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RESEARCH ARTICLE

Cedrus atlantica - Possible Alternative Tree Species under Changing Climate Conditions in Central Europe

Muhidin Šeho[1]✉ • Barbara Fussi[1] • Darius Kavaliauskas[1,2,3]

[1]Bavarian Office for Forest Genetics (AWG), Forstamtsplatz 1, Teisendorf/Germany
[2]Vytautas Magnus University Agriculture Academy, Kaunas/Lithuania
[3]Lithuanian Research Centre for Agriculture and Forestry, Institute of Forestry, Kaunas/Lithuania

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ABSTRACT

The effects of climate change are becoming increasingly visible and affect entire ecosystems and their services. Following more frequent dry years and the invasive spread of harmful organisms, interest in drought- and frost-tolerant alternative tree species in forestry practices is growing. The two cedar species, Atlas and Lebanon cedar are discussed as possible alternative tree species in Bavaria and Germany due to their high climate tolerance (drought and frost), wood quality and their potential to be integrated into local forests. Both cedar species can contribute to the stability of weakened spruce and pine forest stands and thus ensuring the supply of conifer stem wood in the long term. As there is hardly any cultivation experience in Bavaria so far, potential alternative tree species should be evaluated through provenance and practical cultivation trials. Particular attention should be paid to the origin of the forest reproductive material (FRM), as this plays a decisive role in adaptability and successful cultivation. The suitability and vitality of seed stands should be evaluated before use. In addition to evaluating the phenotype, it is essential to assess the genetic diversity and differentiation of plantations and populations within their natural distribution range. In this study 467 *Cedrus atlantica* (Endl.) Manetti ex Carrière tress from 11 populations were sampled and genotyped based on 15 variable nuclear microsatellite markers. Results showed that the applied markers are able to clearly differentiate between *C. atlantica* and *C. libani.* Genetic diversity varies among sampled *C. atlantica* populations and clear differentiation of *C. atlantica* from France and Morocco was found. Based on our results, all investigated Atlas cedar populations can be proposed as seed stands and conservation units. Future studies should include the Atlas cedar populations from Algeria.

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1. Introduction

The aim of the current discussion of introducing of alternative tree species is the formation of mixed forests with an increasing number of forest tree species, including non-native drought adapted tree species. Adaptive forest management can diminish, and split the risks raised by climate change by expanding the existing range of tree species and thereby spread the cultivation risk (Spiecker, 2006; Knoke et al., 2008; De Hemery et al., 2010; Bauhus et al., 2017; Thurm et al., 2018; Avila & Albrecht, 2018; Šeho & Janßen, 2019; Šeho, 2020; Kavaliauskas et al., 2021, 2022). The tree species intended for use should be both ecologically and economically compatible with forest ecosystem (İmal et al., 2024). As part of the “CorCed” project, funded by the Federal Ministry of Food and Agriculture (BMLE, Germany), the suitability for cultivation of Atlas cedar, Lebanon cedar and Turkish hazel as

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✉ Correspondence
E-mail address: muhidin.seho@awg.bayern.de

possible alternative tree species in Germany was investigated (Šeho, 2018; Šeho et al., 2019; 2023). The Atlas cedar is drought and late frost tolerant tree species which grows on shallow to deep, dry to almost wet, nutrient-poor to nutrient-rich sites. The average annual temperature in the main distribution area is 7.5 - 15.0 °C, where annual rainfall ranges from 500 to 2,000 mm. The coldest monthly averages can range from -1 to -8 °C (Cheddadi et al., 2017; Laaribya et al., 2024; Linares et al., 2011). It is a semi-shade tree species characterized by low invasion potential and high compatibility for mixed stands (Šeho, 2018; 2019). It occurs on calcareous and siliceous soils (Aoujdad et al., 2015). The natural distribution area of the Atlas cedar is fragmented and is limited to the North African mountains at elevations between 1,300 and 2,600 m above sea level and regions of Rif, Atlas, and Aures Mountains in Morocco and Algeria (Figure 1, Cheddadi et al., 2017). The Atlas cedar is an endangered tree species that has been heavily overexploited in its natural range and only occurs in small populations. There are currently around 184,000 hectares of cedar forest left in Morocco and around 14,000 hectares in Algeria, most of which have been placed under protection by the countries (Šeho, 2018; Laaribya et al., 2024). Slimani et al. (2014) observed that tree growth in Algerian Atlas cedar forest was mainly influenced by precipitation variability. The Saharan Atlas populations have a better adaptation to water shortage (xerothermic adaptation) by reducing their leaf area, which makes them interesting due to their drought resistance (Nedjahi & Zanndouche, 2011).

