and 12 years, a rapid decrease in wood density was noted, together with an increase in the values of height and root collar diameter [70].

Comparing trees left standing with those that died, DeSoto et al. observed that dead trees were less resilient to previous droughts; thus, there is a link between reduced drought resilience and mortality risk [183]. In the Dorna Candrenilor trial, provenances with a high percentage of survival had low recovery, resilience, and relative resilience, while in the Zărnești trial, provenances with a high percentage of survival had high recovery and relative resilience and low resilience. A negative correlation between percentage survival and resistance as well as recovery was also obtained in 10 populations of maritime pine, *Pinus pinaster*, tested in two field trials in Spain [184].

In terms of longitude, the eastern provenances had lower latewood and a lower latewood percentage than the western ones in the Dorna Candrenilor comparative trial. In the Turda comparative trial, they achieved a lower earlywood growth and a higher latewood percentage. In the comparative Zărneşti trial, the correlations between the annual radial growth and the longitude of the provenances were not significant.

The provenances that had large ring widths, resistance, and/or good recovery in all three comparative trials are: 67-Frasin, 70-Coşna, 71-Moldovița, and 75-Broşteni, from the Eastern Carpathians; 53-Neustift, 49-Redl-Zipf-Fuchsberg, 40-Wietersdf, from the Eastern Alps; 19-Kerns and 25-Wassen, from the Central Alps; 31-Bremenhagen, from NE Germany; and 99-Zelesna Ruda, from the Bohemian Plateau.

Differences between the sites' environmental conditions are also reflected in the correlations between survival percentage and recovery, resilience, and relative resilience of trees. These were negative in the Dorna Candrenilor comparative trial, which is in a high-quality forest site, and positive in the Zărnești comparative trial.

4.3. Analysis of the influences of climatic conditions on the biometric traits of Norway spruce provenances

4.3.1. Genotype x environment interaction and performance stability

Significant differences between provenances were highlighted for several traits. The effect of the test site was significant for all analysed traits, and the effect of the provenance x trial interaction was not significant for D1.30m, Suprav and DCL. The effect of repetition in each comparative trial was significant for all traits except D1.30m and DCL.

The best results for HT, HE, D1.30m and Suprav were obtained in the Dorna Candrenilor trial (Figs. 22, 23, 24 and 25). The trial average of HT in the Dorna Candrenilor trials was 20.6% higher than the average of the Turda comparative trial and 20.9% higher than the average obtained in the Zărnești comparative trial.

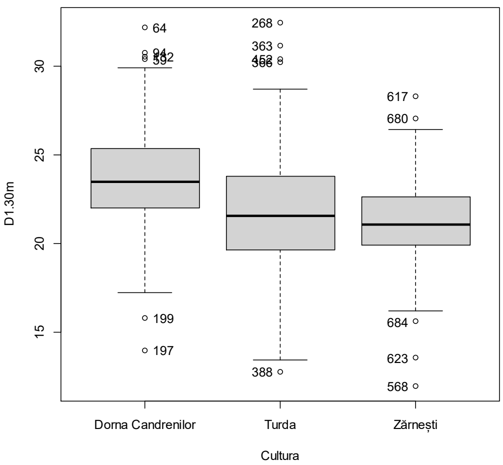


Fig. 22. Variation in diameter at breast height in each Norway spruce provenance trial at 49 years

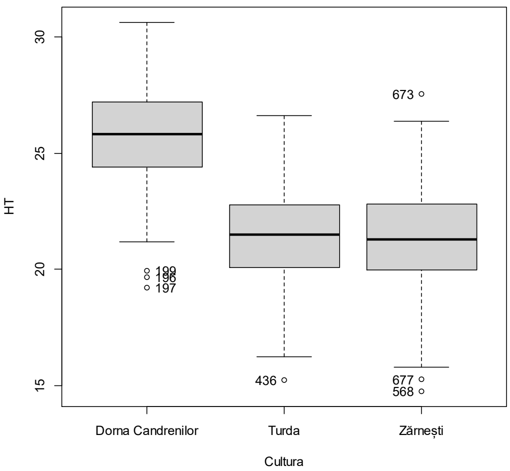


Fig. 23. Total height variation in each comparative Norway provenance spruce trial at age 49

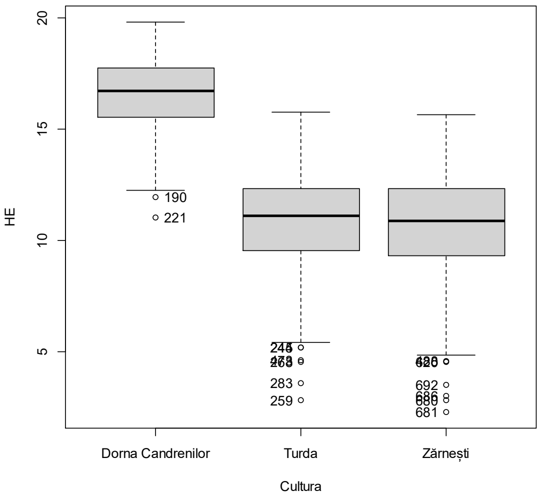


Fig. 24. Variation in grafted height in each comparative Norway spruce provenance trial at age 49

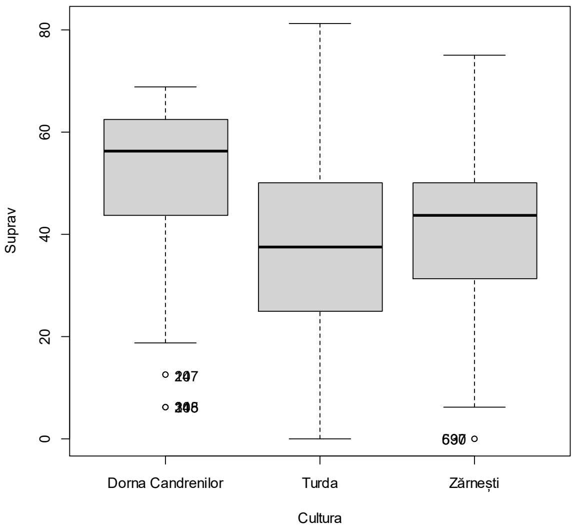


Fig. 25. Variation in survival percentage in each Norway spruce provenance trial at age 49

Analysing genetic variation between trials for DCL, provenance and the provenance x trial interaction were not significant. There were significant, although not impressive differences between trials: the highest value was obtained in the Zărnești comparative trial, 0.341 ± 0.032 g/cm^3, and in the Dorna Candrenilor trial, a 2.85% lower value was obtained, of 0.331 ± 0.027 g/cm^3 (Fig. 26).

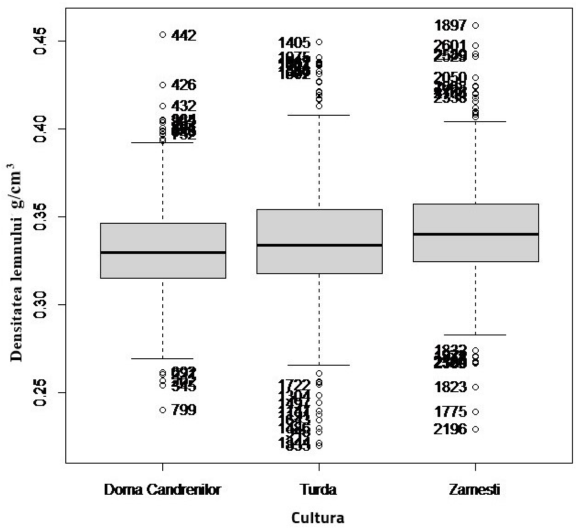


Fig. 26. Variation of conventional wood density in the three comparative Norway spruce provenance trials, at the age of 49 years

The average ring width per trial was between 2.55 mm, in the Zărnești trial, and 2.81 mm, in the Turda trial.

Regarding the latewood, its average per trial was between 0.65 mm, in the Zărnești trial, and 0.78 mm, in the Turda trial.

The lowest value of the average growth in the earlywood was also achieved in the Zărnești trial - 1.90 mm, and the highest value, in the Dorna Candrenilor trial - 2.08 mm.

The highest average value of the percentage of latewood was obtained in the Turda trial - 30.76%, and the lowest value, in the Dorna Candrenilor trial - 27.06% (Fig. 27).

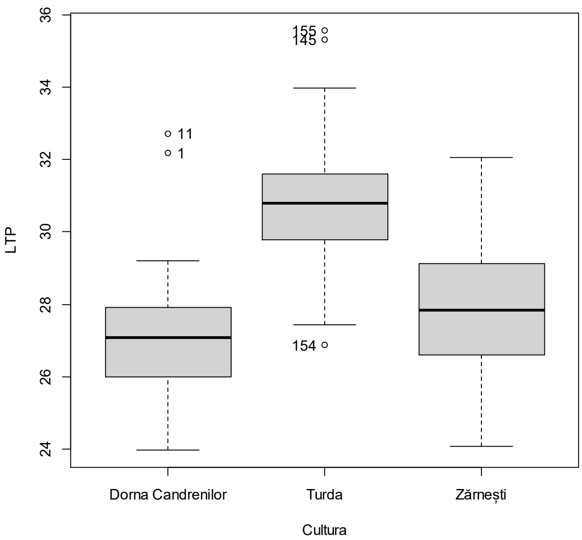


Fig. 27. Variation of latewood percentage in the three comparative Norway spruce provenance trials, at the age of 49 years

The provenance 56-Anfasterod, from Northern Europe, had a high DCL in all three comparative trials, the values being between 0.350 and 0.356 g/cm^3 in the comparative trials Turda and Dorna Candrenilor, respectively.

The provenance 55-Munkahus, also from Northern Europe, had low values of conventional wood density in all three comparative trials, between 0.319 and 0.330 g/cm^3 in the Turda and Zărnești comparative trials, respectively.

Among the Romanian provenances, 64-Gheorghieni and 67-Frasin performed well in two of the three comparative trials; Dorna Candrenilor and Zărnești, respectively Turda and Zărnești. The provenance 68-Breaza performed above average in the three comparative trials, even good in the comparative trial Zărnești.

Analysing the provenance x trial interaction for annual radial growth, it was highly significant for all traits. The year x provenance interaction was significant only for mean ring width and mean earlywood.

The differences between trials, between years, between repetitions, as well as the locality x years interaction were highly significant for all annual radial growths, as well as for latewood percentage.

From the point of view of the stability of the performances, the highest correlation coefficient was obtained for the pruned height between the Dorna Candrenilor trial and the Zărnești trials. This denotes an instability of performances and a pronounced provenance x trials interaction.

