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Multi-Trait Selection and Stability in Norway Spruce (*Picea abies*) Provenance Trials in Romania

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Abstract: Provenance trials replicated in multiple environments allow the selection of populations with high and stable performances. In this study, two methods have been applied to select stable Norway spruce provenances with high performances in three provenance trials established in Romania in 1972, where 81 provenances have been tested. Four traits were assessed: total and pruned height, diameter at breast height and survival rate. Two multi-trait indices have been used: multi-trait genotype-ideotype distance index (MGIDI) for each provenance trial and multi-trait stability index (MTSI) across provenance trials. The selection differential was between 0.2 and 17.8% better than each site means. Several Norway spruce provenances showed stability and high performances, as confirmed by both selection indices. Our results provide valuable information for the genetic improvement program and seed transfer guidelines based on assisted migration in this ecologically and economically important forest tree species.

Keywords: Norway spruce; provenance trials; stability; GxE interaction; multi-trait selection

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

Academic Editor: Filippos A. Aravanopoulos

Received: 19 January 2023
Revised: 17 February 2023
Accepted: 21 February 2023
Published: 22 February 2023

1. Introduction

Norway spruce (*Picea abies* (L.) H. Karst.) is one of the most important coniferous species in Europe, covering a distribution area of about 30 million ha, representing 38% of the total coniferous species area. Its range is separated into three areas: (i) Alpine, (ii) Hercyno-Carpathian, and (iii) Baltic-Nordic Region [1]. More than 20% of its distribution area represents the extension beyond its native range [1]. In Romania, Norway spruce covers an area of 1.37 million ha, representing 21% of the total forest area [2]. More than 25% of this area (around 360,000 ha) are plantations outside its natural range [3]. Although recent studies revealed that Norway spruce is a species sensitive to increasing temperature and water deficit, it remains one of the most economically important species in Europe and has a significant role in European forestry [4].

Norway spruce was among the first species for which breeding was started in Europe in the late 1940s under IUFRO auspices [5]. Norway spruce breeding programmes were initiated in many European countries, but breeding objectives vary across Europe depending on the use of the genetic material. Thus, in Romania, the Norway spruce breeding program was started in the 1960s by seed stands and plus trees selection, setting up 78 ha of seed orchards and 15 provenance trials where 50 autochthonous and 71 foreign provenances have been tested [6,7].

The main goals of the Norway spruce breeding programmes, regardless of the country, were to increase the yield per area unit, shorten the rotation age, improve the adaptability and economic value of the wood harvested.

However, traits of economic value and importance in tree breeding programmes possess polygenic variation and are strongly influenced by environmental factors. The climate and soil conditions often lead to different responses in populations of various origins. Campbell and Jones [8] define GxE interaction as the different responses of a group of genotypes for a given trait in different environments. In recent years, GxE has been of great importance for forest trees because the rate of their natural migration is too slow to track their ecological optimum when the environmental conditions change swiftly, as expected under climate change [9,10]. For this reason, studies on genotype x environment interaction (GxE) and phenotypic plasticity for selecting populations with high and stable performances in a broad range of environmental conditions become of significant importance in breeding programmes. Also, sstudies of GxE interactions allow the identification of unstable genotypes; one strategy to minimise the GxE interaction would be their elimination from the breeding population [11]. There are many studies for nearly all commercially important forest tree species which have reported significant GxE, such as: Scots pine [12], eucalypts [13], Douglas-fir [14], Norway spruce [7,15,16], poplar [17].

To evaluate GxE interaction, there are many methods, including analysis of variance, principal components analysis and linear regression. Recently, the factor-analytic method and parametric approaches was introduced to decompose the GxE interactions and to explore the relationship between population variation/stability and environmental gradients.

Heinrich et al. [18] define the stability of one character as the ability of a genotype to avoid substantial fluctuations over a range of environmental conditions. Laing [19] made the difference between spatial stability, 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 [20], stability has two contrasting concepts: static and dynamic. The static concept implies that the provenance is stable when it maintains its performance across different environments. Dynamic stability is when there is no genotype x environment (GxE) interaction; the performance of the provenance across sites parallels the mean response of the tested provenances.

The provenance trials replicated across multiple sites allow comparison of tree populations within a trial site to assess the genetic component of variation and also allow comparison of the same populations amongst trial sites to assess the environmental component of variation (phenotypic plasticity). Gianoli and Valladares [21] defined phenotypic plasticity as the inherent and ecological phenomenon that refers to changes in the phenotype induced by the environment.

Therefore, the provenance trials provide essential information for selecting the most valuable and adapted provenances [22]. However, a superior genotype in one environment might be inferior in another environment [23]. For tree breeding, the interaction of GxE can be addressed in two ways: selecting stable genotypes, which are not sensitive to environmental changes, or selecting genotypes suitable for specific environments [24]. Furthermore, evaluation of the GxE interaction at the adult stage, close to or exceeding half of the rotation age, is more meaningful from the perspective of commercial forestry [25,26].

