ANALYSIS OF LATVIAN AND BELARUSIAN OAK (*QUERCUS ROBUR* L.) POPULATION PROVENANCE AND GENETIC STRUCTURE USING CHLOROPLAST MARKERS

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In this study, oak specific chloroplast simple sequence repeat (SSR) markers were used to analyse Latvian and Belarusian oak (Quercus robur L.) population provenance and genetic structure. Chloroplast haplotypes were compared between Latvian and Belarusian pedunculate oak, and several common haplotypes were identified. The SSR haplotypes were compared to previously reported PCR-RFLP haplotypes, and haplotypes from the A (eastern European) and C (central European) lineages were identified. C lineage haplotypes were only found in the western region of Latvia. Haplotypes shared between Latvia and Belarus were all from the A lineage. Despite the much smaller population size of oak in Latvia in comparison to Belarus, the level of genetic diversity identified using the chloroplast SSR markers is similar. Provenance trials will need to be established in order to determine the suitability of Belarusian oak reproductive material for deployment in Latvia. Based on the results from this comparison of chloroplast haplotypes, as well as climatic similarities, it is probable that Belarusian oak material will be better suited to the eastern regions of Latvia compared to the western regions of Latvia.

Keywords: pedunculate oak, glacial refugia, haplotypes, forest reproductive material.

INTRODUCTION

Oak species have a wide distribution range in Europe, but in Northern Europe, only two species are found — *Quercus robur* L. (pedunculate oak) and *Q. petraea* (Matt.) Liebl. (sessile oak). In Latvia, only *Q. robur* is found in natural forest stands. The current area of oak in Latvia is very small (0.35% of the forest area) (Gailis and Smaukstelis, 1998); however, historically and culturally this species is very important in Latvia. In contrast, oak is widely distributed in Belarus, with oak stands covering more than 287 000 ha or 3.5% of forest area. The distribution of oak in Belarus is distinctly zonal. The majority (63.5% of the total area of oak forests of the country) are found in southern Belarus, while oak is less common in the north and northwest areas. Most of the oak trees are found in mixed or pure stands, and

provenance regions and genetic reserves have been established (Kovalevich *et al.*, 2010).

Oak is thought to have arrived in the territory of present-day Latvia approximately 7400 years before present (ybp), reaching a maximum coverage of approximately 18% ~3000 ybp (Zunde, 1999). Oaks were widely distributed in Latvia, but intensive felling and changing land use has greatly diminished their distribution. There are very few oak stands, and many trees are found in isolated patches comprising of one or a few trees. In addition, the provenance of the oaks is not known in Latvia, and it is possible that there have been repeated introductions of unknown reproductive material. Most of the oak stands registered in the Latvian Forest Service database are mixed stands with other coniferous and deciduous species. In order to determine the anthropogenic impact on oak renewal, not only natural stands

were sampled, but also single trees found close to existing or former dwellings, as well as old oak individuals which are found in the register of noble trees.

There are many factors influencing the low proportion of oak in Latvian forests. However, in response to predicted climate changes, the distribution of the species is expected to experience latitudinal shifts. In addition, the range of forest tree species under management is increasing in Latvia, where forestry is dominated by Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* L.), and to a lesser extent, birch (*Betula* spp.). Therefore, whether by natural or artificial regeneration, the proportion of oak growing in Latvian forests can be expected to increase in the future. A further impact of climate change will be the increase of pathogen and pest infestations, both established and novel (Bergot *et al.*, 2004). No provenance or breeding zones for oak have been delimited within Latvia. As a result, there is a shortage of tested and certified oak reproductive material in Latvia. One solution would be the exchange of oak reproductive material between Latvia and Belarus. Seeking to use certified oak material in Latvia, experimental trials must be established to determine the suitability of Belarusian oak material growing in Latvian conditions, and to identify which provenances are most suitable for use in reproductive material exchanges.