Total height and survival percentage were the only traits for which there were significant correlations between all three comparative trials. The values of the correlation coefficients were between 0.4387 and 0.581, for total height, and 0.327 and 0.505, respectively, for the survival percentage.

4.3.2. Evolution in time of the correlations between climate variables and standardised ring width

Analysing the moving window correlations, the rainfall in July was always positively correlated with the standardised ring width in the comparative Dorna Candrenilor trial (Fig. 28), but they became significant only after 1991.

In contrast, the correlation coefficients with April precipitation gradually decreased, reaching negative values for the last sub-period, 1996-2020. The correlation coefficients with March temperature were also positive, more pronounced after 1990. The correlation coefficients with May temperature, although positive in the first sub-periods, starting from 1987-2011 were negative.

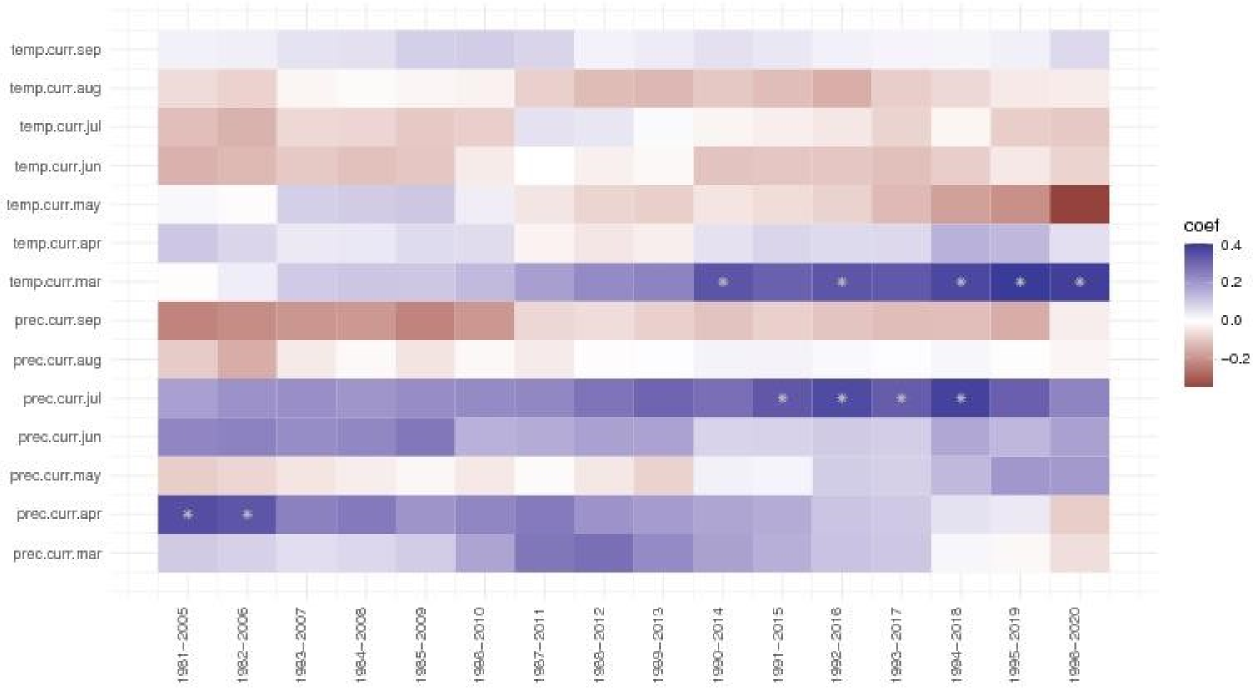


Fig. 28. Analysis of the moving window correlations for the comparative trial Dorna Candrenilor

In the Zărnești trial, the precipitation in June was significant for the sub-periods from 1981 to 2007, and then, although the correlation coefficient values remained positive, they started to decrease (Fig. 29). Although insignificant, the correlations with September precipitation and May temperature were always negative, but more pronounced in the last sub-periods.

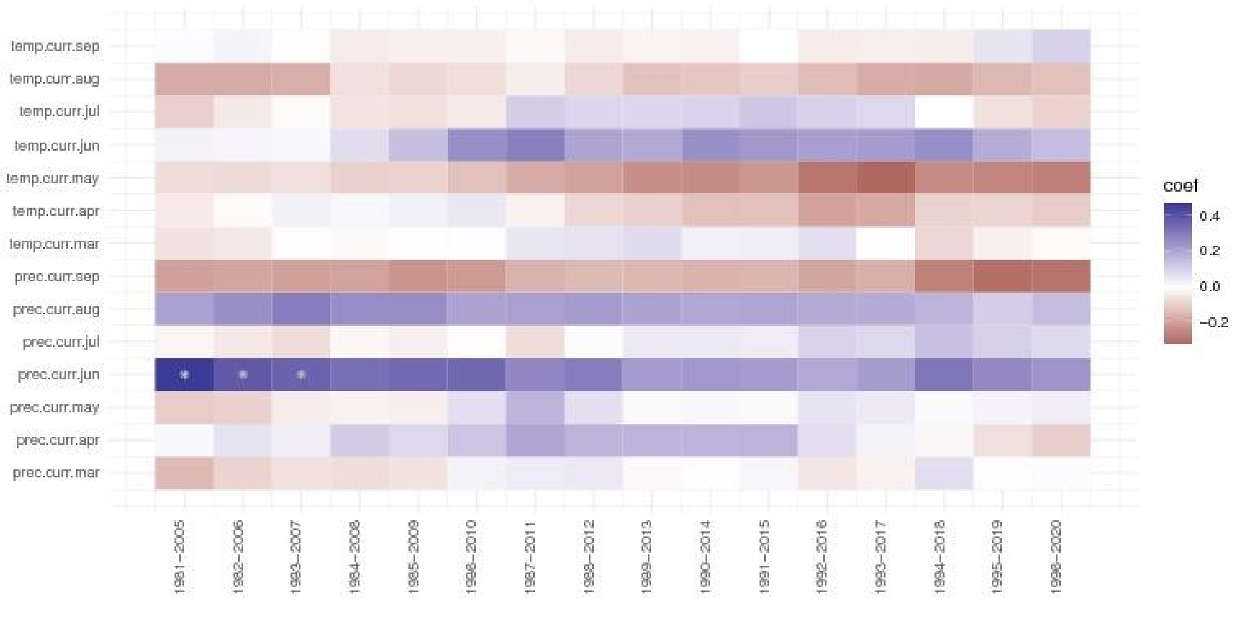


Fig. 29. Analysis of the moving window correlations for the comparative trial Zărnești

In the comparative trial Turda, the correlations with the precipitation in June and July were always positive, but more accentuated in the last three-four sub-periods (Fig. 30). The negative correlation of March temperature in the first analysed sub-period, 1981-2005, became positive starting from the 1983-2007 sub-period, and even significant in the 1993-2017 sub-period. The correlation with the temperature in May, which was significant for the sub-periods 1987-2011 and 1988-2012, was negative for all the sub-periods analysed, except for the last three, when the correlation coefficient values were close to zero.

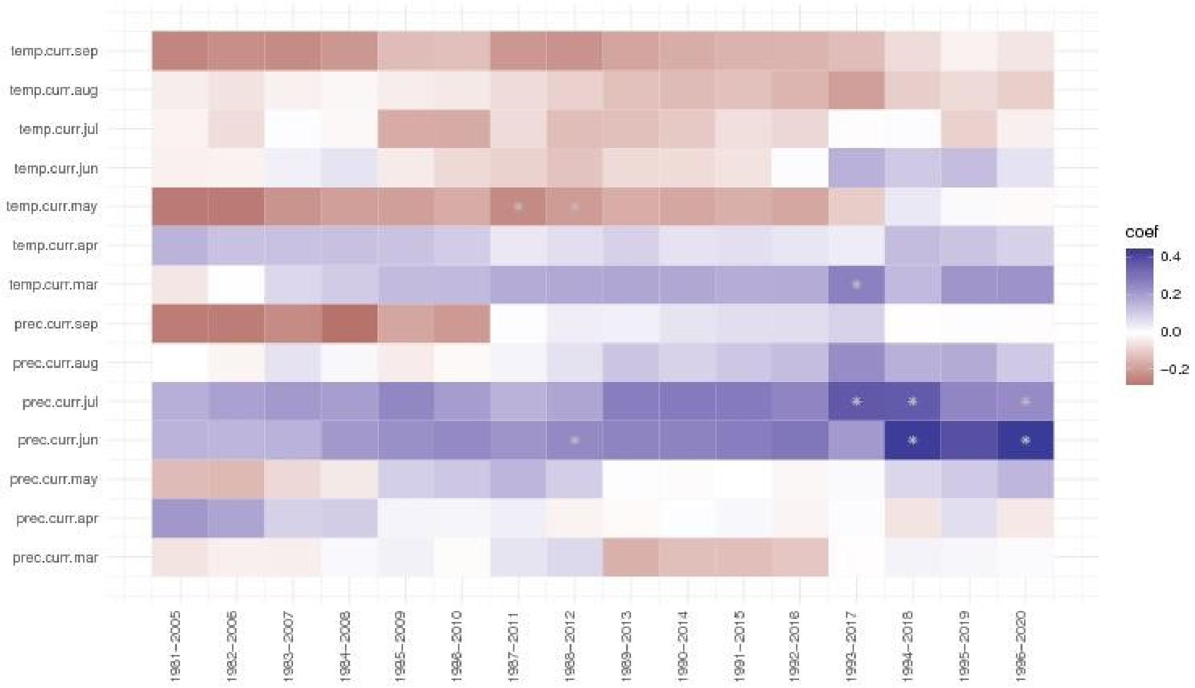


Fig. 30. Analysis of the moving window correlations for the comparative trial Turda

4.3.3. Response functions to the climatic conditions of the testing site

4.3.3.1. Response functions for latewood percentage

The response patterns for LTP were significant, with adjusted R^2 ranging from 0.143 to 0.247. The average temperature of the warmest three-month period had a positive influence on LTP in the comparative trial Zărneşti. For this trial, the quadratic model that considered the number of frost-free days obtained a higher adjusted R^2 of 0.163.

In the comparative Dorna Candrenilor trial, the quadratic model with the highest adjusted R^2 was the one with degree-days above 0°C and precipitation of the rainiest month, and the influence of these terms was 22.2% and 8.6%, respectively.

In the comparative trial Turda, the best quadratic model was the one that had as terms the degree-days above 5°C and the summer heat moisture index, (SHM index), which had an influence of 22.2%, respectively 6.4% on the percentage of latewood, LTP.

