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Genetic variation in European elms

Genetic characterisation of populations of *Ulmus laevis* and of the *U. minor-U. glabra* complex

Karen Cox, An Vanden Broeck and Kristine Vander Mijnsbrugge

Redacteurs:
Karen Cox, An Vanden Broeck en Kristine Vander Mijnsbrugge
Instituut voor Natuur- en Bosonderzoek

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Vestiging:
INBO Geraardsbergen
Gaverstraat 4, B-9500 Geraardsbergen
www.inbo.be

e-mail:
karen.cox@inbo.be

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Coppiced *Ulmus laevis* (Kristine Vander Mijnsbrugge)

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Summary

Dutch Elm Disease, habitat loss and fragmentation have reduced the European elm populations enourmously and are still persisting threats to their survival. As genetic variation plays an essential role in evolution and adaptation, we assessed the genetic diversity within and among remaining elm populations in Flanders (northern Belgium). This report is devided in two parts. The first part entails the study of *Ulmus laevis*, the second the study of the *U. minor-U. glabra* complex. For both studies Amplified Fragment Length Polymorphic (AFLP) markers were used, with 191 and 389 polymorphic loci, respectively. Also, samples from surrounding countries were included as a reference. As expected, the genetic diversity of the generally small *U. laevis* populations is low and population differentiation is moderately high (F_{ST} = 0.14 when F_{IS} = 0). No logical population structure was found, which could be related to the species' phylogeographic history and/or caused by past translocation.

Only 27% of the Belgian samples taken from *U. minor*, *U. glabra* and their hybrids seemed to be from pure *U. glabra* and again 27% from pure *U. minor*. Consequently, ca. 45 % of the samples appeared to be hybrids between both species or backcrosses, of which 77 % was identified as one of both pure species based solely on their morphology. Whereas *U. laevis* does not seem to reproduce vegetavily often, 76% of the Belgian locations with more than one sample of the *U. minor-U. glabra* complex contained multiple ramets of the same genet or had a genet shared among locations. Clonal reproduction was only found among *U. minor* and hybrids with *U. glabra* (*U.* x *hollandica*) which confirms the inability of *U. glabra* to produce root suckers or sprouts. Since the majority of the sampled locations holds a mixture of pure species and hybrids, genetic diversity and differentiation were calculated within and among these mixed populations. Both parameters were higher compared to *U. laevis*, wich could be due to the combination of species. Furthermore, various elm cultivars were included in the study. After clarifying their taxonomy genetically, we investigated their influence on the Belgian populations of *U. minor-U. glabra.* 'Klemmer' was found on two locations. Also, several samples were assigned as offspring of 'Belgica', 'Klemmer' and 'Major'. Considering the history of the use of elms, their hybrids and cultivars, it is possible that reproductive material has been moved around a lot, obscuring the genetic structure of the populations. Moreover, this could explain the species mix and the abundant hybrids present in the studied populations.

Index

List of figures and tables

Introduction

Only three *Ulmus* ssp. are native in Europe: *U. minor*, *U. glabra* and *U. laevis*. Besides habitat loss and fragmentation, the Dutch Elm Disease (DED) severely reduced the number of elm trees starting from around 1910. These threats still exist, making the conservation of the remaining trees a necessity. DED is caused by the alien fungi, *Ophiostoma ulmi* (Buisman) Nannf. and *O. novo-ulmi* Brasier, which are spread by bark beetles of *Scolytus* Geoffroy (Coleoptera, Scolitidae; Brasier 2001). The main vectors in Europe are *S. scolytus* and *S. multistriatus* (Webber 2004). DED resistant cultivars are developed with varying success. Also, some of these cultivars have been widely planted in the past, possibly posing an influence on the genetic diversity of existing natural populations of *U. minor* and *U. glabra* through hybridisation and introgression. Certain cultivars and many ornamentals are non-European elms or hybrids between European and non-European elms. When hybridisation with native elms is possible, it may change the genetic makeup of the latter (Soltis and Soltis 2009). An example is *U. pumila*, or the Siberian elm, which was introduced in Spain and Italy. Its hybrid with the native *U. minor* is now common in both countries (Cogolludo-Agustin et al. 2000).