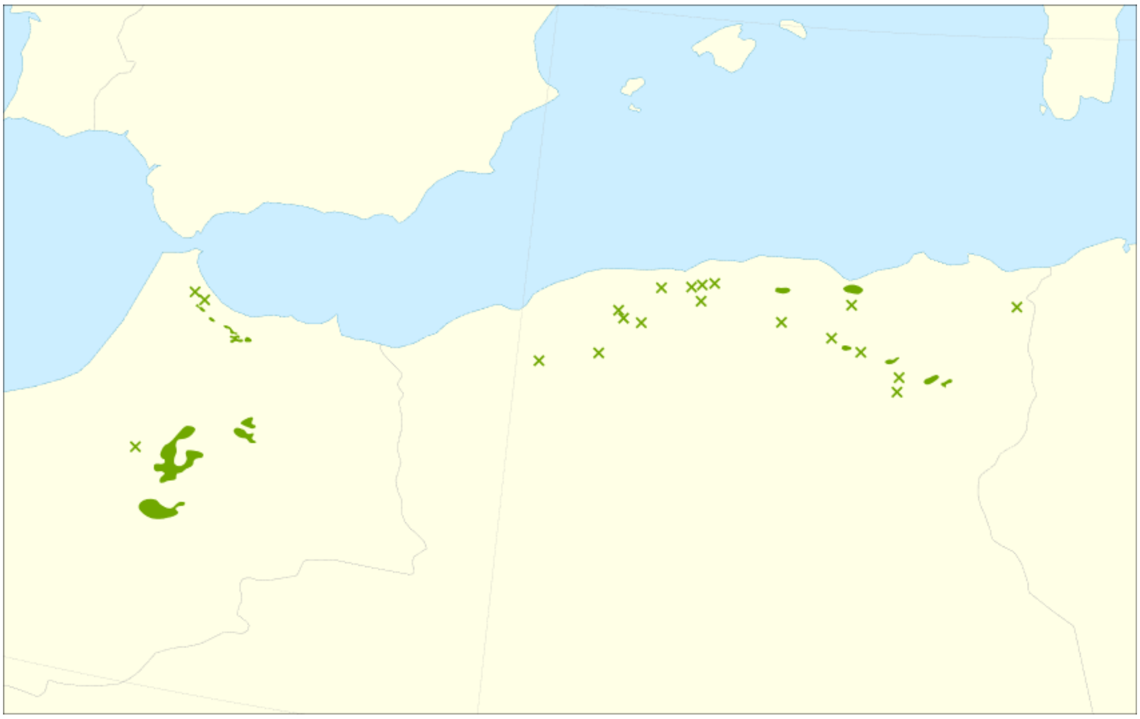

Figure 1. The natural range of the Atlas cedar according to Caudullo et al. (2017). Green = Contiguous natural distribution area, X = Isolated populations.

In addition to climate change, grazing is among the biggest challenge for the long-term conservation of Atlas cedar forests, as sheep and goat farming is an important source of livelihood for the population dependent on agriculture in the mountain regions. One of the largest contiguous cedar areas is located in the Middle Atlas on a plateau south of Azrou (Middle Atlas) on basalt bedrock. Trees up to 700 years old can still be found there. Due to their sparse growth, however, the oldest trees bear mostly coarse branches, but the trunks are of considerable size. In the largest cultivation area outside its natural distribution in France, there are around 20,000 hectares of cedar forest. In France, it has been used since the middle of the 19th century for the reforestation of devastated and erosion-prone areas. The FRM used for afforestation was of Algerian origin coming from the Tell Atlas and was able to adapt to the difficult site conditions in France. A plantation from 1970 which was established to test different provenances in the field allowed the selection of three stands as reproductive material in the category “tested” (Bariteau & Vauthier, 2011). A provenance test comparing *C. atlantica* and *C. libani* demonstrated better height growth for Atlas cedar and a great variability within the species. Phenological observations from an Italian provenance test showed 7-15 day difference in the starting of the vegetative activity between *C. atlantica* provenances from Rif and High Atlas (Fusaro, 2011). Investigation after the extreme heat and drought of 2003 showed a resistance of Lebanon Cedar provenances to long dry summers on calcareous soils (Bariteau & Vauthier, 2011). In France, two Atlas cedar populations were visited on Mont Ventoux and in Ménerbes in the Luberon within CorCed project. The trees exhibit high-quality trunk shapes and can be utilized without restrictions as seed stands. Seeds of the highest category “tested” are produced and distributed from these stands across Europe. Prior introducing new tree species like Atlas cedar to Germany, attention should be paid to the selection of the appropriate provenance as well to the quality and sustainable production of seed and planting material. The production, import, export and marketing should be carried out in compliance with the legal requirements regulated by the German Forest Reproductive Material Act (FoVG) (Šeho & Janßen, 2019; 2020). In Germany, there was hardly any forestry experience with Cedar species at the beginning of the CorCed project and suitable seed were not available. For the successful implementation of the project, it was necessary to develop close cooperation with local institutions in the countries of origin in the field of FRM and plant propagation. This was followed by field visits and the evaluation of possible seed stands. The next step was the selection and harvesting of seeds and the import of suitable provenances to Germany. In addition to the phenotypic evaluation of seed stands, it is very important to know the genetic make-up of the stands that are recommended for later use, especially for tree species with a small and fragmented natural distribution area. Finally, the findings from provenance tests should be extended through the use of genetic markers to obtain even more precise information on the genetic variability of the species. Genetic samples were obtained during the evaluation of the stands.