4.3.3.2. Response functions for total height and diameter at breast height

The patterns of the response functions for diameter at breast height and total height were significant, with adjusted R^2 ranging between 0.289 and 0.665, respectively.

The high average temperature during autumn had a negative influence on both diameter at breast height and total height. The partial R^2 for this factor had values of 29.4% and 66.4% for the diameter at breast height and the total height, respectively.

Conversely, abundant precipitation in the warmest three-month period had a positive influence on the two traits (Figs. 31 and 32). The influence of this factor was somewhat lower than that of the average temperature during autumn, the partial R^2 being between 19.9% and 58.8%, for the diameter at breast height and the total height, respectively.

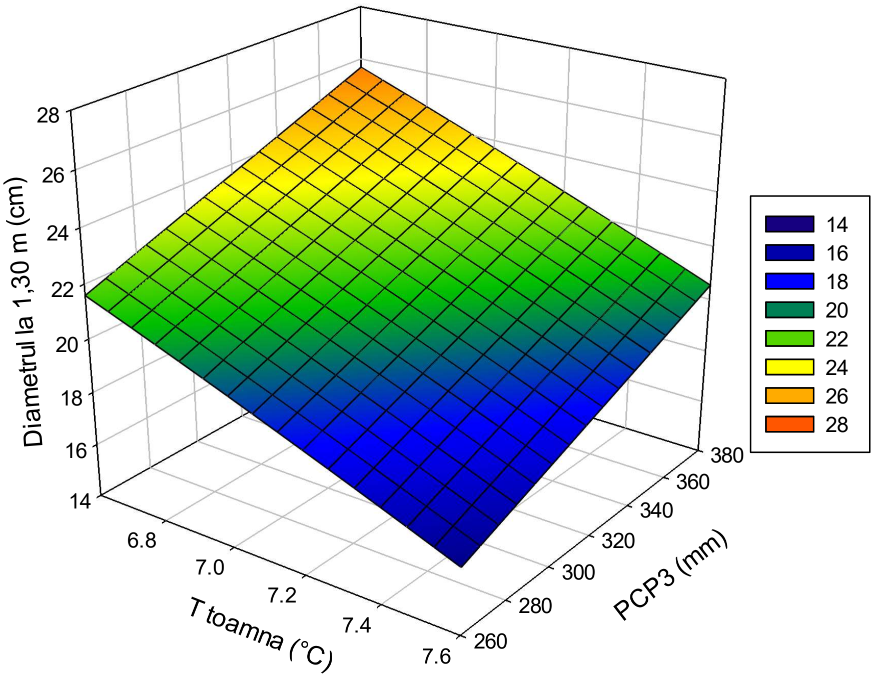


Fig. 31. Response function for diameter at breast height of Norway spruce provenances at age 49

Ttoamna – the average temperature during autumn; PCP3 – sum of precipitation in the warmest 3-month period (June, July, August).

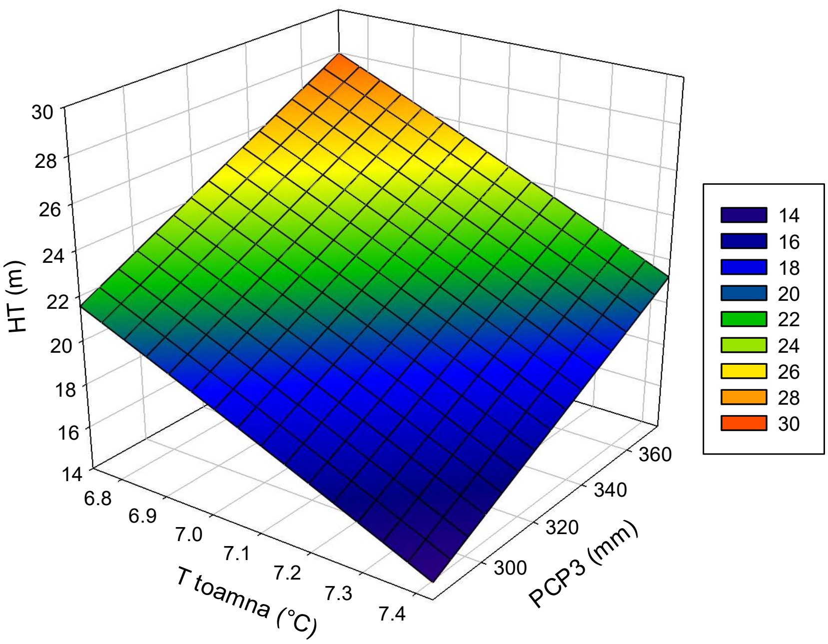


Fig. 32. Response function for total height of Norway spruce provenances at age 49

4.3.4. Transfer functions for the tested Norway spruce provenances

4.3.4.1. Transfer functions for total height

The difference in precipitation in the warmest 3-month period and the difference in the average temperature of the rainiest 3-month period between the planting site and the place of origin of the provenances were the variables that influenced the total height in the Zărnești comparative trial (Fig. 33).

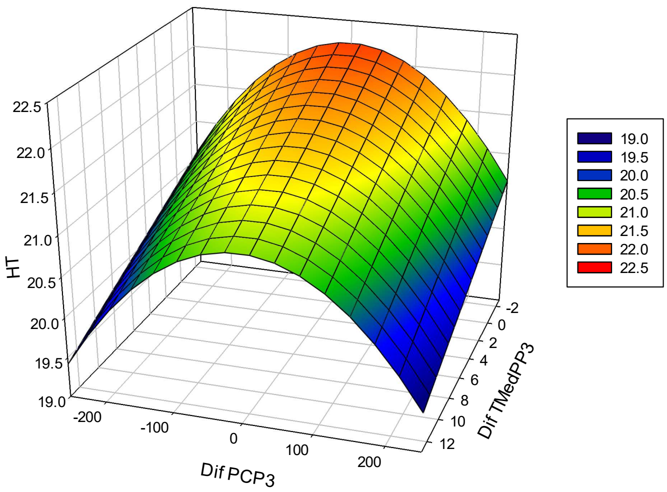


Fig. 33. The transfer function for the total height (HT) of the Norway spruce provenances at the age of 49 years in the comparative trial Zărnești

Dif PCP3 – the difference in precipitation in the warmest 3-month period between the planting site and the place of origin; Dif TMedPP3 – the difference in the average temperature of the rainiest 3-month period between the site and the place of origin of the provenances.

After running the linear model with all climate variables, the differences between the warmest month's maximum temperature and the warmest period precipitation influenced the total height in the comparative trial Dorna Candrenilor (Fig. 34).

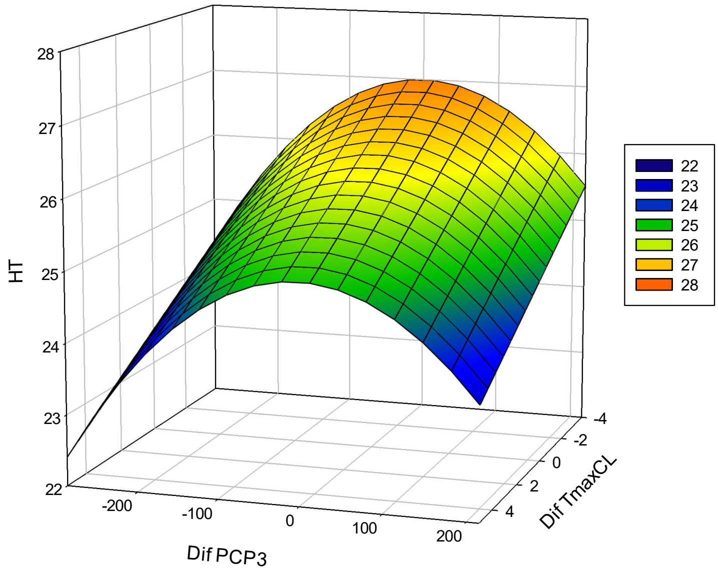


Fig. 34. Transfer function for the total height (HT) of Norway spruce provenances at the age of 49 years in the comparative trial Dorna Candrenilor

Dif PCP3 – the difference in precipitation in the warmest 3-month period between the planting site and the place of origin; Dif TMaxCL – the difference in the maximum temperature of the warmest month between the place of planting and the place of origin of the provenance.

In the comparative trial Turda, the variables that influenced the total height of the provenances were the difference in precipitation from the coldest 3-month period and the difference in the average temperature of the wettest 3-month period between the planting site and the place of origin of the provenances (Fig. 35).

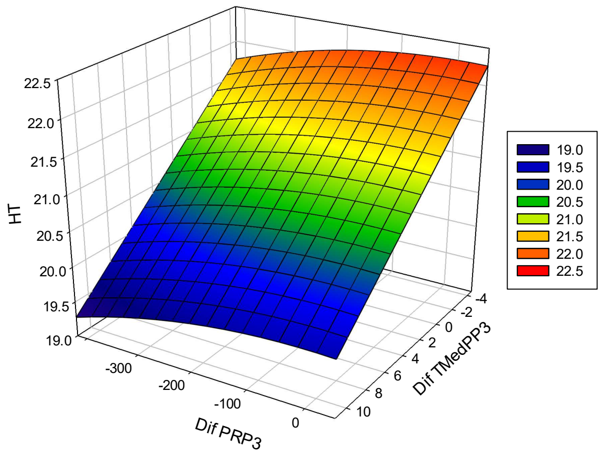


Fig. 35. Transfer function for total height (HT) of Norway spruce provenances at the age of 49 years in the comparative trial Turda

Dif PRP3 – the difference in precipitation in the coldest 3-month period between the planting site and the place of origin; Dif TMedPP3 – the difference in the average temperature of the rainiest 3-month period between the place of planting and the place of origin of the provenances.

4.3.4.2. Transfer functions for the survival percentage

The differences between the average diurnal amplitude (MAD) and the seasonality of precipitation (SP) were the ones that had a negative and positive influence, respectively, on the survival percentage of the Norway spruce provenances in the Zărnești comparative trial. The partial R^2 for these factors was 0.095 and 0.042, respectively (Fig. 36).