Considering the severe threats European elms are under, actions were taken to conserve the remaining germplasm on a national basis. In turn, this has led to the initiative within the European Forest Genetic Resources (EUFORGEN) cooperative program to realise a conservation plan on a European level (Collin 2002). Furthermore, an EU project on the "Co-ordination for conservation, characterisation, collection and utilisation of genetic resources of European elms" ran from 1997 till 2001 (RESGEN CT96-78).

In Flanders (northern Belgium), new individuals of native elms are still being added to *ex situ* collections, even after the RESGEN project ended. They are collected in potential autochthonous populations, to preserve the remaining genetic resources and to eventually use the collections as seed orchards. In order to promote the use of local planting stock for (re)forestation and the creation of small landscape elements, reproductive material needed to be available. Once a seed orchard is established, it is a more convenient source of such planting material, as opposed to the fragmented and scattered populations *in situ*. Nevertheless, source populations as well as the *ex situ* collections required to be screened genetically, in order to confirm assumptions of autochthony and to evaluate the level of genetic diversity and structure.

This study entails two sections. First we took a closer look at the *U. laevis* populations. This study was done separate from the *U. minor-U. glabra* complex, because *U. laevis* is known not to crossbreed with these species (Mittempergher and La Porta 1991). Although *U. laevis* is susceptible to DED, it suffered considerably less losses. The reason for this is that the species seems less attractive to the *Scolytus* vectors than *U. minor* and *U. glabra* (Sacchetti et al. 1990, Webber 2000, Martin-Benito et al. 2005). Because of its lower infection rate in Western Europe, interest has been renewed to use it as a tree species, e.g. in urban plantings. However, habitat loss reduced the number and size of its populations in Europe. The typical habitat of *U. laevis*, riparian deciduous forest, has undergone severe changes due to the canalisation of rivers, land drainage and/or land reclamation for agriculture (Collin 2003). We tried to detect how much genetic diversity was left in the remaining populations, especially of Flanders. To compare results with populations of surrounding countries, samples mainly from France and the Netherlands were included. Furthermore, genetic variation among populations and population genetic structure were investigated. In addition, we needed to ensure that the *ex situ* collection is representative for the *in situ* genetic diversity. Based on the results, guidelines for conservation were given.

In the second section, we tried to unravel the *U. minor-glabra* complex in Flanders. Because both species hybridise with each other, their taxonomy becomes extremely difficult (Goodall-Copestake et al. 2005). Identifying the species origin of individual trees is necessary to determine the species composition of populations and thus helps to understand their ecology. Moreover, the results of the species identification could also shed some light on the species composition of the *ex situ* collections, which were created in Flanders with pure species in mind. As is the case with *U. laevis*, *U. minor* and *U. glabra* generally occur in scattered, small groups. Although *U. minor* is found

more often, it might be because of its ability to reproduce clonally through root suckering, an ability that its hybrid with *U. glabra* shares. It is therefore necessary to detect clones among individuals and characterise the populations' genetic diversity and structure.

As cultivars of elms have shared space with natural elm populations for some time now, introgression is not unthinkable. In this study, we included several well-known cultivars to investigate their influence on the Flemish populations of *U. minor-U. glabra*. Also, the taxonomy of the cultivars was evaluated.