The aims of this study were (*i*) to select and test DNA markers for *Cedrus* species identification, (*ii*) to visit and sample selected Atlas cedar populations for DNA marker-based study of the intra-species genetic variation (structure and diversity) of Atlas cedar populations in France and Morocco, (*iii*) to infer stands for conservation and seed harvesting and (*iv*) to provide practical implementation and recommendations for FRM selection under changing environmental conditions in Germany.

2. Materials and Methods

Needle samples from Atlas and Lebanon cedars were used for the genetic analyses. The Lebanon cedar was sampled in its natural distribution area as part of the CorCed project and is used for species differentiation in this study. DNA markers were tested and optimized in the AWG laboratory and the following 15 nuclear microsatellite markers (nSSR) were selected for genotyping: CaTssr_41, CaTssr171, CaTssr31, CaTssr175 (Karam et al., 2015); EQJYX_A, DWOTR_A, GN16, GN19, GN24, GN_02, GN_18 (Karam et al., 2019); CatXITcE11, CatXiiTcC6, CatITgD4, Cat_D12 (Chaïb et al., 2006).

2.1. Microsatellite Data Analysis

Based on the multilocus genotypes determined for the sampled 467 *Cedrus atlantica* trees, the allele frequencies and subsequent parameters describing the genetic variation within populations were calculated. The following genetic parameters were calculated using the GenAlEx 6.5 program (Peakall & Smouse, 2012): mean number of alleles (*Na*), private alleles (*Np*, alleles that only occur in this population), mean number of effective alleles (*Ne*), observed (*Ho*) and expected (*He*) heterozygosity, fixation index (*F*) as the ratio between (*Ho*) and (*He*). The rarified allelic richness (*Ar*) based on the lowest number of samples (25 individuals) was calculated with Fstat software version 2.9.3. (Goudet, 2001). The heatmap representing private alleles was prepared using R package Poppr (Kamvar et al., 2014).

The analysis of molecular variance (AMOVA) was carried out using GeneAlEx 6.5 (Peakall & Smouse, 2012). AMOVA enables a hierarchical partitioning of genetic variation between regions, between populations and within populations. For the AMOVA significance tests, 999 random permutations were performed.

Two cedar species identification and genetic population structure was determined using the following approach: We used a Bayesian clustering approach, which is implemented in the software STRUCTURE 2.3.3 (Pritchard et al., 2000) and the empirical statistic DeltaK (Evanno et al., 2005, implemented in STRUCTURE HARVESTER (Earl & Von Holdt, 2012), to determine the number of clusters (K) into which the populations under study can be divided with the highest probability. Each run consisted of 20,000 iteration loops and 200,000 datasets repetitions and was repeated 20 times. The results were visualized using CLUMPAK (Kopelman et al., 2015).

3. Results

3.1. Species Differentiation

DNA was extracted from 13 Lebanon cedar and 11 Atlas cedar populations (Table 1). The 15 nuclear microsatellite produced reproducible alleles in both tree species and were highly polymorphic.

Table 1. Cedar populations examined and genetically analysed.

No.	Pop_ID	Tree species	Country	Provenance	North	East	Elevation [m]	No. of samples
1	1_FRA	*C. atlantica*	France	CAT900	44.600000	4.500000	500-600	48
2	2_FRA			Mont_Ventoux	44.116667	5.183333	780–930	48
3	3_FRA			Mont_Ventoux2	44.116667	5.183333	780–930	30
4	4_FRA			Saumon	44.100000	6.233333	820–950	48
5	5_FRA			Menerbes	43.833333	5.200000	660	48
6	6_FRA			Menerbes2	43.800000	5.250000	714	30
7	7_MOR	*C. atlantica*	Morocco	Rif	34.822500	-4.410833	1765	26
8	8_MOR			Talzemt	33.633333	-4.000000	1990	48
9	9_MOR			Marmoucha	33.578611	-4.216944	1800	47
10	10_MOR			Azrou	33.425000	-5.180000	1814	48
11	11_MOR			Ifrane	33.316667	-5.233333	1653	48
12	1_TUR	*C. libani*	Türkiye	Antalya/Kaş/Karaçay	36.398056	29.44028	1550	48
13	2_TUR			Antalya/Finike/Aykırıçay	36.450278	30.17944	1300	48
14	3_TUR			Isparta/Isparta/Kapıdağ	38.08972	30.70556	1600	48
15	4_TUR			Eskişehir/Afyon/Sultandağı	38.53389	31.15194	1400	48
16	5_TUR			Konya /Ermenek/Kazancı	36.53528	32.77722	1750	48
17	6_TUR			Mersin/Anamur/Abanoz-1	36.33750	32.93750	1430	48
18	7_TUR			Mersin/Mersin/Aslanköy	37.00000	34.23333	1000	48
19	8_TUR			Adana/Pozantı/Pozantı	37.50889	34.96056	1325	48
20	9_TUR			Amasya/Niksar/Çatalan	40.79167	36.57778	1100	48
21	10_TUR			Amasya/Niksar/Çatalan-2	40.79167	36.57778	1100	28
22	11_TUR			K.Maraş/Andırın/Elmadağı	37.61750	36.46889	1550	48
23	12_LBN	*C. libani*	Lebanon	Ain Zhalta	33.74278	35.73083	1580	48
24	13_LBN			Ehden	34.31000	35.99000	1565	48
							Total	**1.073**