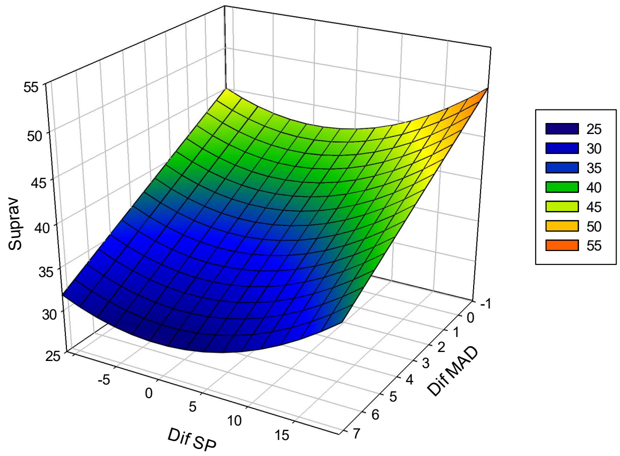


Fig. 36. Transfer function for the percentage of survival (Suprav) of Norway spruce provenances at the age of 49 years in the comparative trials Zărneşti

In the comparative trial Dorna Candrenilor, the differences between the average annual temperature of the planting site and that of the place of origin of the provenances, as well as those of the precipitation in the warmest period, had a negative influence on the survival percentage (Fig. 37).

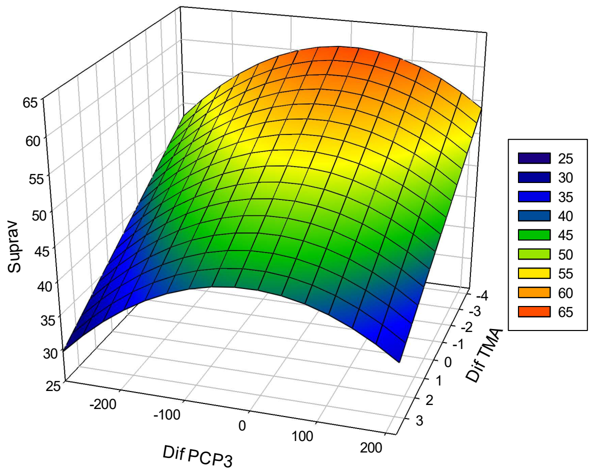


Fig. 37. Transfer function for the percentage of survival (Suprav) of Norway spruce provenances at the age of 49 years in the comparative trial Dorna Candrenilor

Differences in the average temperature of the warmest 3-month period had a positive influence on the percentage of survival in the comparative trial Turda. Here, as in the comparative Dorna Candrenilor trial, the differences between the precipitation in the warmest period had a negative influence (Fig. 38).

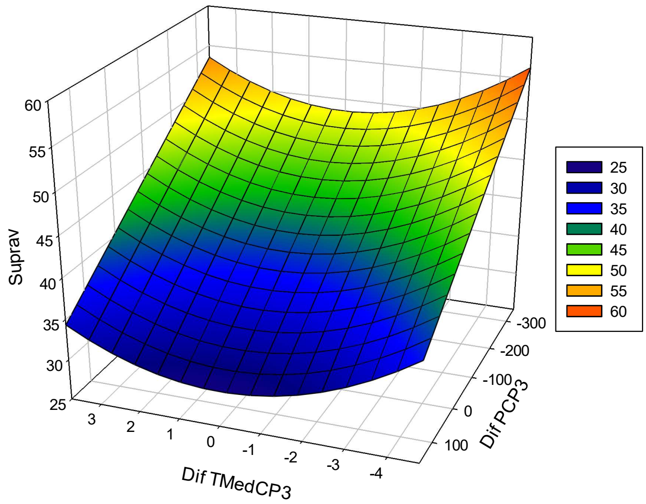


Fig. 38. Transfer function for survival percentage (Suprav) of Norway spruce provenances at the age of 49 years in the comparative trial Turda

4.3.5. Discussion

The genotype x environment interaction (GxE) was highly significant for HT and HE, but non-significant for D1.30m, Suprav and DCL. The results are consistent with those of Chen et al. [185], who observed a highly significant GxE interaction for total height of Norway spruce *half-sib* progeny in Sweden.

Through this study, the importance of GxE interaction in Norway spruce improvement and reforestation programs is ascertained, especially in areas exposed to drought or other risk factors. Identification of stable provenances reduces long-term risks, but the selection of provenances adapted to specific environments maximises genetic gains for all environments [186]. Similar results for Norway spruce were obtained for height [187], and height and diameter in a study with 20 Romanian provenances at the age of 34 [3]. Also, in another series of comparative Norway spruce trials installed in Romania, the GxE interaction was not significant for D1.30m [157].

Also, the fact that the GxE interaction for D1.30m, Suprav and DCL was small but large for other traits indicates a high plasticity of Norway spruce. Although not all phenotypic plasticity is adaptive, it can facilitate the manifestation of well-adapted phenotypes in new environmental conditions, thus allowing the perpetuation of a population [188].

The differences between provenances in terms of conventional wood density were not significant, but very close to meeting this criterion, p= 0.0503. The GxE interaction was not significant, indicating high stability of provenances with respect to conventional wood density. Test sites influenced conventional wood density, with differences between trials being significant. In another study, regarding other Norway spruce provenance trials from Romania, the differences between provenances were significant, and the GxE interaction was also insignificant, with the provenances having stable performances in terms of DCL [162].

From the analysis of the moving windows correlations, the positive influence that the temperature in March has on the annual growth of the Norway spruce in the comparative trials Dorna Candrenilor and Turda can be observed. This can be explained by a longer growing season.

Changes in snow cover and its melting, as well as frozen ground dynamics, have a negative impact on tree growth [189], [190]. A low snowpack and its early thaw affect the water supply obtained by snowmelt, which supports tree growth in areas affected by water stress [189]. In addition, early snowmelt can promote spring phenology (tree budding), thus increasing the length of the growing season [143], but exposes trees to late frosts [191], [192]. Weigel et al. [193], [194] showed the importance of winter climate change since marginal populations in cold areas become more sensitive to low winter temperatures, specifically from February in his case, and less sensitive to precipitation from June.

A negative effect of increasing temperature on growth traits in conifers was also observed in the study by Gómez-Aparicio et al. [195], which may be associated with a greater demand for atmospheric water, intensifying drought stress. Even if precipitation is abundant, high temperatures can increase soil water loss through evaporation and reduce soil moisture [196], [197], [198].

Precipitation amounts in June and July also became important for pine growth [199], a novelty compared to previous studies [200]. Roibu et al. [201], also analysing 25-year sub-periods, observed the mobility of the correlations with temperature and precipitation for ash and oak in the Republic of Moldova. The amount of summer precipitation was a factor with a stable influence on the radial growth of four analysed species in Northern Germany, beech, oak, pine, and Douglas fir [202].

The climatic variables with influence on the percentage of latewood were the average temperature of the warmest three-month period (summer), the number of degree-days above 0 and 5 °C, the number of frost-free days, the amount of precipitation in the rainiest month and SHM. Apart from the SHM in the comparative trial Turda, all other climatic variables had a positive impact on the latewood percentage.

Norway spruce is a very sensitive species to drought, the density of its crown is affected, especially in the case of droughts that occur at the beginning of summer [203]. Solberg reported that summer droughts affect Norway spruce crown and survival [204]. Norway spruce, Douglas fir, fir and cedar were classified as heat-sensitive species [205].

The sum of the precipitation in June, July, and August, the warmest 3-month period, had a positive influence on the total height and diameter at breast height of the Norway spruce provenances. High average temperatures during autumn negatively influenced these two analysed traits. High temperatures at the end of the growing season reduce soil moisture by increasing evapotranspiration [206], and high rainfall during autumn increases the amount of water in the soil and the amount of water available in early spring [207]. It is also possible that high temperatures in late summer and early autumn reduce carbohydrate reserves, which are an important element in needle development and cambium growth, from the early stages of the next growing season [56].

For the transfer functions for the total height, regarding the influence of temperature, the variables were different for each comparative trial: the difference in the warmest 3-month period for Zărnești, the difference in the maximum temperature of the warmest month, for Dorna Candrenilor, and the average temperature difference of the wettest period of 3 months, for Turda. However, the same trend can be observed for all of them: provenances from places where the previously mentioned temperatures were higher than those of the planting site (origins from warmer places) had higher total heights.

The closer the amounts of precipitation in the warmest 3-month period of the planting site were to those of the place of origin of the provenances, the higher the percentage of survival and total height were in the comparative trial Dorna Candrenilor. The same is true for total height in the Zărnești comparative trial. In the comparative trial Turda, however, provenances from places where precipitation in the warmest 3-month period exceeds that of the planting site had a higher survival percentage.

The differences in precipitation between the planting site and the place of origin of the provenances had a greater influence than the temperature differences on the total height in the Zărneşti and Dorna Candrenilor trials. Similar results were obtained for other 2 out of 5 comparative trials from Romania, in which only Romanian provenances were tested at the age of 34 [3].

4.4. Selection of the best provenances based on selection indices

4.4.1. Selection of provenances in each trial, using the MGIDI index

In each comparative trial, factor analysis grouped the traits into a single factor. The group effect was abandoned to be able to select provenances from the entire area. Not considering the influence of this effect, the differences between the Norway spruce provenances from the comparative trial Turda are also significant regarding D1.30m and Suprav (Table 7).

Table 7. Analysis of the variability of the traits analysed for the MGIDI calculation in each Norway spruce trial at 49 years

Provenance trial	Trait	LRTp	Vp	Vr	MS rep
Dorna Candrenilor	D1,30m	61,11***	2,42	28,87	16,95 ns
	HT	304,50***	2,34	8,14	62,90***
	HE	430,20***	1,48	3,44	104,90***
	Suprav	42,19***	81,97	104,50	533,50**
Zărnești	D1,30m	2,44 ns	0,33	22,25	90,94*
	HT	57,88***	1,11	11,13	208,30***
	HE	258,50***	2,35	6,31	319,70***
	Suprav	0,00 ns	0,60	185,4	504,90 ns
Turda	D1,30m	4,66*	0,73	30,31	36,27 ns
	HT	75,78***	1,29	9,44	53,89**
	HE	98,14***	1,24	7,03	21,17*
	Suprav	7,76**	37,02	160,30	906,80**

D1,30 – diameter at breast height; HT – total height; HE -prunned height; Suprav – survival rate

The provenances selected in the Dorna Candrenilor comparative trial are: 72-Dorna Candrenilor, 74-Galu, 66-Marginea, 71-Moldovița, 64-Gheorghieni and 70-Coșna, all from the Romanian Carpathians; 51-Herfenberg, from the Bohemian Plateau; 39-Klaunz Bannwald, 53-Neustift and 41-Eppenstein from the Eastern Alps; 101-Valke Karlovice and 61-Nyugatbukki Allami from the Western Carpathians.