1. Population genetics of *Ulmus laevis*

1.1. Material and methods

1.1.1. Samples and DNA extraction

During the period 2006-2009 leaves of *Ulmus laevis* trees were collected in Flanders, the Netherlands, France and Kyrgyzstan and stored on silica gel. The locations are listed in Table 1.1 and shown in Fig. 1.1. Except for 18 samples of location BEHE, the samples of the locations FRDV, FRVA8, FRVA9, FRVA10, FRVA13, FRVA14, FRVA23, KYBI and a few samples of the Netherlands, all leaves were collected in a seed orchard/ gene bank containing ramets of the orginal ortets. All samples are listed in Table A in the Annex. In general, only a few samples per location of France and the Netherlands were included as reference samples.

Total DNA was extracted from ground leaf samples, partly with QuickPick™ SML Plant DNA purification kit in combination with the PickPen 8-M magnectic tool or the MagRo 8-M robotic workstation (Isogen Life Science) on 5 mg of dried leaf tissue, and partly with DNeasy Plant Mini Kit (Qiagen) on 20 mg of dried leaf tissue. The integrity and quantity of DNA were assessed on 1.5% agarose gels and spectrophotometrically with the ND-1000 Nano-Drop (NanoDrop Technologies), respectively.

Table 1. 1: List of sampled populations of *Ulmus laevis*. N: number of sampled individuals; N AFLP: number of samples successfully analysed with AFLP; N pop: total number of individuals present on a location; Type LE: type of landscape element.

Location	Country	city	Lon	Lat	N	N AFLP	N pop	Type LE
BEBR	Belgium	Brakel	3.7255	50.7797	5	4	5	Forest edge, wooded bank
BEDP	Belgium	De Panne	2.6133	51.0910	6	6	20	Small forest
BEEG	Belgium	Egenhoven	4.6682	50.8576	7	7	15	Forest, along river
BEGE	Belgium	Geraardsbergen	3.9265	50.7704	3	3	5	Forest
BEHE	Belgium	Heers	5.2484	50.7211	22	18	30	Wooded bank, forest
BEKE	Belgium	Kermt	5.2587	50.9361	5	4	5	Small forests, forest edge
BELI	Belgium	Lille	4.8039	51.2804	4	4	4	Forest
BEPL	Belgium	Ploegsteert	2.8754	50.7405	1	1	1	Forest edge
BEPO	Belgium	Poperingen	2.6327	50.8196	6	5	6	Lane plantation
BESH	Belgium	Sint-Lievens-Houtem	3.8427	50.9045	8	7	10	Pollard trees at forest edge
BETO	Belgium	Tombeek	4.5808	50.7581	2	1	3	Forest, wooded bank, along river
BEVO	Belgium	Ruiselede	3.3692	51.0680	5	4	5	Forest
BEWO	Belgium	Wortegem-	3.4574	50.8651	1	1	1	Forest, pollard tree
BEZA	Belgium	Zandhoven	4.6785	51.2186	2	2	4	Forest edge
BEZO	Belgium	Zoersel	4.6757	51.2535	6	6	10	Small forests
FRCO	France	Colmar	7.3533	48.0740	1	1		
FRDE	France	DESVRES	1.8338	50.6690	1	1		
FRDV	France	Chabrillan	4.9513	44.7352	5	5		
FRER	France	Erstein	7.6585	48.4200	2	2		
FRGG1	France	Grenade-sur-	1.2897	43.7713	2	2		
FRGG2	France	Grenade-sur-	1.0078	43.7542	1	1		