For all markers, the mean allele number, the mean observed heterozygosity, the genetic diversity and the polymorphism information index were high. The analysis of molecular variance (AMOVA) showed that 63% of the total genetic variation was within populations, 26% between populations and 11% between individuals (Supplementary Figure 1). The Bayesian cluster analysis with the STRUCTURE software resulted in the highest probability for two genetic clusters (maximum value Delta K = 92.9 for K = 2). In Figure 2, the populations are separated by vertical lines and labelled on the X-axis with the Pop.ID corresponding to Table 1. Based on the STRUCTURE results, a clear separation of the two cedar species was observed with populations of *Cedrus atlantica* in green (populations 1-11) and *Cedrus libani* in red (populations 12-24) using the CLUMPAK software. The 15 markers used are thus very well suited for species differentiation.

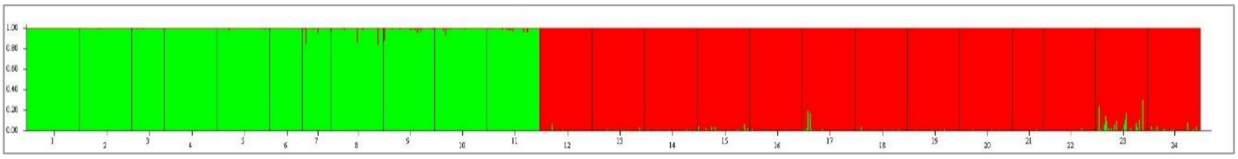

Figure 2. Cluster analysis for species identification using genetic markers (15 nSSRs). The colour distributions K1 and K2 indicate clear grouping: Green = *Cedrus atlantica*; Red = *Cedrus libani*. Histogram of the genetic structures of the 24 cedar populations.

3.2. Genetic Variation and Structure of *Cedrus atlantica*

The microsatellite data analyses showed an average genetic diversity among the studied Atlas cedar populations (Table 2). The number of alleles (*Na*) varied between 3.53 (population 4_FRA_ Saumon) and 6.40 (population 5_FRA_ Menerbes) with an overall mean of *Na* = 5.10. The allelic richness (*Ar*) varied between 3.19 (population 4_FRA_ Saumon) and 5.53 (population 5_FRA_ Menerbes) with an overall mean value of *Ar* = 4.65. The mean number of effective alleles (*Ne*) varied from 2.10 (population 4_FRA_ Saumon) to 3.18 (population 9_MOR_Marmoucha) with an overall mean of *Ne* = 2.71. A total of 31 private alleles were present, distributed over 8 populations (Figure 4). The highest number of private alleles was found in population 5_FRA_ Menerbes (*Np* = 7) (Figure 3). Expected heterozygosity (*He*) was also medium in all populations studied (mean = 0.499). The fixation index (*F*) varied from -0.059 (population 10_MOR_ Ifrane) to 0.265 (population 9_MOR_ Marmoucha, Table 2).

Table 2. Parameters of genetic variation within the eleven Atlas cedar populations.

Pop	PopName	*N*	*Na*	*Ne*	*Ar*	*Np*	*Ho*	*He*	*F*
1_FRA	CAT900	48	5.60	3.00	4.99	3	0.460	0.535	0.156
2_FRA	Mont_Ventoux	48	5.33	2.75	4.78	0	0.470	0.509	0.085
3_FRA	Mont_Ventoux	30	5.33	2.85	5.15	0	0.504	0.524	0.045
4_FRA	Saumon	48	3.53	2.10	3.19	3	0.325	0.407	0.169
5_FRA	Menerbes	48	6.40	3.06	5.53	7	0.498	0.542	0.093
6_FRA	Luberon	30	5.47	2.99	5.28	0	0.507	0.535	0.044
7_MOR	Rif	26	5.07	2.92	5.04	6	0.477	0.490	0.059
8_MOR	Talzemt	48	5.07	2.54	4.39	2	0.509	0.497	0.031
9_MOR	Marmoucha	47	5.20	3.18	4.76	2	0.417	0.538	0.265
10_MOR	Azrou	48	4.60	2.22	4.03	4	0.492	0.445	-0.059
11_MOR	Ifrane	48	4.47	2.23	4.04	4	0.419	0.468	0.110
Total		**467**	**5.10**	**2.71**	**4.65**	**2.8**	**0.462**	**0.499**	**0.091**

N	Sample numbers	***Np***	Private alleles
Na	Mean number of alleles	***Ho***	Observed heterozygosity
Ne	Mean number of effective alleles	***He***	Expected heterozygosity
Ar	Mean allelic richness (based on the minimum sample number of 25 Individuals)	***F***	Fixation index