The provenances selected in the Zărnești comparative trial are: 72-Dorna Candrenilor and 74-Galu from the Romanian Carpathians, 27-Bodenseichen from Germany; 60-Keletbukki Allami from the Western Carpathians; 51-Herfenberg, 52-Sandl-bei-Freistadt and 100-Kasperske Hory from the Bohemian Plateau; 26-Winterthur, 25-Wassen and 38-Val Di Fiemme, from the Central Alps; 39-Klaunz Bannwald and 41-Eppenstein from the Eastern Alps.

The provenances selected in the Turda comparative trial are: 70-Coşna, 66-Marginea and 72-Dorna Candrenilor from the Romanian Carpathians; 60-Keletbukki Allami from the Western Carpathians; 40-Wietersdf, 42-Rotlgut Liezen, 50-Hoyos-Ernest-reith, 49-Redl-Zipf-Fuchsberg and 41-Eppenstein from the Eastern Alps; 25-Wassen from the Central Alps; 100-Kasperske Hory and 99-Zelesna Ruda from the Bohemian Plateau.

Selected provenances outperformed trial averages for all traits. The differences were larger, with values between 0.18 and 16.5% (Table 8).

Table 8. Differences obtained by selection using the MGIDI index of Norway spruce provenances at the age of 49

Traits	Trial average			Selected provenances average			Difference %		
	Dorna Candrenilor	Zărnești	Turda	Dorna Candrenilor	Zărnești	Turda	Dorna Candrenilor	Zărnești	Turda
D1,30 m (cm)	23,8	21,1	21,6	25,7	21,5	22,2	8,1	1,6	2,9
HT (m)	25,9	21,4	21,5	28,1	22,7	22,8	8,4	5,9	6,1
HE (m)	16,7	11,0	11,2	18,2	12,8	12,4	9,0	16,5	10,3
Suprav (%)	50,0	40,7	36,8	56,0	40,7	40,2	12,0	0,2	9,3

4.4.2. Selection of provenances based on the MTSI index

If we consider the superiority (with a weight of 75%) and the stability (with a weight of 25%) of the analysed traits, the provenances selected using the MTSI index are the following: 72-Dorna Candrenilor, 41-Eppenstein, 60-Keletbukki Allami, 70 -Coșna, 100-Kasperske Hory, 66-Marginea, 40-Wietersdorf, 39-Klaunz Bannwald, 99-Zelesna Ruda, 71-Moldovita, 52-Sandl-bei-Freistadt and 63-Nyugatbukki Allami (Fig. 39). However, the provenances 25-Wassen, 61-Nyugatbukki Allami, 73-Stulpicani, 51-Herfenberg and 74-Galu are also highlighted.
The selected provenances performed better compared to the trial average for all traits analysed. The differences were higher with values between 6.4 and 17.8% (Table 9).

Table 9. Differences obtained by selection using the MTSI index of Norway spruce provenances at the age of 49

Traits	Trial average			Selected provenances average			Difference %		
	Dorna Candrenilor	Zărnești	Turda	Dorna Candrenilor	Zărnești	Turda	Dorna Candrenilor	Zărnești	Turda
D1.30m (cm)	23,8	21,1	21,6	25,5	22,5	23,2	7,0	6,4	7,3
HT (m)	25,9	21,4	21,5	27,7	23,2	23,0	6,9	8,6	6,9
HE (m)	16,7	11,0	11,2	18,0	12,7	12,3	7,7	15,8	9,6
Suprav (%)	50,0	40,7	36,8	57,2	44,8	43,4	14,4	10,0	17,8

D1,30m – diameter at breast height; HT – total height; HE -prunned height; Suprav – survival rate.

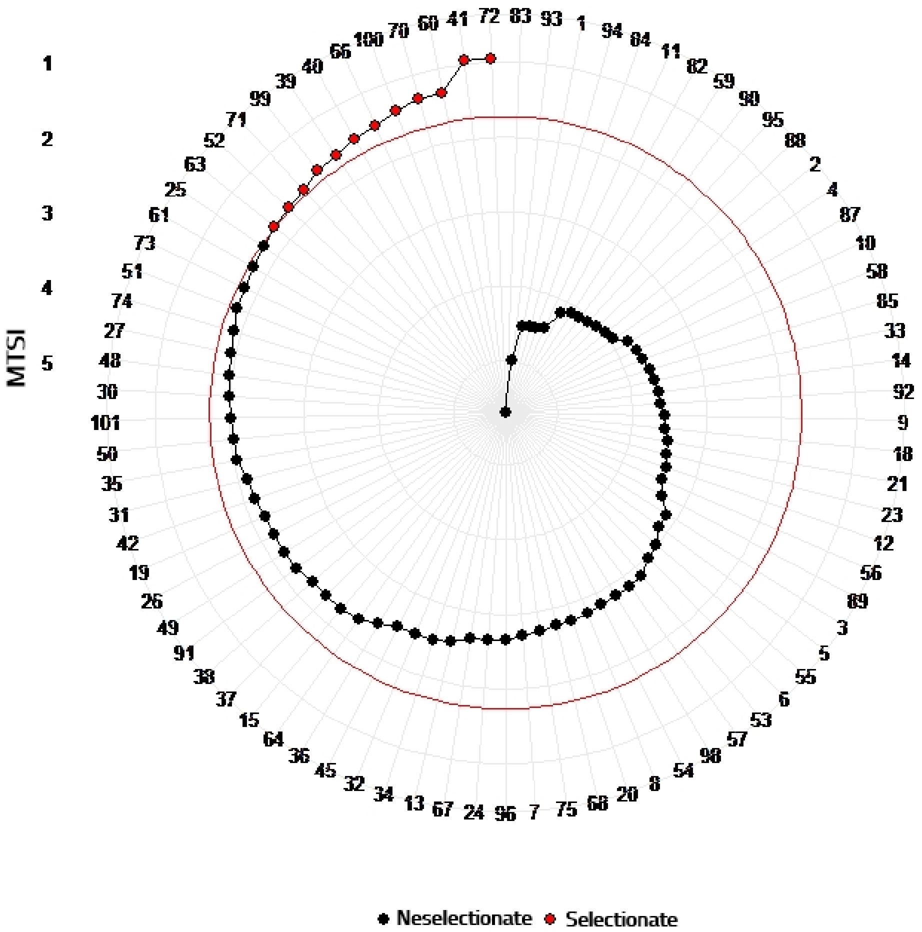


Fig. 39. Ranking of Norway spruce provenances using the MTSI index

The red line represents the selection intensity (15%). The points represent the values of the MTSI index. The red dots correspond to the selected provenances.

The classification of provenances for each characteristic used in the MTSI calculation is shown in Fig. 40 - 43.

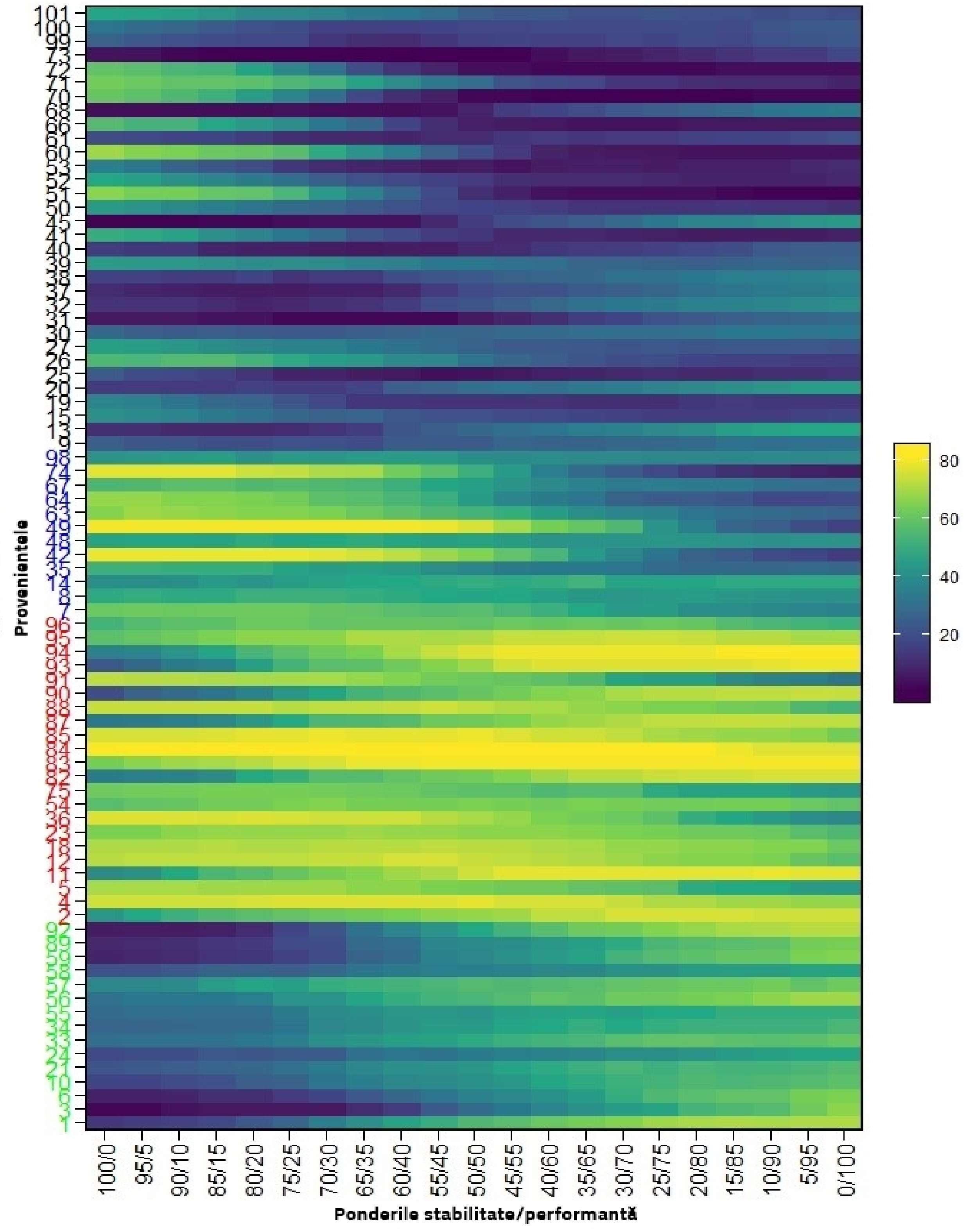


Fig. 40. Classification of provenances by assigning different weights to stability and average performance regarding diameter at breast height