Stability analysis is often performed for a single trait, especially in forest tree species. The first simultaneous selection index was proposed by Smith [27] and Hazel [28]. But if multicollinearity exists between variables, a biased index coefficient can appear [29]. Allen [30] defined multicollinearity as the strong correlation between two or more variables/characteristics. Multicollinearity is an issue in multivariate analyses, which often appear in tree populations and can cause problems with the proper interpretation of results, leading to erroneous conclusions [31]. One issue with the S.H. index is the difficulty of expressing the economic value of traits [32].

Selection for increasing growth rates, wood yields and quality, and adaptability is the primary goal of many tree breeding programmes. Therefore, the simultaneous selection is required to produce simultaneous responses to selection in the intended direction in several traits [33].

Since the 1980s, the selection based on multiple traits has been used for many forest tree species: *Pseudotsuga menziesii* and *Picea sitchensis* [34], *Pinus elliottii* [35], *Pinus pinaster* [36], and more recently, *Prosopis alba* [37], *Pinus kesiya* [38], *Populus ussuriensis* Kom [39], *Picea abies* [40], *Picea glauca* [41], *Catalpa bungei* [42]. In the present study, we aimed to determine two selection indices that were not used so far in forest species (multi-trait genotype-ideotype distance index—MGIDI [29] and multi-trait stability index—MTSI [43]) by combining growth with quality traits and survival rate in order to select the most valuable and stable Norway spruce provenances. The objectives of this study were to: (1) assess genotype by environment interaction (GxE); (2) select Norway spruce provenances with high performances through multiple traits selection in each trial site, (3) analyze stability of selected provenances across sites and (4) select Norway spruce provenances with the highest breeding values and stable performances based on multiple desired traits using simple and easy-to-compute methods. The results not only provide valuable information for the genetic improvement program of this species and conservation of the unique tree lineages, but also provide for seed transfer guidelines based on assisted migration.

2. Materials and Methods

2.1. Genetic Material, Experimental Desing and Measurements

In 1972, four Norway spruce trials were established in Romania [44]: Dorna Candrenilor, Zarnesti, Turda and Novaci. In 1998, because of windfalls, the Novaci field trial was disaffected; our study was carried out in the remaining three field trials. Ten Romanian Norway spruce provenances and 71 from 12 other European countries were tested. They cover the European species' natural and planted distribution range, from 41.6° to 63.28° northern latitude and from 6.03° to 34.62° eastern longitude. Also, the altitudinal range of provenances is very wide, being between 20 m (some provenances from Germany, Sweden and Finland) to 2000 m (Bulgaria). The locations of the common garden trials and the provenances are shown in Figure 1. According to the geographic regions, provenances were divided into 11 groups: 1. Northern Europe, 2. NE Germany, 3. NE Poland, 4. Bohemian, 5. French (Vosges and Jura Mountains), 6. Western Alps, 7. Central Alps, 8. Eastern Alps, 9. Western Carpathians, 10. Eastern (Romanian) Carpathians, and 11. Bulgarian (Rila and the Rhodope Mountains). Details on the Norway spruce provenances and trial location are in the Supplementary Materials (Table S1).