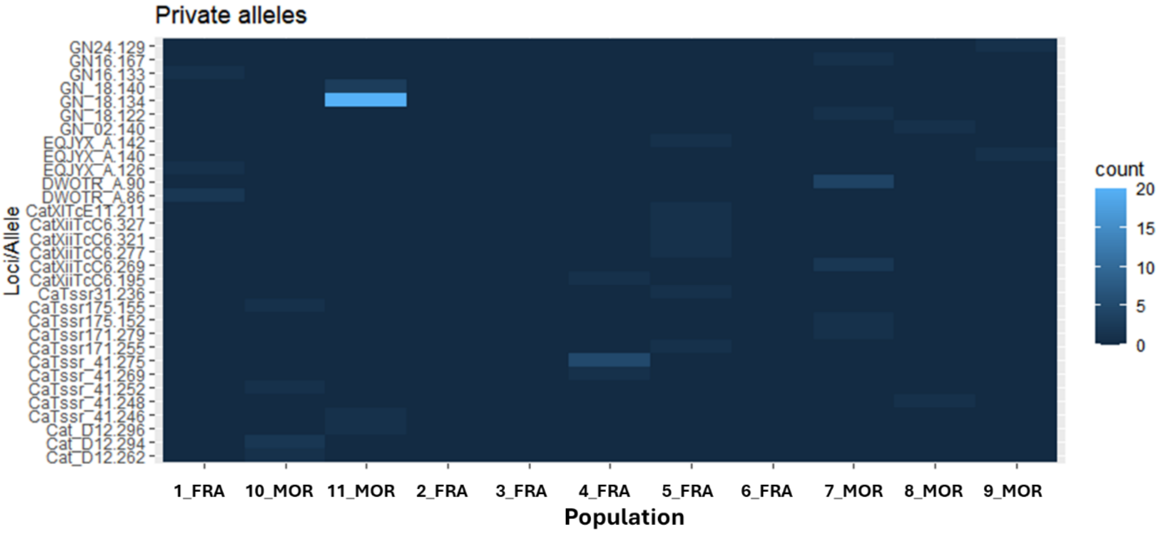

Figure 3. Private alleles in *Cedrus atlantica* populations.

The analysis of molecular variance (AMOVA) showed that 79% of the total genetic variation occurs within populations and 12% between populations (Supplementary Figure 2). The result of the cluster formation based on the 15 nSSR loci yielded a K value of 2. The deltaK value was very high at around 475 (data not shown). The two colours indicate different STRUCTURE clusters. Figure 4 provides a summarized overview of the spatial genetic structures of the atlas cedar populations, in particular the affiliation of the individual populations to one of the two identified groups.

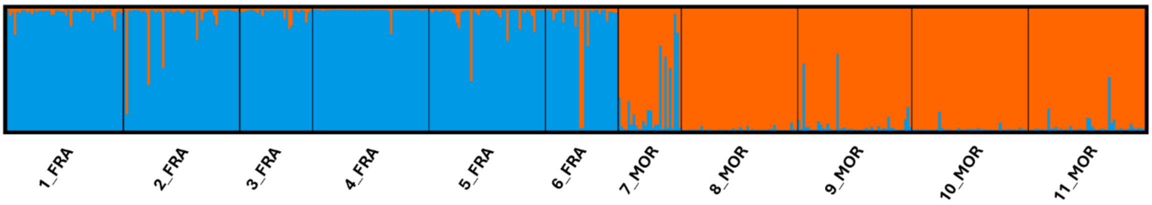

Figure 4. Histogram of the genetic structures of the 11 cedar populations based on Bayesian clustering population structuring using 15 nSSRs. Blue = *Cedrus atlantica* from France; Orange = *Cedrus atlantica* from Morocco.

The two genetic groups shown in the histogram (Figure 4) can be also clearly divided spatially into two areas. There is a clear separation between the populations from France (K1, blue) and the populations from Morocco (K2, orange). The pie charts in Figure 5 show the assignment of the individuals within populations to the two STRUCTURE clusters.