Coding on the OY axis: ***Black-performant and stable****; Blue-performant but unstable; Red - underperforming and unstable; Green - underperforming but stable. The colours in the graph represent the ranking of the respective origin, depending on the scenario: dark blue – is best ranked; yellow - is the last place in the ranking.*

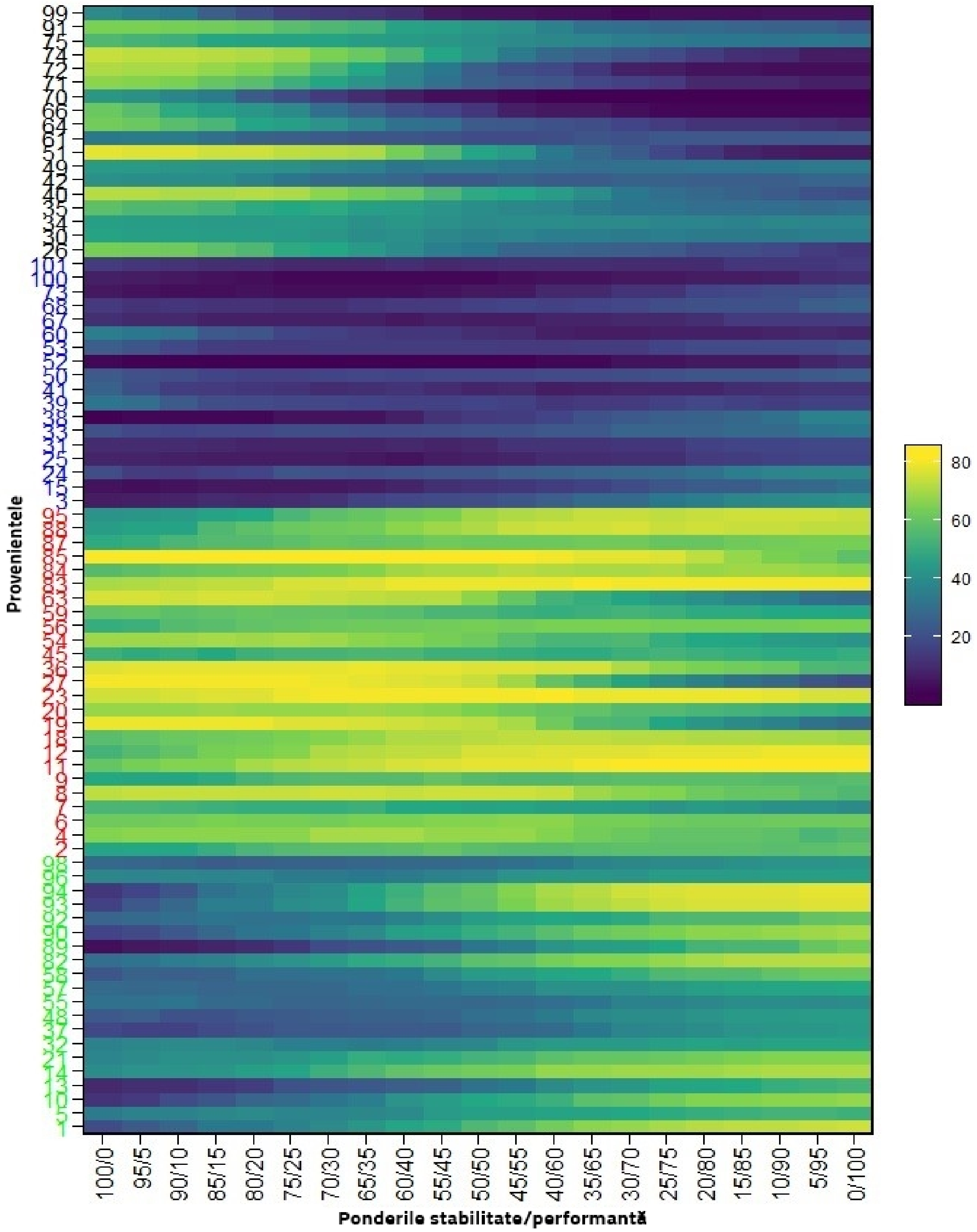


Fig. 41. Classification of provenances by assigning different weights to stability and average performance regarding total height

Coding on the OY axis: Black-performant, but unstable; ***Blue – performant and stable****; Red – underperforming and unstable; Green – underperforming, but stable.*

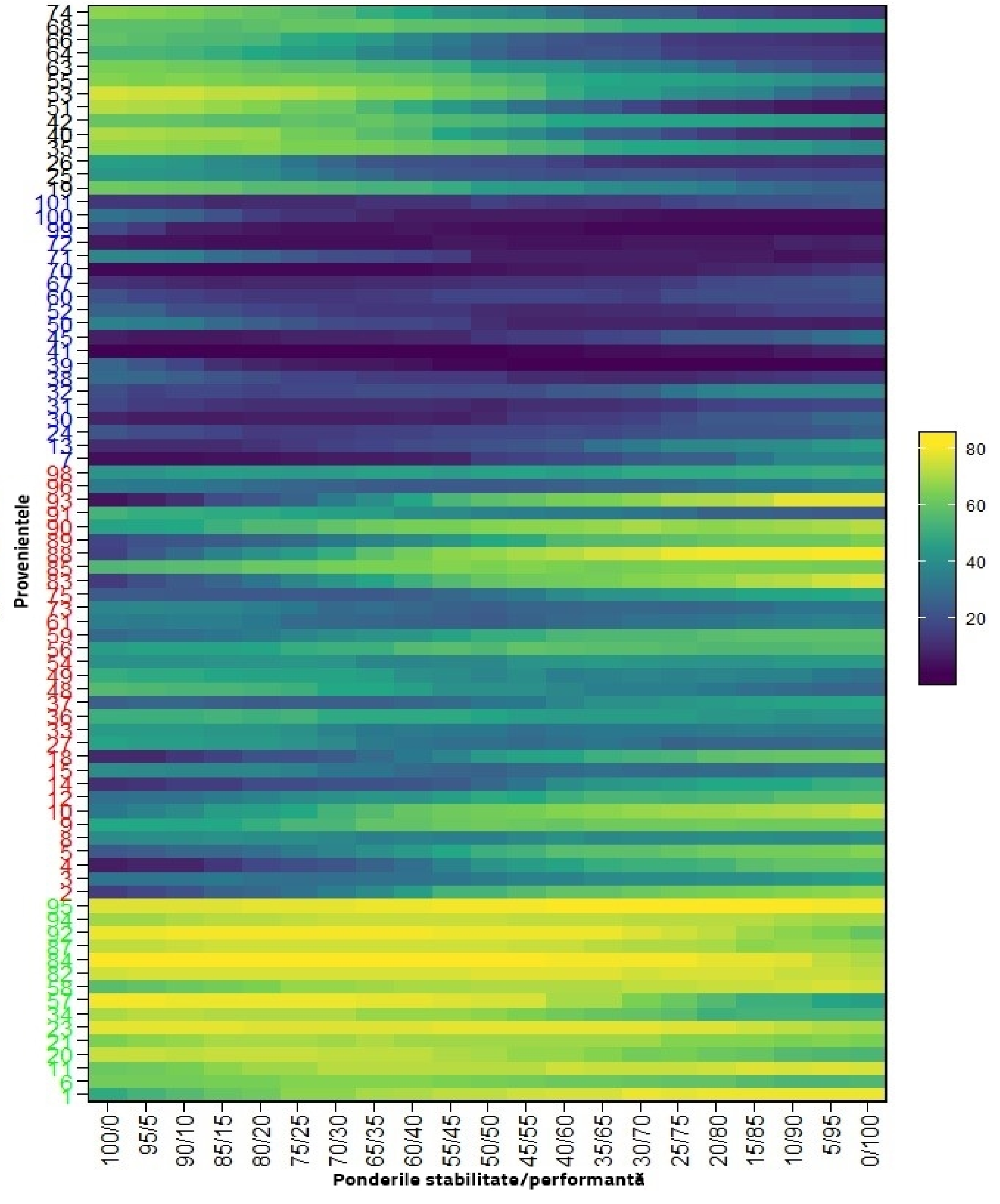


Fig. 42. Classification of provenances by assigning different weightings to stability and average performance regarding pruned height

Coding on the OY axis: Black - performant, but unstable; ***Blue – performant and stable****; Red - underperforming but stable; Green - underperforming and unstable.*