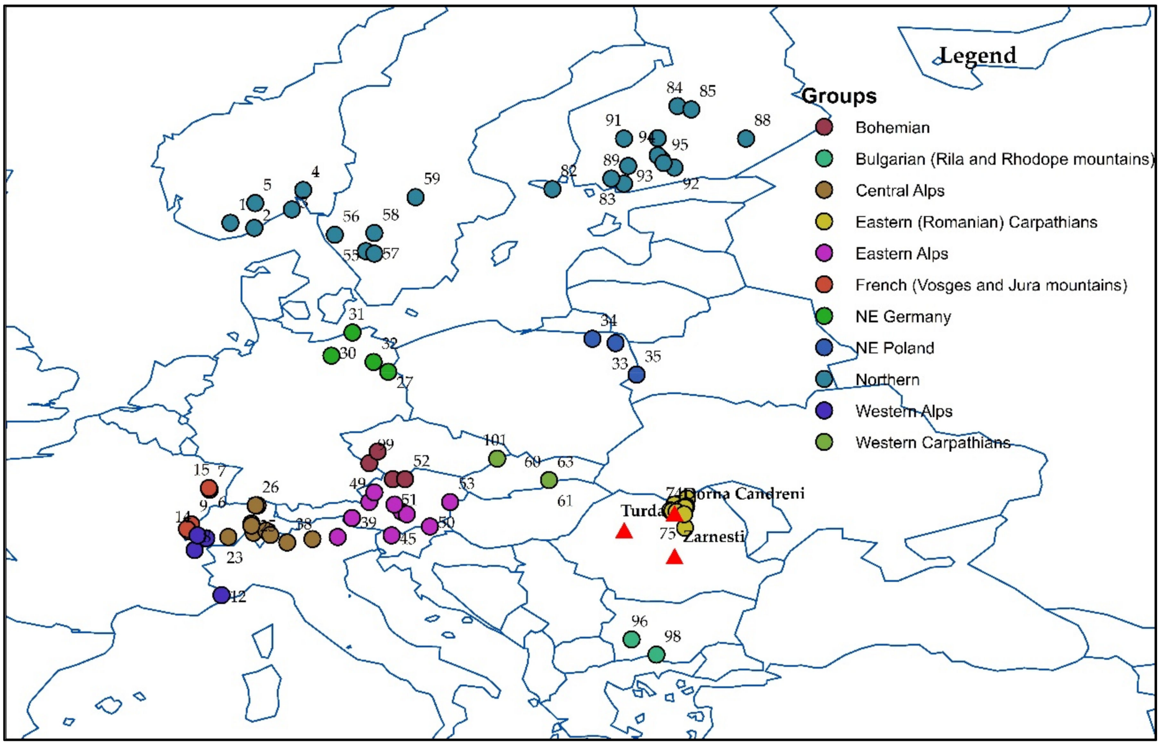

Figure 1. The locations of the Norway spruce provenances (dots and numbers) and of the provenance trials (red triangles).

The provenance trials analysed in this study were established in three forest districts located in Romania's Northeastern, Western, and Southern Carpathians, in the mixed beech and coniferous species zone (Zarnesti) and Norway spruce zone (Dorna Candrenilor and Turda), respectively. The testing sites show different climate conditions, continental with Scandinavian-Baltic influences in the north (Dorna Candrenilor), and temperate-continental with oceanic influence in the west (Turda) and central parts (Zarnesti) [45,46].

Provenances were planted in a randomised complete block design, each plot with 16 (4×4) individuals per provenance at 2×2 m spacing and three blocks. No thinning or artificial pruning was made in these provenance trials. After 49 years, the number of remaining trees per provenance in each block varied between 4 and 13, the sample per provenance ranging from 12 to 31 trees, which has ensured a good precision of the results.

The measurements were made in the fall of 2020, 49 years after planting, which represents about half the rotation age of Norway spruce in Romania. The traits chosen to assess the adaptive variation were: total height (Th) (m), diameter at breast height (Dbh) (cm), pruned height (Ph) (m), and survival rate (Surv). Pruned height represents the height of the lowest green branch.

Total height is considered, in many studies, a proxy for local adaptation [47,48] because taller trees can compete more effectively for light, water and nutrients, and can possibly have a higher reproductive success at maturity [49]. However, assessing other adaptive traits, such as survival rate, can result in a better understanding of the provenance's response to environmental conditions. Total and pruned height were measured with the help of a Vertex IV with a precision of 0.1 m; the diameter at breast height was measured using a calliper with a precision of 0.1 cm. The survival rate was calculated as the ratio between the number of remaining trees and the number of planted trees on every plot.

2.2. Statistical Analysis

The genetic variance analysis of each trait was performed at two levels: at each trial site and across sites. The residual histograms were used to assess whether the residual distribution of the four traits approached the normal distribution (S2) reasonably well.

In each trial site, a mixed linear model was used, where provenance was considered random effect, and as fixed effects, group and block [50]:

$$Yijk = \mu + Gi + Pj + Bk + Pj \times Bk + eijkl \quad (1)$$

where μ is the general mean, Gi is the effect of the ith group, Pj is the effect of the jth provenance, Bk is the effect of the kth block, $Pj \times Bk$ is the provenance-by-block interaction and eijkl is the error term associated with ijkl trees.

The provenance-by-block interaction was not statistically significant, so it was dropped from the model. The linear mixed effects models and their testing were computed using lmerTest R package [51].

Across sites, analysis was based on the following mixed linear model, where provenance and provenance x site interaction were considered random effects while site as fixed effect:

$$Yijk = \mu + Si + Pj + Bik + Si \times Pj + eijkl \quad (2)$$

where μ is the general mean, Si is the effect of the ith site, Pj is the effect of the jth provenance, Bik is the effect of kth block within Si site, $Si \times Pj$ is the provenance-by-site interaction and eijkl is the error term associated with ijkl trees. The group effect was not accounted for in this model because we have aimed to select the Norway spruce provenances which highlighted stability and high performances and not geographical groups.

The stability and adaptability of Norway spruce provenances of various origins were estimated based on multiple traits—MGIDI [29] in each trial and MTSI [43] across trials.

A mixed linear model analysis was necessary for REML estimation of variance parameters and to attain the BLUP of every provenance effect in the data, which is used to compute the indices.