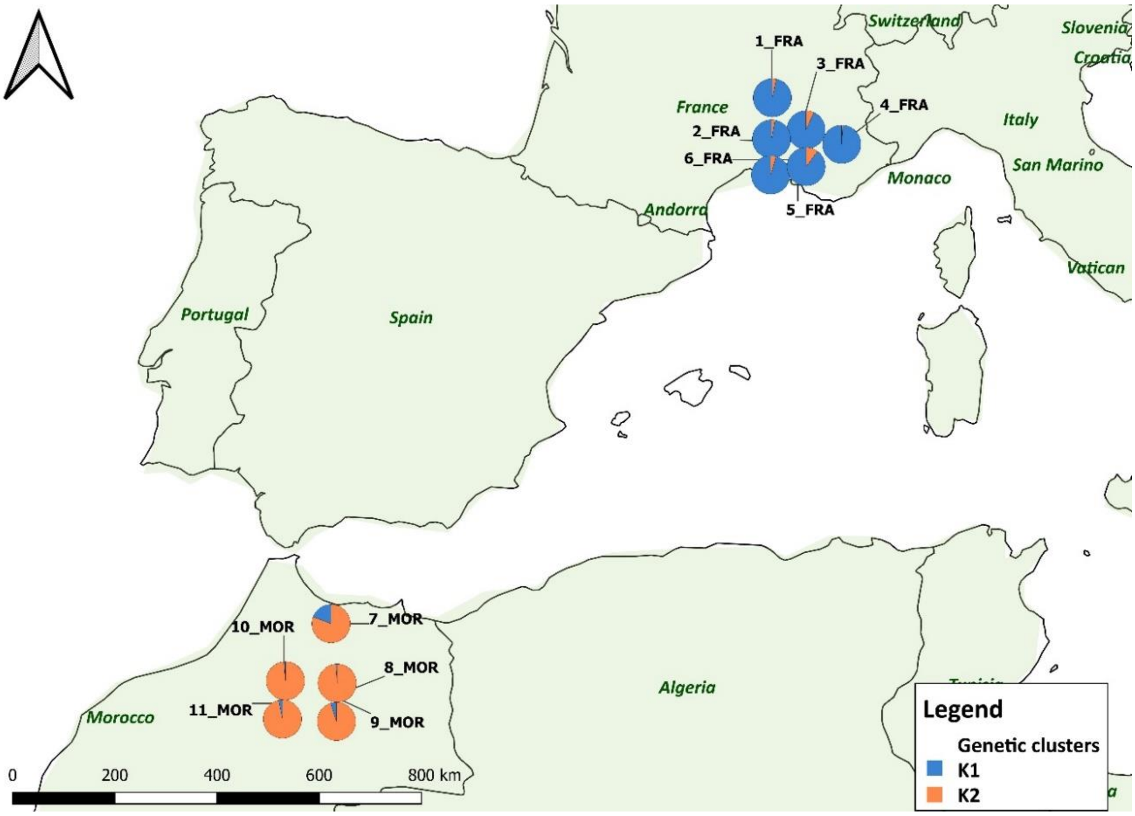

Figure 5. Distribution of the spatial genetic structures of the *Cedrus atlantica* populations. The colours K1 and K2 show clear geographical grouping. Cluster colours correspond to the histogram in Figure 4.

4. Discussion and Conclusion

The two cedar species Atlas and Lebanon cedar are increasingly being discussed as possible drought-resistant alternative tree species in Germany and Central Europe. Main interest is to increase resilience of unstable Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) stands and thus avoid bottlenecks in the supply of timber in the long term. Both cedar species have a high climate tolerance (drought and frost tolerance), occurs on calcareous and siliceous soils and can be integrated into European forests (Bariteau & Vauthier, 2011; Carvalho et al., 2011; Fusaro, 2011; Gökdemir & Dağdaş, 2011; Aoujdad et al., 2015; Šeho, 2018, 2019; İmal et al., 2024; Laaribya et al., 2024). Recent studies of Atlas cedar in northwestern Algeria shows that drier winters accompanied by positive North Atlantic Oscillation phases affected tree growth and resilience of these forests (Sarmoum et al., 2024). Particular attention should be paid to the origin of the forest reproductive material, as this plays a decisive role in performance of provenance, adaptability, and successful cultivation (Bariteau & Vauthier, 2011; Fusaro, 2011, Šeho & Janßen, 2020). In Bavaria, cedar species have so far mainly been planted as parks and street trees. Until the start of the CorCed project in 2015, there was hardly any experience of cultivation in Bavarian forests. In order to test the suitability for cultivation of different provenances of Atlas cedar and Lebanon cedar under Central

European climatic conditions and to evaluate their suitability for cultivation, possible seed stands in the natural distribution area were phenotypically evaluated and genetically characterized.

Thus, in our study we used a set of 15 nuclear microsatellite loci which produced fragment patterns that were easy to evaluate in both cedar species. The derived fragment length differences made it possible to genetically clearly separate the two cedar species. For the investigation of species differentiation, 24 populations were analysed. We observed strong and significant genetic differentiation between the two cedar species. Correspondingly, Bou Dagher-Kharrat et al. (2001) shows interspecific differentiation in the genus *Cedrus* based on karyotype analysis. Within the Atlas cedars, the Bayesian clustering method also showed clearly distinguishable geographical patterns. For example, populations from Morocco and France, the latter ones being secondary populations of Algerian origin, can be clearly separated. The strong differentiation arose from distinct glacial refugia in Algeria, Morocco, and Tunisia after the last Quaternary glacial cycle (Cheddadi et al., 2022). Renau-Morata et al. (2005) identified two to three genetic groups across the Atlas cedar's natural distribution range, within genetically distinct subpopulations. Cheddadi et al. (2022) stated for the microrefugia within Rif mountains that the progressive reduction of population and habitat fragmentation will lead to a reduction of gene flow and increases genetic drift and inbreeding. These effects may increase the chances of