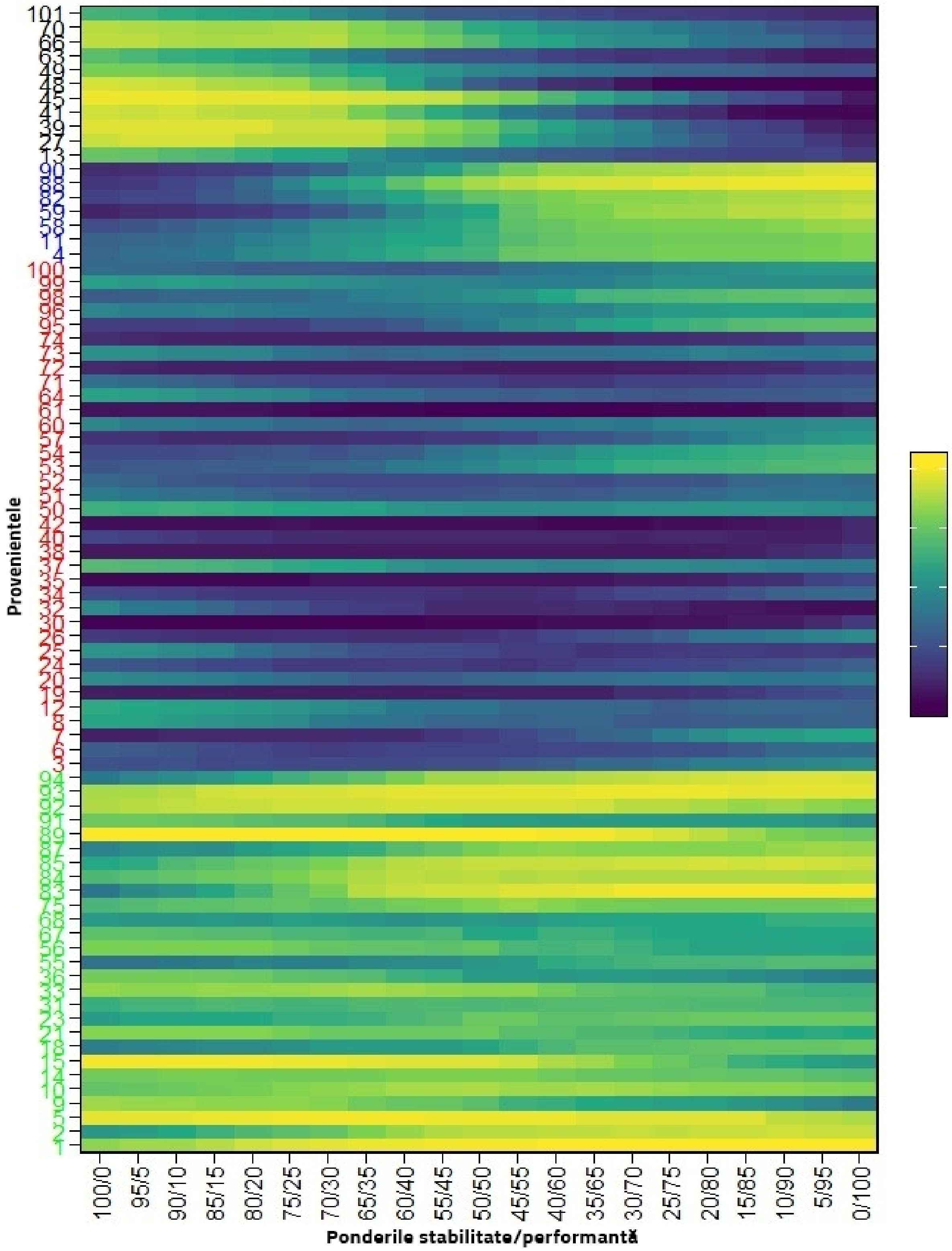


Fig. 43. Classification of provenances by assigning different weights to stability and average performance regarding survival percentage

Coding on the OY axis: Black - performant, but unstable; Blue - underperforming, but stable; ***Red - performant and stable****; Green - underperforming and unstable.*

Among those selected, provenance 60-Keletbukki Allami, from the Western Carpathians, 100-Kasperske Hory and 52-Sandl-bei-Freistadt, both from the Bohemian Plateau, were classified as stable and performing (group 1) for all four traits (Fig. 44).

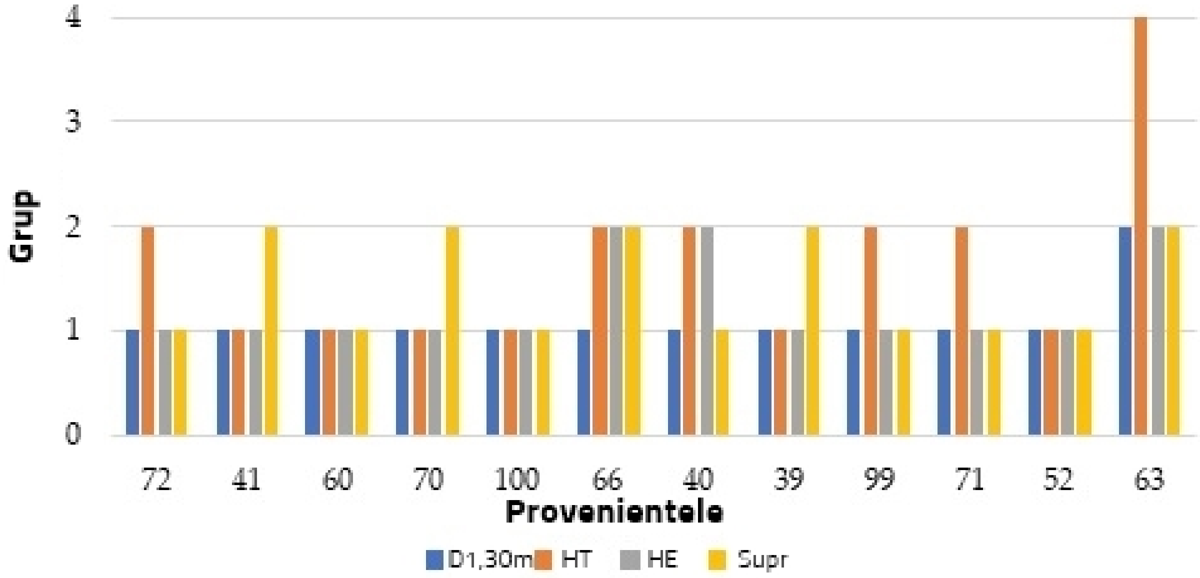


Fig. 44. Grouping of selected provenances using the MTSI index

1 - performing and stable; 2 – performing, but unstable; 3 – non-performing, but stable; and 4 – non-performing and unstable.

The 41-Eppenstein and 70-Coșna provenances were stable and performing (group 1) for D1.30 m, HT and HE, but in terms of survival, they were classified as performing but unstable (group 2).

The provenances 71-Moldovița, 72-Dorna Candrenilor and 99-Zelesna Ruda were stable and performing in terms of D1.30 m, HE and Suprav, and performing but unstable in terms of HT.

The 66-Marginea and 40-Wietersdf provenances were stable and performing in terms of D1.30 and performing but unstable in terms of both heights. According to Suprav, provenance 66 was performing but unstable, and provenance 40 was stable and performing.

The 39-Klaunz Bannwald provenance was stable and performing for all traits except Suprav, where it was classified as performing but unstable.

The 63-Nyugatbukki Allami provenance was performing but unstable in all traits except HT, where it was classified as non-performing and unstable (group 4).

Among the other Romanian provenances, the 73-Stulpicani provenance was performing and stable for all traits, except for HT, where it was non-performing but stable (group 3). The 74-Galu and 64-Gheorghieni provenances were performing but unstable for D1.30 m, HT and HE and stable and performing with respect to Suprav.

4.4.3. Discussion

Stability analysis is often performed for a single feature, especially for tree species. The first indices of simultaneous selection were proposed by Smith [208] and Hazel [209]. But, if there is multicollinearity between the variables, the coefficient of the index can be influenced [153]. Allen [210] defined multicollinearity as the strong correlation between two or more variables. Multicollinearity is a problem in multivariate analyses, which occurs frequently in tree populations, and can create problems in the correct interpretation of results, leading to erroneous conclusions

[211]. One aspect of the Smith-Hazel index is the difficulty of expressing the economic value of the traits [212].

Selection for larger growth, quantity and quality of wood, and adaptability are among the main objectives of tree breeding programs. Thus, simultaneous selection is necessary to obtain results in the desired direction for several traits simultaneously [213].

The increase in the possibility of using fast and powerful computers has made it possible to use selection indices in forest tree breeding [214]. The first mentions of multiple trait-based selection indices in forest tree breeding were in the mid-1980s [215], [216]. By using the methodology of mixed models, the best linear unbiased predictions (BLUP) of the genetic values are obtained, which have many advantages over the predictions obtained by previously used analysis methods [217]. The most important advantage is that the ranking of genotypes using the genetic values estimated by BLUP is very close to the real ranking of genotypes [217]. Also, mixed models can efficiently process unbalanced databases and remove the influence of non-genetic factors or heteroscedasticity between trials [218].

Multi-trait selection was performed within each trial and between trials. The method was based on the calculation of some selection indices that reflect the superiority for all the traits analysed in each trial (MGIDI) and the superiority and stability of the traits between trials (MTSI). If selection indices based on multiple traits are used, care must be taken that if too many traits are used, it is possible to identify genotypes that are close to average for all traits but extraordinary for none [217]. The selection indices used allowed the identification of superior provenances in terms of several traits, thus increasing the selection response. Thus, their use has proven effective in responding to selection in the direction of multiple trait-based breeding.

When the selection of provenances was made in each comparative trial, by using the MGIDI index, the ranking of the provenances was different for each trial. However, two provenances performed well in all three comparative trials: 72-Dorna Candrenilor and 41-Eppenstein. Among the 12 provenances selected with the MTSI index, 11 were also selected with the help of the MGIDI index, in at least one comparative trial. The only one not selected was the provenance 63-Nyugatbukki Allami, ranking 17th in Turda, 20th in Dorna Candrenilor and 21st in Zărnești, according to the MGIDI index.

Provenances selected with the help of these two indices have a high value for the improvement and use of forest reproductive material. They have demonstrated good growth performance and stability and belong to the Eastern and Western Carpathian, Bohemian Plateau and Eastern Alps groups. Also in other studies, provenances from the Eastern Carpathians, the Bihor Mountains, and the region between the Beskizi Mountains and the Erz Mountains to the foothills of the Harz Mountains performed well in different ecological conditions [219] [220]. Schuler [221] also found that the most productive provenances and with potential in Austria's future climatic conditions come from the Bohemian Massif and the south-eastern edge of the Alps. Some Romanian provenances performed well regarding total height and volume, at the age of 32 years, in a Norway spruce provenance trial, from Latvia, one of them being Dorna Candrenilor [109]. Carpathian and Baltic Norway spruce provenances have shown superior growth [222], even in Canada [223]. Romanian Norway spruce provenances had higher growth than local provenances, even at low altitudes in eastern Norway [113].

Another important element of the MTSI index is that the 63-Nyugatbukki Allami provenance was selected through its use, although it was classified as unstable and underperforming in terms of overall height. If the selection had been made according to this characteristic, this provenance would not have been selected.

5. CONCLUSIONS. PERSONAL CONTRIBUTIONS. DISSEMINATION OF RESULTS. FUTURE RESEARCH DIRECTIONS

5.1. Conclusions

Regarding the evaluation of the genetic variability of the main economic and adaptive traits in provenance trials

◘ The genetic variability of Norway spruce [*Picea abies* (L.) Karst.] was evaluated in three common garden experiments from Romania. A total of 81 Norway spruce provenances from Romania and 12 other European countries from 11 geographical groups were analysed and compared 49 years after planting. Significant differences were observed between provenances, geographic groups, and field trials for diameter at breast height, total and pruned height, and survival percentage.

◘ High genetic variability in annual diameter growth and drought response of tested Norway spruce provenances was observed. These results can be used in breeding programs as well as genetic conservation, but also represent a step in the development of an adaptation strategy for this species.

◘ The drought response of the provenances was influenced by the years in which the droughts occurred, as well as the seasonal conditions of the planting site.

◘ A longer period was required for recovery, indicating a reduced revitalisation capacity of Norway spruce after drought episodes. However, some provenances with high radial growth and good strength and/or recovery have been identified.

Regarding the evaluation of the genotype x environment interaction in the case of Norway spruce provenances tested in comparative trials from Romania

◘ The results confirm that Norway spruce has high phenotypic plasticity, and there is potential for important genetic gains in the next phases of breeding programs.