Oak species have been widely studied using chloroplast markers, and detailed maps of haplotype distribution on a European scale have been published (Petit *et al.*, 2002a and references therein). These phylogeographic studies allow determination of post-glacial re-colonisation pathways and are used to detect or to confirm provenance regions (Pliura *et al.*, 2009), as well as to investigate the genetic consequences of human impact on oak populations (König *et al.*, 2002). The majority of these studies have been undertaken using universal chloroplast PCR-RFLP markers (Taberlet *et al.*, 1991; Demesure *et al.*, 1995). Additionally, the focus of these studies has been Western Europe, and the Iberian, Italian, and Balkan refugia and the subsequent re-colonisation pathways have been well studied and defined. Other potential refugia, such as more easterly regions such as the Caucasus and more northerly cryptic refugia (Stewart and Lister, 2001) are less well characterised. PCR-RFLP markers have been utilised to genotype oak populations from both Latvia and Belarus (Csaikl *et al.*, 2002a; Petit *et al.*, 2002b); however, only a small number of populations were analysed (eight and three populations, respectively). In Latvia, a total of six PCR-RFLP haplotypes were identified from two lineages (A and C) (Csaikl *et al.*, 2002a). The haplotypes identified in Latvia from lineage C (E8 and E11) were rare haplotypes. In addition, of the four lineage A haplotypes identified in Latvia (4, 5, 7, E22), one was a rare haplotype. A total of 47.5% of the Latvian oak individuals analysed were rare haplotypes. The origin of these rare haplotypes is not known; they are also found in Estonia, but not in Lithuania or Poland. In addition, the presence of one of the lineage C rare alleles (E8) has been reported in Austrian populations in the Danube valley (Csaikl *et al.*, 2002b). All

three Belarusian oak populations had chloroplast haplotypes belonging to lineage A.

In this study, we utilised oak specific chloroplast SSR markers. These markers have been previously used to investigate oak populations in France (Deguilloux *et al.*, 2004). A much larger study of oak in Europe has been undertaken using PCR-RFLP markers (Petit *et al.*, 2002a). However, we decided to utilise the SSR markers as they could be expected to exhibit higher levels of genetic diversity (Provan *et al.*, 2001), and the genotyping of them is potentially more accurate and complete. The genotyping was done using fluorescently labelled primers, and a capillary sequencer. In contrast, the PCR-RFLP method relies on the discovery of genetic polymorphisms using restriction enzymes, which may not reveal the full amount of genetic diversity due to the choice of restriction enzyme. A sub-set of samples was also genotyped using the PCR-RFLP markers, to facilitate the comparison with the European-wide phylogeographic study (Petit *et al.*, 2002b). The aim of this study was to compare the chloroplast haplotypes found in Latvian and Belarusian pedunculate oak. The results were utilised to confirm the existing provenance regions and to determine the necessity for the establishment of additional genetic reserves in Belarus, as well as to compare the oak haplotypes between Latvia and Belarus in order to identify provenances that potentially could be most suitable for the establishment of trials in Latvia.

MATERIALS AND METHODS

All oak samples collected were *Q. robur*. In Latvia, leaf samples were collected from individual oak trees as well as from oak stands. In addition, oak trees registered in the database of noble Latvian trees were also collected where possible. In total, 415 oak samples were collected in Latvia. Oak samples in Belarus were collected from over 110 oak stands throughout the territory of Belarus. The sampled oak stands included young, mature and old stands, as well as plus forest stands, and genetic reserves. Buds, leaves and wood sampled from five to ten individuals with a minimum distance of 50 m from each other were collected from each stand.

DNA was extracted using a modified CTAB method (Doyle and Doyle, 1990). Chloroplast SSR marker analysis was done using five markers — μ dt1, μ cd4, μ kk4, μ dt3, and μ dt4 (Deguilloux *et al.*, 2003). For each marker, one primer was fluorescently end-labelled in order to facilitate analysis on an ABI Genetic Analyser 3100xl. Genotyping was performed using GeneMapper v4.0 (ABI). Latvian and Belarusian oak samples were analysed separately in each respective country, and a subset of each haplotype jointly genotyped in order to standardise haplotype nomenclature between the two countries. The obtained genotypes were analysed separately and also combined into haplotypes for further analysis. Genetic analysis was done using the softwares GenAlEx v6.4 (Peakall and Smouse, 2012) and Arlequin 3.1 (Excoffier *et al.*, 2005). Minimum spanning trees

and networks were plotted using the Darwin software (Perrier and Jacquemoud-Collet, 2006) and HapStar 0.7 (Teacher and Griffiths, 2011).