For the MGIDI calculation, the effect of the ith group was dropped from the model (1). Because the primary goal of many tree breeding programmes is the selection for increasing growth rates, wood yields and quality, as well as adaptability, we have designed the ideotype as having a higher diameter, total and pruned height, and a greater survival rate. The selection intensity was 15%, i.e., 12 provenances out of the total of 81 were selected. The MGIDI was computed in four steps: (1) rescaling the traits in a 0–100 range; if an increase for the trait is desired, the maximum equals 100 and the minimum 0; if a decrease is desired, then the maximum is 0 and minimum is 100; (2) computing an exploratory factor analysis with the rescaled values to group traits that are correlated into factors and estimate the factorial scores for each provenance; (3) establishing an ideotype based on desired values for the traits—by definition, the ideotype has the rescaled value of 100 for all analysed traits; and (4) computing the distance between each genotype and the ideotype [29]. The equation used is:

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

where $MGIDI_i$ is the multi-trait genotype-ideotype distance index for the ith genotype, y_{ij} is the score of the ith genotype in the jth factor, and y_j is the jth score of the ideotype. The lower the MGIDI of a genotype, the closer it is to the ideotype and has desired values for the analysed traits.

MTSI was computed in the following steps:

(1) After the WAASB (Weighted Average of Absolute Scores for quantifying the stability of *g* genotypes conducted in *e* environments using linear mixed-effect models) was calculated, it and the performances (values of traits) were rescaled in a 0 to 100 range.
(2) Then, the WAASBY index was computed, which allowed weighting between stability (WAASB) and mean performance (Y) [52]. Different weights can be used for prioritising the performance or the stability of the provenances. In our study, the used weights were 25 for stability and 75 for performance, i.e., performance was put above stability.
(3) After that, the steps were similar to those of MGIDI, the difference being that the ideotype now had the maximum value of 100 for the WAASBY.
(4) Finally, MTSI was estimated according to the equation:

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

where the $MTSI_i$ = the multi-trait stability index for the ith genotype; F_{ij} = the jth score of the ith genotype; F_j = the jth score of the ideotype.

The lower the MTSI for a genotype, the closer it is to the ideotype; in addition, it has a high performance and stability for all the variables analysed. The multi-trait indices were computed with the help of metan package [53] in R [54].

After the model for the MTSI index was fitted, different scenarios of weights for stability and performance (from 100/0 to 0/100) were computed and plotted (Supplementary Materials S3). The provenances were grouped into four clusters for each trait: (i) performant and stable genotypes; (ii) performant but unstable genotypes; (iii) underperforming but stable genotypes; and (iv) underperforming and unstable genotypes.

3. Results

3.1. Genetic Variability Analysis within Trial Sites

The results of the linear mixed model for the analysed traits in each Norway spruce provenance trial at 49 years are presented in Table 1.

Table 1. The results for random- and fixed-effects of the four traits in each Norway spruce provenance trials evaluated at age 49.

	Trait	LRTp	Vp	Vr	MS g	MS b	Mean ± SD
Dorna Candrenilor	Dbh	5.07 *	0.56	28.87	264.06 ***	15.19 ns	23.75 ± 5.58
	Th	55.39 ***	0.70	8.14	108.68 ***	62.44 ***	25.90 ± 3.24
	Ph	152.53 ***	0.62	3.44	33.74 ***	104.27 ***	16.74 ± 2.21
	Surv	12.31 ***	34.31	104.5	680.76 ***	533.53 **	49.97 ± 13.73
Zărnești	Dbh	0.44 ns	0.14	22.24	49.73 *	82.91 *	21.14 ± 4.76
	Th	21.55 ***	0.6	11.12	50.90 ***	206.67 ***	21.43 ± 3.53
	Ph	98.84 ***	1.16	6.31	44.59 ***	322.91 ***	10.96 ± 2.95
	Surv	0 ns	0	178.2	365.38 *	504.92 ns	40.66 ± 13.71
Turda	Dbh	0 ns	0	30.12	151.61 ***	25.25 ns	21.57 ± 5.57
	Th	14.35 ***	0.49	9.45	64.60 ***	58.99 **	21.48 ± 3.28
	Ph	55.53 ***	0.94	7.04	18.22 *	24.78 *	11.21 ± 2.86
	Surv	0.16 ns	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; Vg—variance for provenance random effect; Vr—residual variance; MS—mean squares for group (g) and block (b); Dbh—diameter at breast height; Th—total height; Ph -pruned height; Surv—survival rate.

The group factor was significant in all field trials for all traits. For provenance factor, significant differences were found at Dorna Candrenilor trial for all traits, while no significant differences were found at the Zarnesti and Turda trials for Dbh and survival rate.

Given the large areas occupied by the field trials, there was heterogeneity within each site. The block effect was significant for all traits in all trials, except for the survival rate in the Zarnesti trial and Dbh in the Dorna Candrenilor and Turda trials. A large effect for the block was also obtained in the study of two Romanian Norway spruce provenance trials [55].