◘ The effect of planting sites is greater than that of provenances, which underlines the necessary attention to seasonal conditions in reforestation works.

Regarding the analysis of phenotypic correlations between traits of economic and adaptive interest and between them and the geographic gradients of origin of the provenances tested

◘ There were significant and positive correlations between the altitude of origin of the provenances and their survival percentage in all three comparative trials. Thus, provenances from higher altitudes obtained higher survival percentage values.

◘ Southern provenances obtained higher survival percentages and diameters at breast height than northern provenances in all three comparative trials.

◘ Likewise, the southern provenances had higher pruned heights than the northern ones in the Dorna Candrenilor and Zărnești trials.

◘ Low-elevation provenances had higher resilience and relative resilience than high-elevation provenances in the Turda trial but lower recovery and relative resilience in the Zărnești trial.

◘ The northern provenances had a higher relative recovery and resilience compared to the southern ones in the Dorna Candrenilor and Turda trials, but their values were lower compared to the southern ones in the Zărnești trial.

◘ The eastern origins had a lower resistance compared to the western ones in the Dorna Candrenilor trial, but a greater resistance compared to the western ones in the Zărnești trial.

◘ Provenances with a high percentage of survival had lower relative recovery and resilience in the Dorna Candrenilor trial, compared to those with a lower percentage of survival. In the Zărnești trial, the situation was the opposite; those with a high survival percentage had a high relative recovery and resilience.

◘ Diameter at breast height, total and pruned height, and survival were all highly significantly correlated, except for the correlation between diameter at breast height and survival percentage in the Zărnești trial.

◘ The performances of the provenances were not very stable, according to the correlation coefficients. The interaction of provenance x trials and the influence of the place of planting is thus highlighted.

Regarding the analysis of the influence of climatic conditions on the biometric traits of Norway spruce provenances

◘ Significant changes in correlations between climate variables and standardised annual growth have been observed over the past 40 years.

◘ Response functions revealed the positive influence of high summer temperatures on latewood percentage.

◘ The negative influence of the high temperature during autumn on the diameter at breast height and the total height was also highlighted, as well as the positive influence of the sum of precipitation in June, July, and August (the warmest 3-month period) on the two analysed traits.

◘ The transfer functions highlighted the fact that the differences in precipitation in the warmest period, between the place of planting and the place of origin of the provenances, had a greater influence on the total height, compared to the temperature differences, in the Dorna Candrenilor and Zărnești trials, and on the percentage of survival in the Turda trials.

Regarding the selection of the best Norway spruce provenances using selection indices

◘ The indices used for the selection of provenances according to several traits do not have problems with multicollinearity and are easy to calculate and interpret. MGIDI can be used to select provenances adapted to certain seasonal conditions, and MTSI can be used to select provenances with good performance in several environmental conditions.

◘ They were established based on four traits, but more valuable results can be obtained if this number is increased.

◘ Different MTSI weights can also be used to prioritise either stability or average performance of provenances.

◘ Using the MTSI index, 12 provenances were identified from the entire range of the species, from the groups of the Eastern and Western Carpathians, the Bohemian Plateau, and the Eastern Alps, which had stability and high growth and adaptive performance.

◘ Considering the high vulnerability of genetic resources to climate change, it would be desirable for these unique lineages to be conserved *in-situ* and used in assisted migration as part of the forest adaptation strategy.

◘ The study of these provenances must be continued since the age of the field trials is only 49 years, half the age of the exploitability of Norway spruce in Romania.

5.2. Personal contributions

◘ Analysis of the genetic variability of the Norway spruce in provenance trials, half of the age of rotation of the Norway spruce in Romania.

◘ Analysis of the response of the provenances to extreme droughts by calculating the resilience parameters.

◘ Carrying out analysis of mobile periods for four decades in each field trial.

◘ Analysis of response functions in each field trial to determine the local climate variables with the most significant influence on total height, diameter at breast height, annual growth in diameter, and latewood percentage of Norway spruce provenances.

◘ Analysis of transfer functions in each field trial to determine the climatic differences between the planting site and provenance site that had the most significant influence on total height and survival percentage of Norway spruce provenances.

◘ Use of two new selection indices for the first time in a forest tree species, combining growth, quality, and provenance survival.

◘ Identification of 12 provenances from the entire distribution range of the species, from the groups of the Eastern and Western Carpathians, the Bohemian Plateau and the Eastern Alps, which showed stability and high performance for growth and adaptive traits.

5.3. Dissemination of results

A. Papers published in journals indexed by Clarivate Analytics (formerly ISI Web of Science):

As lead/corresponding author:

Alexandru, A.-M., Mihai, G., Stoica, E., & Curtu, A. L. (2023). Multi-Trait Selection and Stability in Norway spruce (*Picea abies*) Provenance Trials in Romania. Forests, 14(3), 456. https://doi.org/10.3390/f14030456

Mihai, G.; **Alexandru, A.M.**; Stoica, E.; Birsan, M.V. Intraspecific Growth Response to Drought of *Abies alba* in the Southeastern Carpathians. *Forests* 2021, *12*, 387. https://doi.org/10.3390/f12040387

Alexandru, A.-M.; Mihai, G.; Stoica, E.; Curtu, A. L. Drought Resilience Indices of Norway spruce Provenances Tested in Long-Term Common Garden Experiments in the Romanian Carpathians. *Preprints* 2024, 2024011040. https://doi.org/10.20944/preprints202401.1040.v1, sent for publication

As a co-author:

Mihai, G., Teodosiu, M., Birsan, M.-V., **Alexandru, A.-M.**, Mirancea, I., Apostol, E.-N., Gârbacea, P., & Ioniță, L. (2020). Impact of Climate Change and Adaptive Genetic Potential of Norway spruce at the South–eastern Range of Species Distribution. Agricultural and Forest Meteorology, 291, 108040. https://doi.org/10.1016/j.agrformet.2020.108040

B. Works published in journals indexed in international databases (BDI):

As lead/corresponding author:

Alexandru, A.-M., Mihai, G., Stoica, E., & Curtu, A. L., Variation in wood density among *Picea abies* provenances in the Romanian Carpathians, Bulletin of the Transilvania University of Braşov, Series II: Forestry, Wood Industry, Agricultural Food Engineering, Vol. 17(66) No. 1 – 2024. https://doi.org/10.31926/but.fwiafe.2024.17.66.1.1

C. Papers presented at national or international symposiums and conferences:

ALEXANDRU A.M., MIHAI G., CIOCÎRLAN E., CURTU A.L. et al., 2020: Variation of radial growth in Norway spruce provenance trials. International Conference 9th International Symposium Forest and Sustainable Development", Brasov, Romania, 16 October 2020, oral presentation;

ALEXANDRU A.M., MIHAI G., STOICA E., CURTU A. L., 2021: Analyzing adaptive traits of Norway spruce provenances in relation to their place of origin in common garden trials across Romanian Carpathians. International Conference IMER 5 - Integrated Management of Environmental Resources 2021, Suceava, Romania, 29 October 2021, oral presentation;

ALEXANDRU A.M., STOICA E., MIHAI G., CURTU A. L., 2022: Selection of the most adapted Norway spruce provenances for a sustainable forest management in the context of climate change. International Conference Ecology & Safety, Burgas, Bulgaria, 16-19 August 2022, Poster.

ALEXANDRU A.M., STOICA E., MIHAI G., CURTU A. L., 2023: The response to drought of Norway spruce (*Picea abies*) provenances in Romania. Second EVOLTREE Conference 2023 Resilient Forests for The Future, Brasov, Romania, 12-15 September 2023, Poster.

ALEXANDRU A.M., STOICA E., MIHAI G., CURTU A. L., 2023: Selection of Norway spruce (*Picea abies*) provenances from Romanian provenance trials based on multi-trait and stability. International

Conference Forest science for people and societal challenges - The 90th "Marin Drăcea" INCDS Anniversary, Bucharest, Romania, 2-5 October 2023, oral presentation.

5.4. Future research directions

- Use of the two new selection indices for other comparative trials.
- The inclusion in the computing of these indices of other traits, such as attacks by diseases and pests, respiration rate, photosynthesis, water use efficiency, etc.
- Analysis of the resilience parameters of trees for other species, which have not yet been studied or are less studied, in Romania.
- Comparison of tree resilience indices between Norway spruce and other species in a mix of resinous and deciduous stands.
- Realization of "age-to-age" type correlations to analyse the behaviour of the analysed traits over time.
- Considering the competition between individual trees.
- Using of Computed Tomography (CT) to measure cores with X-ray.

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ABSTRACT

Genetic variability is defined as the capacity of an individual or a population to have varying genotypic and phenotypic traits. Quantitative genetic variability is essential for species adaptability to climate change.

This thesis aimed to evaluate the genetic variability of Norway spruce (*Picea abies*)—the most important conifer species from Romania in terms of ecological and economic values—to improve the national breeding strategy and conservation measures of Norway spruce genetic resources from Romania in the context of climate change.

81 Norway spruce provenances from Romania and 12 other European countries have been analysed and compared in three provenance trials from Romania. The provenances are almost half of the rotation age of this species in Romania, 49 years. The provenances cover Europe's species' distribution range well, being from 11 geographical groups.

Significant differences between provenances, geographical groups, and trials have been observed regarding diameter at breast height, total and pruned height, and survival percentage. A high genetic variability of the radial growth and the response to drought of the provenances has also been observed. Regarding conventional wood density, significant differences between provenances were recorded only in the Dorna Candrenilor trial.

Calculating the SPEI-3 for the 1972-2020 period has allowed the identification of the years with severe and extreme drought events.

The correlations between the traits and between them and the provenances' place of origin have been used to examine the extent to which the trait variation is influenced by the local adaptation to the climatic conditions of the place of origin.

The genotype x environment interaction analysis has demonstrated the significant effect of this interaction on the total and pruned height. The planting site had a higher effect than the provenances, emphasising the attention required to the site conditions in reforestation works.

With the moving windows correlation analysis, the changes in the correlations between the climatic variables and the standardised annual radial growth of the provenances have been observed.

The response functions have permitted the identification of the correlations between the different climatic variables of the three trials and the latewood percentage, total height, and diameter at breast height.

Using the transfer functions, the correlations between the differences between the climate variables of the planting site and those from the place of origin have been analysed for total height and survival percentage.

Using the two new selection indices, MGIDI – multi-trait genotype-ideotype distance index and MTSI – multi-trait stability index, 12 provenances were selected from the Eastern and Western Carpathians, Bohemian Plateau, and Eastern Alps groups.