A subset of samples (4–6 individuals) from each haplotype identified using the chloroplast SSR markers was analysed using the PCR-RFLP method described in Petit *et al.* (2002). Three primer/restriction enzyme combinations were analysed: AS/HinfI, CD/TaqI and DT/TaqI. These were previously shown to be informative and to differentiate Lithuanian oak provenances (Pliura *et al.*, 2009), and were sufficient to distinguish lineage A haplotypes from lineage C haplotypes (Petit *et al.*, 2002b).

RESULTS

A total of 415 oak individuals from Latvia were analysed using the five chloroplast SSR markers. Between three and six alleles per locus were detected. However, in most loci, only two alleles were found at a frequency of over 5%, while the locus *pkk4* had three alleles with a frequency over 5%. Over 100 oak stands in Belarus were genotyped (5–10 individuals per stand). The SSR markers amplified two to five alleles per locus. The majority of loci had two alleles with a frequency over 5% in the Belarusian data set, but the locus *pkk4* had only one allele with a frequency over 5%, while locus *mdt3* amplified four alleles with a frequency over 5% (Table 1).

The SSR marker data was combined to identify haplotypes. Haplotypes with a frequency of less than 0.01 in the Latvian and Belarusian data set (corresponding to one to three individuals from the data set) were discarded, as these were either genotyping errors or rare variants with minimal impact on the final analyses. In many cases, these rare haplotypes were distinguished from the haplotypes with a frequency higher than 0.01 by a single nucleotide size difference at one or more SSR loci. This could be attributable to genotyping or scoring errors. In some cases, however, novel alleles were observed, and these individuals could represent either exotic introductions or novel mutations of local origin, which should be studied further, but which is outside the scope of this study.

The Latvian and Belarusian genotypes were compared by genotyping common samples as well as by comparison of allele frequencies (Table 1). In most cases, the allele frequencies were similar. Seven alleles were unique to either Latvian or Belarusian oaks, but of these, five had a frequency of 1–2% in the country where they were found. Where there was a large difference in the allele frequencies between countries, these alleles were found to be predominant in haplotypes that were unique to each country, and which were found in the extremes of the examined range (e.g., the western or northern region of Latvia, and the south-eastern region of Belarus).

A total of 14 haplotypes (with a frequency > 0.01) were identified in the Latvian material, of which 6 had a fre-

Table 1. Chloroplast marker allele frequencies in Latvia and Belarus

Locus	Allele	Allele frequencies	
		LV	BLR
<i>mkk4</i>	110	0.11	0
	111	0.01	0
	112	0.59	0.99
	113	0.29	0.01
<i>mdt1</i>	86	0.17	0.03
	87	0.83	0.87
	88	0	0.10
<i>mdt3</i>	122	0	0.22
	123	0.01	0.11
	124	0.50	0.14
	125	0.47	0.55

quency of over 5%, accounting for almost 80% of the analysed individuals. The most widespread haplotype in Latvia was haplotype 1 (31.7%), followed by haplotype 44 (19.3%), haplotype 7 (11.5%), haplotype 33 (6.2%), haplotype 34 (6.2%) and haplotype 25 (5.0%). Only haplotype 1 was found throughout the territory of Latvia, and the distribution of the remaining common haplotypes showed strong geographical differentiation. Haplotype 25 was found in the north, on the eastern side of the Gulf of Riga, haplotype 7 was found in the east, haplotype 33 in the Vidzeme highlands, haplotype 34 was found in the southern central zone (Zemgale) close to the Lithuanian border, and haplotype 44 was found exclusively in the western region of Latvia — Kurzeme.

A total of 17 haplotypes ($f > 0.01$) were identified in the Belarusian material, of which five had a frequency of over 5%, accounting for 85% of the analysed individuals. The most widespread haplotype in Belarus was haplotype 1 (48%), followed by haplotype 3 (11%), haplotype 7 (10%), haplotype 8 (9%), and haplotype 2 (7%). The frequency of the other alleles varied from 1–3%, and they were found in a limited area. Haplotype 1 was found throughout Belarus, with an increasing frequency from west to east. Haplotype 3 was found in the central and southern regions. Haplotype 2 was predominantly found in the south-east. Haplotype 7 was found mainly in the western region, and haplotype 8 in the north-east and isolated areas in the west.