3.2. Genotype by Environment Analysis

The best growth performances in terms of height and DBH were obtained in the Dorna Candrenilor trial, and the lowest were obtained in the Zarnesti trial. The site average total height was 20.6% greater at Dorna Candrenilor than at the Turda trial and was 20.9% greater than at the Zarnesti trial.

The highest average pruned height per experiment was recorded in the Dorna Candrenilor trial ($\bar{x}$ = 16.74 m), and the lowest was recorded in the Zarnesti trial ($\bar{x}$ = 10.96 m).

The highest survival rate was recorded in the Dorna Candrenilor trial ($\bar{x}$ = 50%), and the lowest survival rate was recorded in the Turda trial ($\bar{x}$ = 37%).

There were significant differences amongst provenances across sites for all traits (Table 2). The site effect was significant for all traits, but the site-by-provenance effect was not significant for Dbh and survival rate. The block-within-environment effect was significant for all traits except Dbh.

Table 2. The results for random- and fixed-effects of the four traits of the Norway spruce provenances evaluated at age 49, across trials.

Trait	LRTg	LRTge	Vg	Vge	Vr	MS Env	MS B (Env)	Mean ± SD
Dbh	39.55 ***	0.12 ns	1.25	0.06	27.17	917.8 ***	42.72 ns	22.30 ± 5.46
Th	63.70 ***	40.93 ***	1.18	0.47	9.45	2109 ***	108 ***	23.23 ± 3.99
Ph	43.04 ***	173.02 ***	0.9	0.79	5.36	2134 ***	149.3 ***	13.34 ± 3.83
Surv	33.6 ***	0.45 ns	35.39	4.48	150.1	3859 ***	480.9 ***	42.47 ± 14.95

***: Significant at 0.1%; ns: not statistically significant, $p > 0.05$; LRTp, LRTge—likelihood ratio test for provenance and genotype x environment interaction effects; Vp, Vge—variance for random effects, provenance and genotype by environment interaction; Vr residual variance; MS—mean squares for environment and block within environment; Dbh—diameter at breast height; Th—total height; Ph—pruned height; Surv—survival rate.

3.3. The Multi-Trait Selection in Each Provenance Trial

In all trials, the factor analysis has grouped the traits into one factor. The results of the linear mixed model for the analysed traits in each Norway spruce provenance trial at 49 years used to compute the MGIDI index are in Supplementary Materials 4 (S4).

At the Dorna Candrenilor trial, the selected provenances are: 72-Dorna Candrenilor, 74-Galu, 66-Marginea, 71-Moldoviţa, 64-Gheorghieni and 70-Coşna, from Eastern (Romanian) Carpathians; 51-Herfenberg, Bohemian; 39-Klaunz Bannwald, 53-Neustift and 41-Eppenstein from Eastern Alps; 101-Valke Karlovice and 61-Nyugatbukki Allami from Western Carpathians.

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

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

The differences among the means of the selected provenances based on MGIDI and the site means are presented in Table 3. The selected provenances had better performances than the site means for all traits. The differences were between 0.18 and 16.5% higher.

Table 3. The selection differential of MGIDI index for Norway spruce provenances at 48 years old.

Traits	Site Mean			Selected Provenances Mean			Selection Differential%		
	Dorna Candrenilor	Zarnesti	Turda	Dorna Candrenilor	Zarnesti	Turda	Dorna Candrenilor	Zarnesti	Turda
Diameter at breast height (cm)	23.8	21.1	21.6	25.7	21.5	22.2	8.05	1.62	2.85
Total height (m)	25.9	21.4	21.5	28.1	22.7	22.8	8.39	5.86	6.1
Pruned height (m)	16.7	11	11.2	18.2	12.8	12.4	8.97	16.5	10.3
Survival (%)	50	40.7	36.8	56	40.7	40.2	12	0.175	9.29

3.4. The Multi-Trait Selection across Provenance Trials

If we consider the superiority (75% weight) and spatial stability (25% weight) of all target traits, the MTSI index (Figure 2) has indicated the following Norway spruce provenances as the most valuable: 72-Dorna Candreni, 41-Eppenstein, 60-Keletbukki Allami, 70-Cosna, 100-Kasperske Hory, 66-Marginea, 40-Wietersdorf, 39-Klaunz Bannwald, 99-Zelesna Ruda, 71-Moldovita, 52-Sandl-bei-Freistadt and 63-Nyugatbukki Allami. Of interest are also provenances 25-Wassen, 61-Nyugatbukki Allami, 73-Stulpicani, 51-Herfenberg and 74-Galu.

The selected provenances had better performances than the site means, for all traits. The differences were between 6.42 and 17.80% higher (Table 4).

By assigning different weights to stability and mean performance (Supplementary Materials S3), the provenances were grouped into four clusters for each trait: (i) performant and stable genotypes; (ii) performant but unstable genotypes; (iii) underperforming but stable genotypes; and (iv) underperforming and unstable genotypes.