Location	Country	city	Lon	Lat	N	N AFLP	N pop	Type LE
FRHA	France	Hasnon	3.3848	50.4198	1	1		
FRHB	France	Harbonnières	2.6690	49.8430	1	1		
FRHE	France	Hem-Hardinval	2.3023	50.1578	1	1		
FRLO	France	Locquignol	3.7177	50.1930	4	3		
FRME	France	Merville	0.9910	43.7205	3	3		
FRQU	France	QUERCAMPS	2.0513	50.7510	1	1		
FRSA	France	SAINT-AMAND	2.5542	50.1585	1	1		
FRVA10	France	Chatêl-de-Neuvre	3.3195	46.4024	8	8		
FRVA13	France	Tilly	3.3198	46.4202	1	1		
FRVA14	France	Bessay-sur-Allier	3.3326	46.4365	6	6		
FRVA23	France	Chemilly	3.3272	46.4767	26	25		
FRVA8	France	Chatêl-de-Neuvre	3.3188	46.3964	2	2		
FRVA9	France	Monténay-sur-Allier	3.3089	46.3866	2	2		
FRWA	France	Wavrans-sur-l'Aa	2.1352	50.6838	1	1		
GELD	Germany	Lüchow-Dannenberg	11.0000	53.2833	1	1		
KYBI	Kyrgystan	Bishkek	74.5879	42.8700	2	1		
NEBA	Netherlands	Barneveld	5.5406	52.1479	2	2		
NEBE	Netherlands	Beilen	6.5306	52.7784	2	2		
NEEN	Netherlands	Enschede	6.8968	52.1786	1	1		
NEGE	Netherlands	Gennep	5.9296	51.7196	2	2		
NEGO	Netherlands	Geulle en Elsloo	5.7556	50.9339	1	1		
NELI1	Netherlands	Liempde	5.3994	51.5710	3	2		
NELI2	Netherlands	Liempde	5.3482	51.5303	4	4		
NEME	Netherlands	Meersen	5.7505	50.9187	4	3		
NEMI	Netherlands	Millingen a/s Rijn	6.0060	51.8793	2	2		
NESO	Netherlands	Sint-Oedenrode	5.4290	51.5462	1	1		
NEUD1	Netherlands	Udenhout	5.1633	51.6318	1	1		
NEUD2	Netherlands	Udenhout	5.1337	51.6109	1	0		
NEVA1	Netherlands	Valkenburg a.d. Geul	5.7764	50.8701	1	1		
NEVA2	Netherlands	Valkenburg a.d. Geul	5.8559	50.8635	2	2		
NEVA3	Netherlands	Valkenburg a.d. Geul	5.8021	50.8790	1	1		
NEWI1	Netherlands	Winterswijk	6.7761	51.9879	2	2		
NEWI2	Netherlands	Winterswijk	6.8029	51.9615	7	7		
NEWI3	Netherlands	Winterswijk	6.7194	51.9908	2	2		
NEWI4	Netherlands	Winterswijk	6.7546	51.9522	2	2		
Total					**197**	**181**		