The unified genotypes were used to identify shared haplotypes. Six haplotypes were in common between Latvia and Belarusian oak samples, of which two had a frequency over 5% in Latvia (haplotypes 1 and 7), while four were rare haplotypes in Latvia (haplotypes 3, 5, 7 and 8). Two haplotypes were identified which had a frequency above 5% in both Latvia and Belarus (haplotypes 1 and 7).

The genetic relatedness of the nine high-frequency haplotypes found in Latvia and Belarus was examined by construction of a minimum-spanning network (MSN) (Fig. 1). The genetically most differentiated haplotype was haplotype 44, which is exclusively found in the western region of Latvia, and was not identified in Belarus. This haplotype is

part of the C haplotype lineage identified in Petit *et al.* (2002), while the remaining alleles in the MSN are from the A haplotype lineage. The genetic relationships between the haplotypes revealed in the MSN corresponded well to the geographical distribution of the haplotypes described previously. The shared haplotypes (1 and 7), occupy the central part of the network, and haplotype 1 has the highest frequency in both Latvia (32%) and Belarus (48%). A separate branch was formed by haplotypes 2 and 3, which were found only in Belarus. Haplotype 3 was localised mainly in places where the Carpathian flora spread to the territory of Belarus in the post-glacial period. Haplotype 2 is apparently the youngest genealogically, and was found in the south-east of Belarus, where the continental climate is most pronounced.

The two most widespread haplotypes (covering the largest territory) in Latvia are haplotypes 1 and 7, which are also found in Belarus. Haplotype 1 is also the most widespread and prevalent haplotype in Belarus. The SSR haplotypes were compared to previously reported PCR-RFLP haplotypes (Csaikl *et al.*, 2002a; Petit *et al.*, 2002b). PCR-RFLP haplotypes from the A and C lineages were identified. SSR haplotype 44 and related lower frequency haplotypes identified in Latvia were from lineage C. The specific haplotypes were not identified, as the lineage C haplotypes previously described in Latvia were rare haplotypes, and the restriction fragment diagrams were not described. Haplotypes from lineage C were only found in the western region of Latvia, and were not identified in Belarus. This is also consistent with differences in climatic conditions, as the climate in the western region of Latvia is influenced by the proximity of the Baltic Sea, and is climatically distinct from the more continental climate regime of eastern Latvia and Belarus. The two common haplotypes between Latvia and Belarus (1 and 7) are both from the A lineage, and the SSR haplotype 1 is probably PCR-RFLP haplotype 5, while SSR haplotype 7 is probably PCR-RFLP haplotype 7. This would be consistent with the previous reports on the PCR-RFLP haplotypes in Latvia (Csaikl *et al.*, 2002a), where PCR-RFLP haplotype 5 had a frequency of 35% (SSR haplotype 1 frequency 32%), and PCR-RFLP haplotype 7 had a frequency of 15% (SSR haplotype 7 frequency 12%). It is possible that the PCR-RFLP and SSR haplotypes are not completely concor-

There is little evidence for high anthropogenic impact on the distribution of oaks in Latvia. The central European haplotype lineage (C) was only found in the western region of Latvia, and corresponds to previous studies (Csaikl *et al.*, 2002a). Oak individuals for this study were collected from a variety of sites in Latvia, including parks and old manor gardens. If this oak material had been imported from central Europe (e.g., Germany), then it is likely that lineage C haplotypes would have also been found in these planted parks and gardens in the eastern regions of Latvia. This identification of probable historic importation of germplasm, by the use of chloroplast markers, has been previously reported in Latvia. Comparative analysis of chloroplast haplotypes of Latvian ash (*Fraxinus excelsior* L.) stands with European lineages revealed that only one population in Ķemeri National Park contained the central European haplotype. This haplotype was also found in the gardens of the nearby sanatorium, which was planted in the mid-19th century, indicating that these central European haplotypes were probably introduced, as they were not found in any other ash populations in the western region of Latvia (Ruņģis *et al.*, 2016). This type of distribution of the current haplotypes contrasts to that found in Latvian oaks, where the central European lineage was found throughout the western region of Latvia, as well as in Poland, Lithuania and western Estonia (Csaikl *et al.*, 2002a), indicating that this distribution is likely to have occurred naturally by the post-glacial recolonisation of the Baltic region by pedunculate oak.