population extinction. Similar findings were observed for Lebanon cedar from Türkiye and Lebanon (Fady et al., 2008). All 11 populations of Atlas cedar in our investigations showed medium values of genetic diversity. The number of alleles (*Na*) varied between 3.53 (Pop 4 Soumon) and 6.40 (Pop 5 Menerbes) in the French populations, while the values of the Moroccan populations were in-between. The population from Soumon (Pop 4) showed the lowest genetic diversity and heterozygosity. The reason for the low diversity parameters could be a bad crop and that seeds were harvested from only a few seed trees. This stand should be representatively sampled and analysed again. If the present result is confirmed, the site should not be recommended for further seed harvesting. On the contrary the 5_FRA Menerbes population showed the highest genetic diversity, which is a good base for further adaptation and should be used as a seed source. This stand is one of the three French stands which produce reproductive material in the category "tested" (Bariteau & Vauthier, 2011). The studied Moroccan populations showed a medium genetic diversity. Cheddadi et al. (2022) observed a low differentiation among populations of Moroccan Atlas cedar, which may be because of moderate genetic flow. Our analysis showed that 79% of the total genetic variation occurs within populations and 12% between populations (Supplementary Figure 2). Renau-Morata et al. (2005), observed similar findings and discussed that effect of gene exchange among populations due to the easy dispersion of the species pollen, despite mountain ranges providing barriers. The highest allelic richness, Ar = 5.04, was observed in the Rif Mountains. As well Cheddadi et al. (2022) observed lower allelic richness in the Middle or High Atlas Mountains. Several Atlas cedar populations are genetically distinct and possess a low genetic diversity which is caused by barriers to their gene flow (Bobo-Pinilla et al., 2022). The further focus should be set on the conservation of this ecologically valuable tree species in all countries of origin (Cheddadi et al., 2017, 2022; Wazen et al., 2018). The planting of so-called "stepping stone populations" can contribute to gene flow and thus to genetic enhancement. In Bavaria the selection of suitable provenances, for example Ménerbes (Supplementary Figure 3), will play a decisive role in the introduction and cultivation success of Atlas cedar. However, all studied Moroccan and French provenances should be tested in provenance tests under different environments in Germany. Based on the present results, possible seed stands and gene conservation stands for the Atlas cedar can be proposed. Following the successful cultivation of the plant material, we established several practical and provenance trials in southern Germany (Kelheim, Kipfenberg, Wüstenrot and Kandern). The provenance trials are established on warm sites (average annual temperature approximately 9.5 °C) along a geographical east-west gradient. These trials should serve as a basis for the evaluation of the suitability of Atlas cedar provenances for cultivation under Central European climatic conditions like in other European countries (e.g., Bariteau & Vauthier, 2011; Fusaro, 2011). Future DNA-based and provenance studies should include more populations of the Atlas cedar from Algeria.