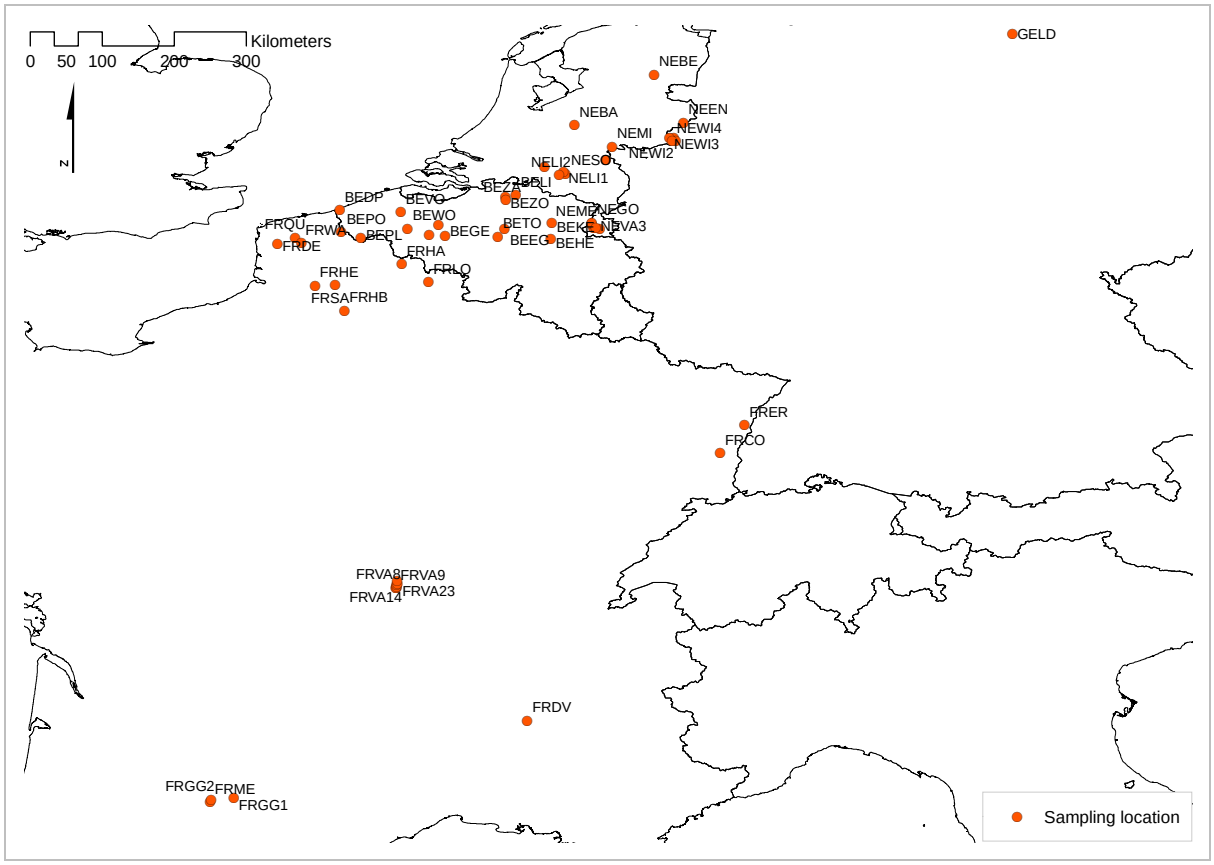

Fig. 1. 1: Location of the sampled populations of *Ulmus laevis*, except for the samples collected near Bishkek in Kyrgyzstan.

1.1.2. AFLP analysis

Amplified Fragment Length Polymorphism (AFLP) fingerprints were generated according to Vos et al. (1995), but with restriction and ligation conducted in one single step. Initially, 39 primer combinations (EcoRI / MseI) were tested on 12 samples. The following three primer combinations were selected for the selective amplifications: EcoRI-ACA(fam)/MseI-CAC (PC1), EcoRI-ACC(ned)/MseI-CAC (PC2) and EcoRI-ACC(ned)/MseI-CTG (PC3). AFLP fragments were separated by electrophoresis on an ABI 3500 Genetic Analyzer (Applied Biosystems). The electropherograms were visualized with 3500 Data Collection Software v 1.0 and GeneMapper v 4.1 (Applied Biosystems). The latter was used to adjust the analysis method of the electropherograms and produce an inputfile for RawGeno v 2.0 R CRAN package Arrigo et al. (2009) for automated scoring. Rawgeno also checks for potential homoplasy, by assessing the correlation between AFLP band size and frequency among samples as recommended by Vekemans et al. (2002). 191 polymorphic loci were retained. 14% of the samples were blindly replicated.

Table 1.2 shows samples with poor quality AFLP electropherograms for one or more primer combinations. To avoid series of missing values, we discarded these samples from further analysis.

Table 1. 2: Samples with poor quality AFLP profiles. The primer combination(s) for which the AFLP fragment analysis failed is indicated.

Sample	PC1	PC2	PC3
SH7			x
RU5	x		
VO1		x	

Sample	PC1	PC2	PC3
BR2		x	
he6.5			x
he8.10			x
he8.11	x	x	x
ker 11		x	
CEM336		x	x
S23N38	x		
TOM1		x	
POP3			x
12202			x
01 Kuilpad Udenhout			x
05 Hezelaar, Liempde	x		
Kyrgystan2			x

1.2. Data analysis and results

1.2.1. Clonality

Because DNA-markers are prone to scoring and sometimes technical errors, it becomes difficult to identify clones among a set of samples. In addition, mutations are possible.