From the selected provenances (Figure 3), provenances 60, 100 and 52 were stable and performant for all four traits.

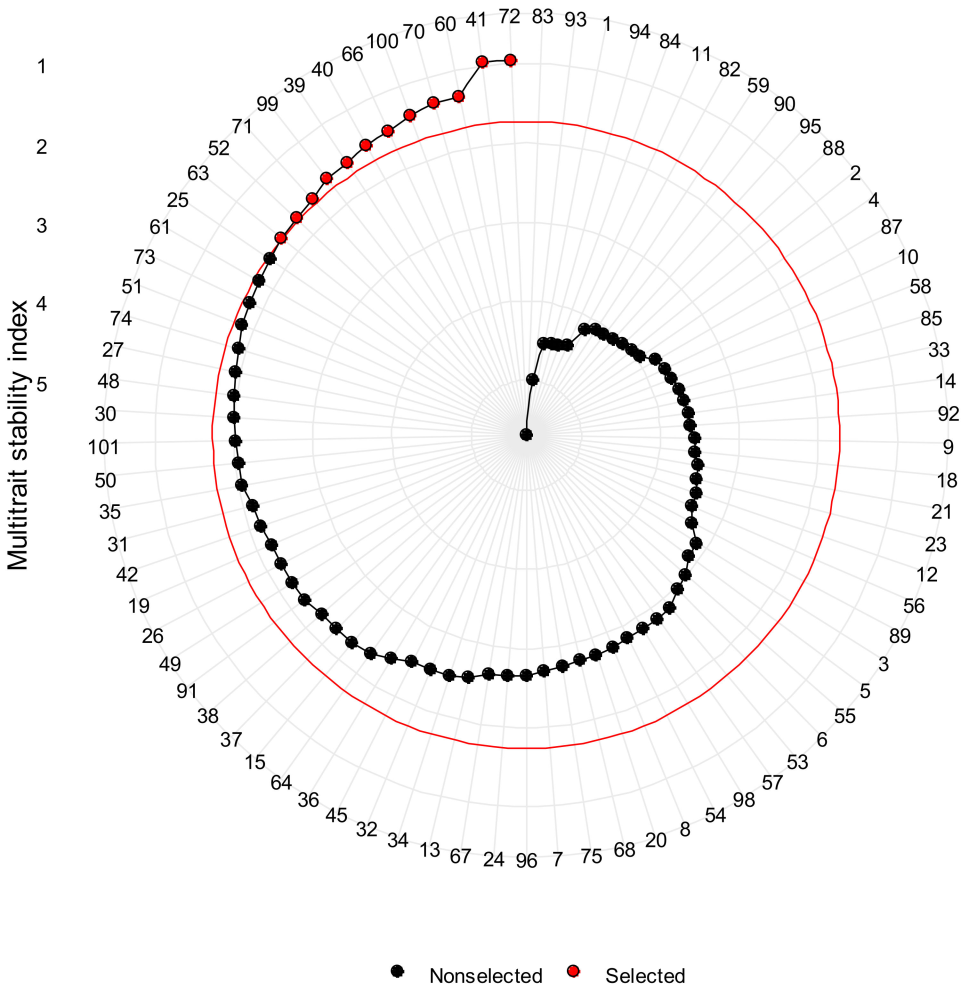

Figure 2. Norway spruce provenances ranking and selected provenances using the MTSI. The red line represents the selection intensity (15%). The dots represent the multi-trait stability index.

Table 4. The selection differential of MTSI index for Norway spruce provenances at 48 years old.

Traits	Site Mean			Selected Provenances Mean			Selection Differential%		
	Dorna Candrenilor	Zarnesti	Turda	Dorna Candrenilor	Zarnesti	Turda	Dorna Candrenilor	Zarnesti	Turda
Diameter at breast height (cm)	23.8	21.1	21.6	25.47	22.45	23.17	7.02	6.42	7.25
Total height (m)	25.9	21.4	21.5	27.68	23.24	22.97	6.87	8.61	6.86
Pruned height (m)	16.7	11.0	11.2	17.99	12.74	12.27	7.71	15.83	9.58
Survival (%)	50	40.7	36.8	57.21	44.79	43.35	14.42	10.04	17.80

Provenances 41 and 70 were considered stable and performant for Dbh, Th and Ph; and for survival rate, they were unstable but performant.

Provenances 71, 72 and 99 were stable and performant regarding Dbh, Ph and survival rate and were performant but unstable regarding Th.

Provenances 66 and 40 were stable and performant regarding Dbh and unstable but performant regarding Th and Ph. Regarding the survival rate, provenance 66 was unstable but performant, and provenance 40 was stable and performant.

Provenance 39-Klaunz Bannwald was stable and performant for all traits, except survival rate, where it was performant but unstable.