4.1. Practical Implementation

The obtained data will be used to assess the suitability of cedar for cultivation in Germany. In addition to the provenance trials, to gain knowledge at different sites (soil and climate) in Bavaria a new instrument of practical cultivation trails was introduced in 2020 (Šeho, 2021). Both instruments can serve as a basis for the development of provenance recommendations in the future. The new instruments involve private and state forest owners and can be used as a real forest laboratory. In 2020, Atlas and Lebanon cedar were included in The Guideline of the Bavarian Forestry Administration "TREE SPECIES FOR THE CLIMATE FOREST". All three tree species from the CorCed project are now being promoted as part of practical cultivation trials for all types of forest ownership making an important contribution to the acquisition of knowledge (Šeho, 2021). Since the beginning of the action in 2020 (Bayerisches Staatsministerium für Ernährung, Landwirtschaft, Forsten und Tourismus, 2020), 11 ha of practical cultivation trials with 28,055 Atlas cedar seedlings from six provenances have been established on 96 subplots (practical cultivation trials) in Bavarian private and municipal forests (Figure 6). According to the data from Bavarian State Institute of Forestry until June

2023 a survival rate of approximately 80% was observed (Wimmer & Šeho, 2024).

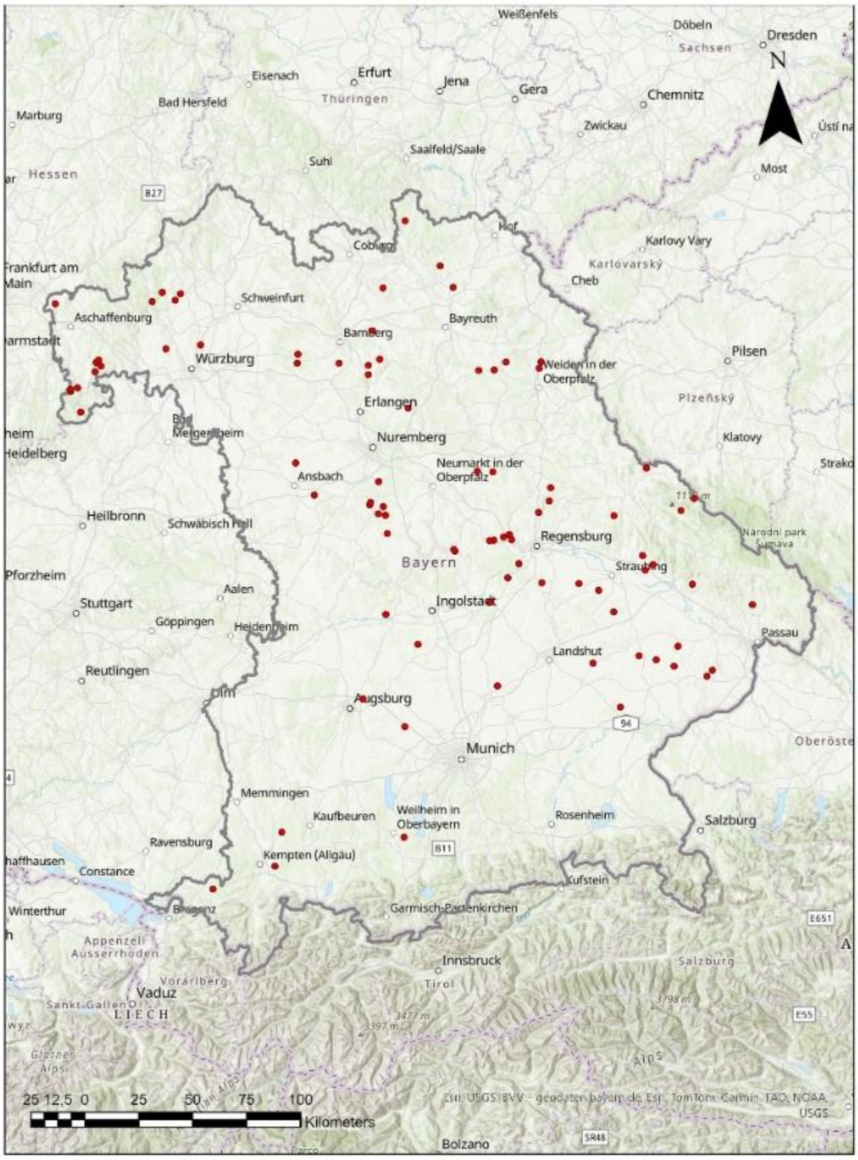

Figure 6. Distribution of practical cultivation trials of Atlas cedar in Bavaria. Data from The Bavarian State Institute of Forestry, map papered by D. Glas, AWG.

In the same period, approximately 4.5 ha of those practical cultivation trials with Atlas cedar were successfully established in the Bavarian State Forests. The genetic analyses within the CorCed project form the basis for the provenance introduction of Atlas cedar provenances in Bavaria. Furthermore, the results obtained can be used for traceability of origin in order to assign FRM to the genotyped stands and to enable a large-scale assignment of the provenances to the natural distribution area.

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Conflict of Interest

The authors declare that they have no conflict of interest.

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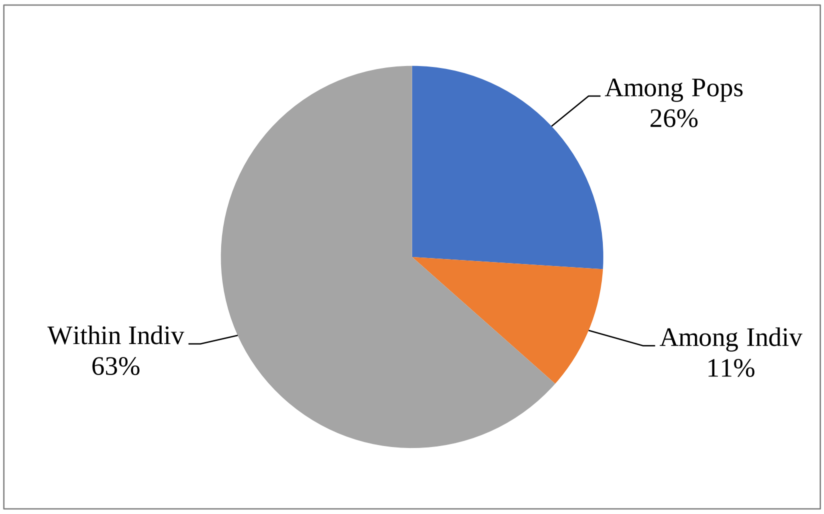
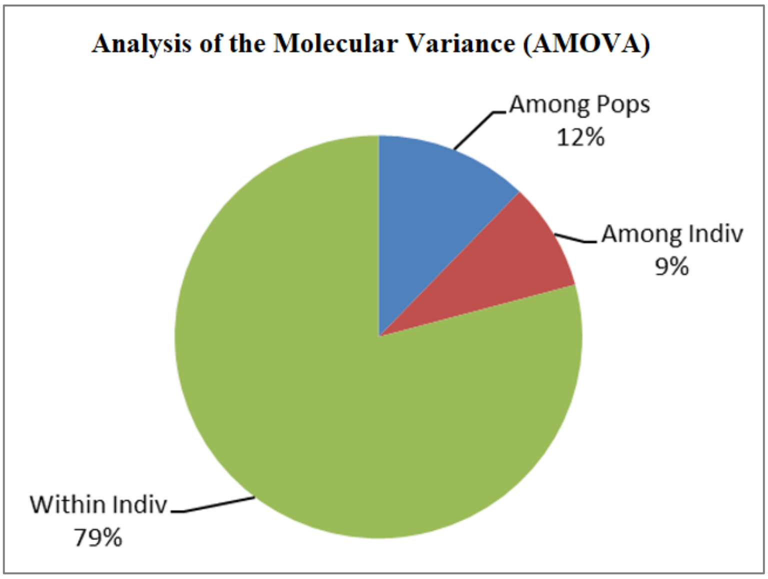
Supplementary Information



Supplementary Figure 1. Analysis of the molecular variance (AMOVA) between the Cedar populations.



Supplementary Figure 2. Analysis of the molecular variance (AMOVA) between the Atlas cedar populations.

Supplementary Figure 3. Seed harvesting stand Ménerbes, France. Photo: M. Šeho.