To infer clonal identity we used GenoType (Meirmans and Van Tienderen 2004). It was difficult to choose a threshold of Dice similarity. If we chose a threshold close to the mean Dice similarity of just above 0.95 calculated for the duplicate samples, only 44 multilocus genotypes remained of the original 181 samples. Although we found no publication that eliminates natural vegetative regeneration, it is hardly likely that this is the case because of the extent of the sampling area. The *U. laevis* trees in our study seem to be closely related or at least show an overall low genetic variation; from a Dice similarity of 0.88 or lower, all the samples share the same multilocus genotype (MLG). Also the similarity between couples of replicates is very diverse (2 to 21 differences of 1% to 10%, with a mean of 8.8 or 4.4%), which makes it difficult to set a reliable threshold.

If we reduce the threshold to 3 differences (i.e. 1.5%) using the infinite allele model, the following samples share the same genotype: S23N35, S23N36 and S23N37. The three trees grow in each other's neighbourhood. They also belong to different diameter classes (S23N35 < S23N36 < S23N37).

1.2.2. Genetic diversity

Because the sampling efforts were quite different depending on the location, we calculated the Shannon index based on a moving window approach, considering a 25 km grid over the sampling area. The Shannon index was computed for samples within a radius of 35 km around each grid point, but only when at least 3 samples were present. To obtain an unbiased Shannon index, 50 resamplings, using 3 samples per cell, were executed. The same was done to calculate the Rarity index ('frequency-down-weighted marker values'; Schönswetter and Tribsch 2005), but here we used a 50 km grid, a 70.7 km radius and again 50 resamplings of 3 samples. We excluded the samples of Kyrgyzstan and Germany from the analysis, because there was only one sample in both countries. The calculations were performed using custom R scripts (R Development Core Team, 2009) written by Arrigo et al. (2010). Fig. 1.2a shows the results for the Shannon Index, Fig. 1.2b for the Rarity index.

In general, the values for the Shannon index are very low (0.039 – 0.09187). Higher values for both the Shannon and Rarity index (0.86247-1.18945) were found in the south of France and in the north near Hasnon and Loquignol (FRHA and FRLO, Fig.1), the Netherlands and the central region of Belgium (i.e. the indices seem to decrease towards the eastern and the western boundaries of the latter country).