Provenance 63 was unstable but performant for all traits except Th, which was underperforming and unstable.

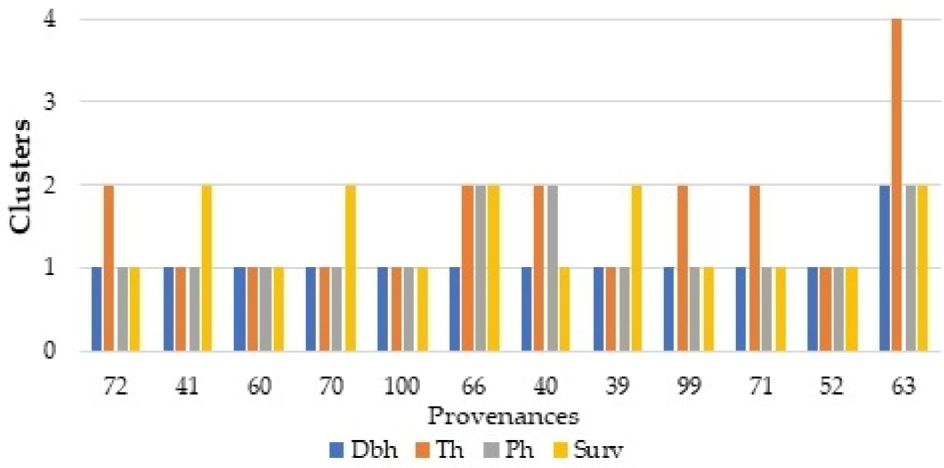

Figure 3. The grouping of the selected provenances using the MTSI index. 1: Performant and stable; 2: Performant but unstable; 3: Underperforming but stable; 4: Underperforming and unstable; Dbh: diameter at breast height; Th: total height; Ph: pruned height; Surv: survival rate.

Regarding other Romanian provenances, provenance 73-Stulpicani was stable and performant for all four traits except Th, which was considered stable, but underperforming. Both 74-Galu and 64-Gheorghieni were performant but unstable for Dbh, Th and Ph and were stable and performant regarding survival rate.

4. Discussion

In this study, we have assessed the genetic variation and stability among 81 Norway spruce provenances covering the entire species distribution range in Europe in three provenance trials using different methods for selecting the provenances with high performances and adaptability to environmental variations. The analyses were focused on four economic and adaptive traits which are highly correlated to the breeding objectives.

Significant differences between provenances, groups and sites for the analysed traits were observed. The high interpopulation genetic variability derived from the wide distribution area of provenances tested in this study, comprising the three post-glacial recolonisation regions in Europe: Scandinavia, Hercyno-Carpathian and Alpine regions. The site conditions with different climates (continental in the north, temperate continental with oceanic influence in the west and central parts) also played an important role in the high level of variation obtained in this experiment. The best performances for all traits were obtained at the Dorna Candrenilor field trial, which is located in the climatic optimum of this species in Romania, while the weakest were obtained at the Zarnesti field trial, which is situated at a lower altitude in the mixed beech and coniferous species zone; the exception was for the survival rate, where the Turda trial had the lowest value, 36.8%. In addition, the provenance x sites interaction (GxE) was significant for total height and pruned height but not for diameter at breast height and survival. Chen [56], who also used factor-analytic models, found highly significant GxE for families of Norway spruce in Sweden.

Findings of this study pointed out that GxE interaction will be important in the Norway spruce breeding program and reforestations, especially in areas exposed to drought or other risk factors. Identifying stable genotypes reduces long-term risks, but selecting genotypes adapted to specific environments maximises genetic gains for all environments [57]. Similar results for Norway spruce were obtained for height [58] and height and diameter at 34 years in the study of 20 Romanian provenances [59]. No significant GxE interaction for Dbh was found in other Norway spruce series of experiments established in Romania [55].

The low value of GxE for Dbh and survival and high value for other traits indicate high phenotypic plasticity of Norway spruce. Although not all phenotypic plasticity is adaptive, the phenotypic plasticity could facilitate the expression of well-adapted phenotypes under new environmental conditions and, therefore, allow a population to carry on [60]. The results obtained by the MTSI index showed that some provenances (60, 100, and 52, respectively) were performant and stable for all traits, while others were performant and stable for some traits but performant and unstable for other traits. Therefore, the level of genetic variation determines the species phenotypic plasticity that could be specific to certain traits and environmental conditions.

In our approach, we have analysed multiple trait selections at each site and across sites. The method was based on the computation of selection indices which reflect the superiority for all target traits in each trial (MGIDI) and the superiority and stability of all target traits across trials (MTSI). A problem when using multi-trait indices for selection is that as more traits are included, the index tends to identify genotypes that are insignificantly above average for all traits but exceptional for none [61]. The MGIDI and MTSI indices have allowed the selection of superior provenances for multiple traits, maximising the selection response. Therefore, their use turned out to be efficient in terms of selection response in the direction of the multiple-trait breeding goal.