Provenance trials will need to be established in order to determine the suitability of Belarusian oak reproductive material for deployment in Latvia. Based on the comparison of distribution of chloroplast haplotypes, as well as due to climatic similarities, it is probable that Belarusian oak material will be better suited to the eastern regions of Latvia compared to the western regions of Latvia. The predominant haplotype found in the western region of Latvia (haplotype 44) is not found at all in Belarus, and it is from a separate

haplotype lineage (lineage C), and is also potentially represents genotypes differentially adapted to the milder and more maritime climate characteristic of the western region of Latvia, contrasting with the more continental climate found in the eastern part of Latvia and in Belarus. Deployment of forest reproductive material outside of their source regions, or ‘assisted migration’ has been proposed as one possible mechanism to mitigate the effects of climate change on forest tree species (Sáenz-Romero *et al.*, 2021). This has, however, been mainly discussed in the context of latitudinal transfer (i.e. south to north). In our case, transfer of oak reproductive material from Belarus to Latvia in most cases would entail a longitudinal transfer (east to west), and from a predominantly continental climate zone into a region more influenced by the proximity of the Baltic Sea. In this case, special attention should be paid to oak from the western part of Belarus (Brest and Grodno regions) at the same longitude with Latvia. The transfer of oak from these regions to Latvia should be carried out in the south-north direction. The haplotype 7 found here growing in the territory of Latvia was also found in Poland in stands near Warsaw and Poznań.

Despite the much smaller population size of oak in Latvia in comparison to Belarus, the level of genetic diversity identified using the chloroplast SSR markers is similar. A further survey of nuclear markers, similarly as described by Jurkšienė *et al.* (2020), would enable a more comprehensive comparison of genetic diversity. The results obtained in this report have enabled comparison of Latvian and Belarusian oak populations, and allowed the identification of specific Belarusian oak provenances that share haplotypes with Latvian oaks. The Belarusian oak provenances are most likely to be suited for growing in eastern regions of Latvia, based on the similarity of haplotype composition and climatic considerations.

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LATVIJAS UN BALTĶRIEVIJAS PARASTĀ OZOLA (*QUERCUS ROBUR* L.) POPULĀCIJU ĢENĒTISKĀS STRUKTŪRAS UN IZCELSMES ANALĪZE

Analizēta Latvijas un Baltkrievijas parastā ozola (*Quercus robur* L.) populāciju izcelsme un ģenētiskā struktūra, izmantojot hloroplastu marķierus. Iegūtie hloroplastu haplotipi salīdzināti starp Latvijas un Baltkrievijas ozolu paraugiem, un identificēti vairāki kopīgi haplotipi. SSR haplotipus salīdzināja ar iepriekš aprakstītiem haplotipiem, un tika identificēti haplotipi no A (Austrumeiropas) un C (Centrāleiropas) līnijām. C līnijas haplotipi tika atrasti tikai Latvijas rietumu reģionā. Latvijai un Baltkrievijai kopīgi haplotipi bija no A līnijas. Neraugoties uz daudz mazāku ozola populācijas lielumu Latvijā salīdzinājumā ar Baltkrieviju, hloroplastu ģenētiskās daudzveidības līmenis ir līdzīgs. Lai noteiktu Baltkrievijas ozola reprodutīvā materiāla piemērotību izvietošanai Latvijā, būs jāizveido izmēģinājumu stādījumi. Ņemot vērā hloroplastu haplotipu salīdzināšanas rezultātus, kā arī klimatiskos apstākļus, iespējams, ka Baltkrievijas ozola stādmateriāls būs labāk piemērots Latvijas austrumu reģioniem.