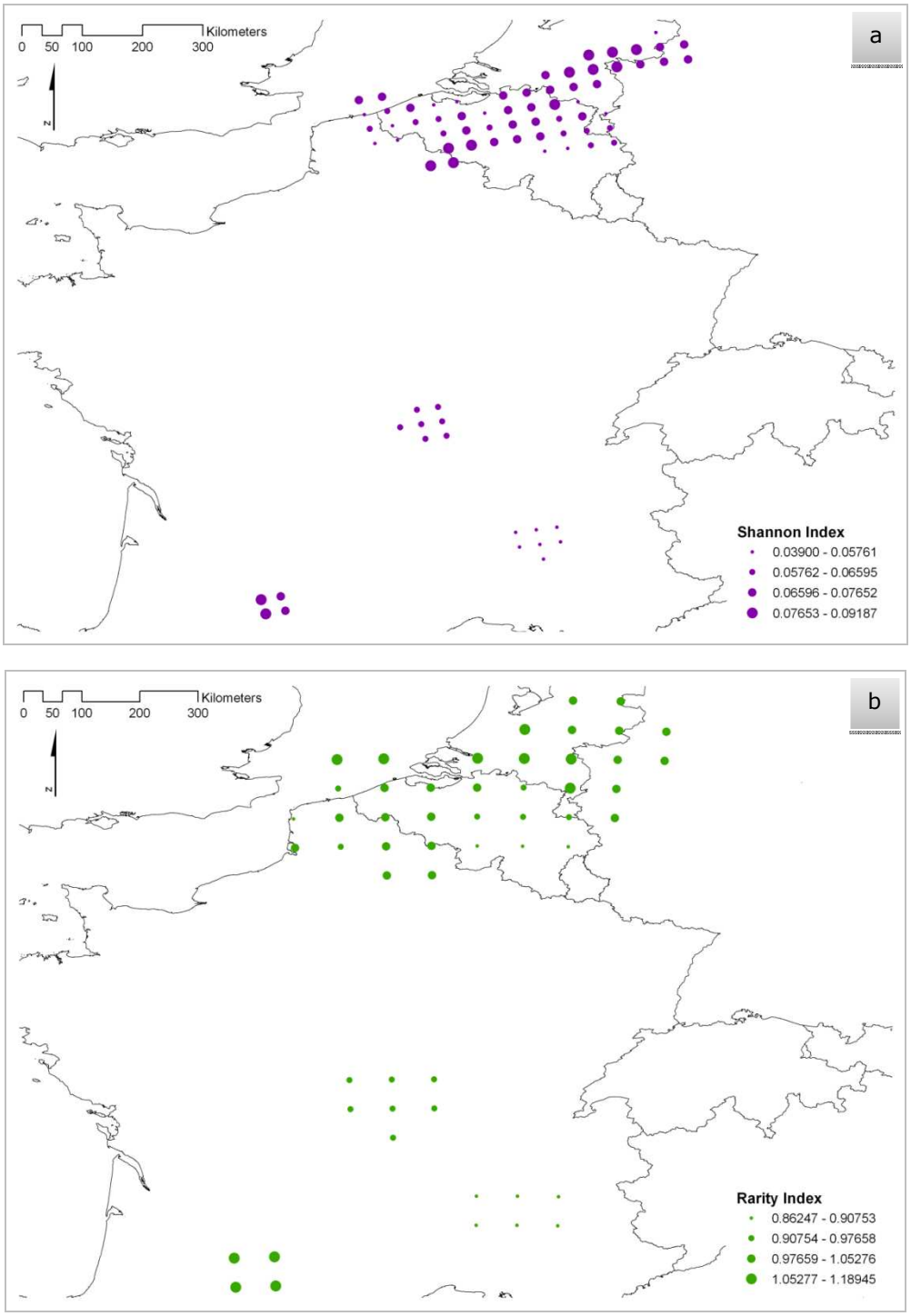

Fig. 1. 2: Regional patterns of genetic diversity of the sampled *Ulmus laevis*; a: Shannon index; using a moving window on a grid of 25 km, 3 individuals were sampled per grid cell and results were averaged over 50 bootstraps; b: Rarity index; here, a grid of 50 km was used.

In addition, we calculated AFLP fragment frequencies with AFLPsurv 1.0 (Vekemans et al. 2002) to estimate allele frequencies for each population, after excluding populations with only one sample. This was based on a Bayesian approach with a non-uniform prior distribution of allele frequencies following Zhivotovsky (1999). We calculated the proportion of polymorphic loci (PPL) with allelic frequencies within the range of 0.05–0.95 and Nei's gene diversity (H_j) We assumed either no (F_{IS} = 0), or some deviation from Hardy–Weinberg genotypic proportions in relation to the outcrossing nature of the species (F_{IS} = 0.1). Results based on both F_{IS} values were very different (Tables 1.3 and 1.4). Naturally, this was especially the case for populations with very low sample sizes.

For comparison, we calculated Shannon's information index with Popgene v 1.32 (Yeh et al. 1997). The results are shown in Table 1.3. The indices did not change much with a F_{IS} value of 0.1 (results not shown). Because of unequal and generally low sample sizes, the values should be assessed with caution. In general, genetic diversity was low, even in substantially larger populations such as FRVA23.