If the selection was based on the MGIDI index, the ranking of the provenances changed from one experiment to another. However, some provenances obtained good performances in all the trials, such as: 72-Dorna Candrenilor and 41-Eppenstein. Comparing the results of the MTSI (with 75% weight for performance) with the ones from the MGIDI, 11 provenances were selected in at least one trial. Only the provenance 63 was not selected using the MGIDI index at a 15% selection intensity. However, it was relatively close, ranking 17th, 20th and 21st in Turda, Dorna Candrenilor and Zarnesti trials, respectively, according to the MGIDI index.

The provenances selected using the MGIDI and MTSI indices have a high value for breeding and deployment of the forest reproductive material. They have shown high growth performances and stability, and they belong to the Eastern and Western Carpathians, Bohemian, and Eastern Alps groups. Provenances from the Eastern Carpathians and Bihor Mountains, as well as from the Beskids and Ore regions to the foothills of the Harz, have demonstrated good performances under very different ecological conditions in other studies as well [62,63]. Schuler [64] found that the most productive and promising provenances for future climate conditions in Austria originate from the Bohemian massif and the southeastern fringe of the Alps. Some Romanian provenances also performed well regarding tree height and stem volume at 32 years in a Norway spruce provenance trial from Latvia, one of them being Dorna Candrenilor [65]. Provenances from the Carpathians and the Baltic region have shown superior growth [66], even in Canada [67]. At low altitudes in Eastern Norway, provenances from Romania had shown growth superior to the local ones [68].

Comparing the selection based on the two indices, at the Dorna Candrenilor trial, which is located in the climatic optimum of this species in Romania, the selection differentials were somewhat greater when selecting genotypes based on MGIDI index, for Dbh, Th and Ph, but the differences were small: 1.03, 1.52 and 1.26%, respectively. For the survival rate, the MTSI gave a better result, but was negligible: 57.21% vs. 56%. At the other two trials, the selection based on the MTSI index gave better results than the MGIDI index, for all traits, except Ph.

5. Conclusions

Our results confirmed that Norway spruce holds high phenotypic plasticity, and there is potential for important genetic gains in the next phases of breeding programmes. Twelve provenances across species range have been identified that belong to the Eastern and Western Carpathians, Bohemian, and Eastern Alps groups, which have shown high growth and adaptive performances and stability. These provenances might be valuable genetic resources for producing forest reproductive material capable of mitigating the impact of climate change.

Considering the high vulnerability of genetic resources in the face of climate change, these unique tree lineages have to be designated as tested seed sources and conserved in situ by including them in the National Catalogues of Basic Material for producing the forest reproductive material from each country. In this way, they could be used in site conditions other than those of origin close to the test sites; this is an activity known as assisted migration.

The site effect is larger than the provenance effect which reinforces the importance of paying close attention to site characteristics in reforestation work. The choice of appropriate seed sources or provenances will improve productivity and adaptation of forests in a changing climate. Given that the populations tested in this experiment already experienced the climate change, results of this study could be used in decision-making regarding selection of the source seed for planting in different countries.

The indices based on multiple traits used in this study are free from multicollinearity issues and easy to compute and interpret. MGIDI can be used for selecting provenances adapted to certain environments, and MTSI for selecting provenances that can perform well across environments. They were based on four traits, but more valuable results could be obtained when the number of traits increases. In addition, different weights for the MTSI could be used to prioritise either the mean performance or the stability.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f14030456/s1, Table S1: Details about the tested Norway spruce provenances and the provenance trials; S2: Histograms and qq-plots for residuals; S3: Different scenarios of weights for stability and performance; S4: The results of the linear mixed models used for the computation of the MGIDI index.

Author Contributions: Conceptualisation, A.-M.A. and G.M.; methodology, A.-M.A.; maps, A.-M.A.; supervision, G.M. and A.L.C.; project administration, G.M.; funding acquisition, G.M.; writing—all authors. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Romanian Ministry of Research, Innovation and Digitalization, in BIOSERV Nucleu Program, within the framework of the project PN 19070303 (Revision of the provenance regions for production and deployment of the forest reproductive materials in Romania to increase the adaptability of forest ecosystems to climate change) and "Programul 1—Dezvoltarea sistemului naţional de cercetare—dezvoltare, Subprogram 1.2—Performanţă instituţională—Proiecte de finanţare a excelenţei în CDI"—project "Creșterea capacității și performanței instituționale a INCDS "Marin Drăcea") în activitatea de CDI—CresPerfInst" (Contract No. 34PFE./30.12.2021).

Data Availability Statement: Data presented in this study are available from the corresponding author upon request.

Acknowledgments: The authors would like to thank the anonymous reviewers for their comments and suggestions that contributed positively to this paper.

Conflicts of Interest: The authors declare no conflict of interest.

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