Using the approach of Dasmahapatra et al. (2008), with FAFLPcalc, an average F_{IS} value of 0.119 was obtained. This method calculates band frequencies from raw AFLP counts. The estimates are then used in simulations to generate data assuming a range of F_{IS} values. The program is based on the premise that inbred individuals are likely more homozygous and carry more null phenotypes than expected by chance. Because it is impossible to estimate both F_{IS} and underlying band frequencies simultaneously, the assumption is made that at least half the individuals are outbred. However, results can be poor due to scoring errors and non-independence between bands.

Table 1. 3: Genetic diversity measures calculated with F_{IS} = 0 and F_{IS} = 0.1, respectively. N: number of individuals; #loc: number of loci; PPL: proportion of polymorphic loci with allelic frequencies within the range of 0.05–0.95; H_j: Nei's gene diversity; S.E.(H_j): standard error of H_j; I: Shannon's information index; St. dev.(I): standard deviation of I.

			F_{is} = 0					F_{is} = 0.1		
Population	**N**	**#loc.**	**PPL**	**H_j**	**S.E.(H_j)**	**I**	**St. dev.(I)**	**PPL**	**H_j**	**S.E.(H_j)**
BEBR	4	191	72.8	0.26299	0.01304	0.188	0.2876	72.8	0.26929	0.01446
BEDP	6	191	72.3	0.19889	0.01314	0.1702	0.2771	72.3	0.21857	0.0132
BEEG	7	191	74.3	0.19501	0.01301	0.1737	0.2775	74.3	0.21394	0.01288
BEGE	3	191	12	0.13806	0.01086	0.0735	0.2019	69.1	0.21677	0.01237
BEHE	18	191	38.2	0.17857	0.01349	0.2239	0.2836	69.6	0.18133	0.01244
BEKE	4	191	72.3	0.26644	0.01332	0.1923	0.2927	72.3	0.27177	0.01475
BELI	4	191	69.6	0.16733	0.01187	0.11	0.2365	69.6	0.21272	0.01266
BEPO	5	191	12.6	0.1034	0.01062	0.0743	0.2028	68.6	0.17093	0.0109
BESH	7	191	14.7	0.10012	0.01053	0.081	0.207	71.2	0.15613	0.01035
BEVO	4	191	15.2	0.13864	0.0109	0.0873	0.2134	71.2	0.20192	0.01161
BEZA	2	191	5.2	0.08228	0.00824	0.0317	0.1351	64.9	0.21826	0.01235
BEZO	6	191	22.5	0.16298	0.01228	0.1305	0.2527	71.7	0.19714	0.01229
FRDV	5	191	18.8	0.15719	0.01252	0.1178	0.2494	69.6	0.20109	0.01265
FRER	2	191	6.8	0.10592	0.00902	0.0412	0.1527	68.6	0.23588	0.01247
FRGG1	2	191	8.9	0.13577	0.00986	0.0538	0.1726	68.1	0.24345	0.01311
FRLO	3	191	71.7	0.1927	0.01127	0.1041	0.2284	71.7	0.24284	0.01292
FRME	3	191	70.7	0.2105	0.01209	0.118	0.2452	70.7	0.25059	0.01377
FRVA10	8	191	26.2	0.15265	0.01201	0.1404	0.2525	75.4	0.18382	0.01142
FRVA14	6	191	22	0.15909	0.01248	0.1285	0.2533	71.2	0.195	0.01243
FRVA23	25	191	30.9	0.14253	0.01236	0.181	0.26	30.9	0.14986	0.01138
FRVA8	2	191	5.2	0.08223	0.00825	0.0317	0.1351	64.4	0.21671	0.0124
FRVA9	2	191	66	0.19038	0.01103	0.0792	0.2045	66	0.25548	0.01438
NEBA	2	191	69.6	0.15782	0.01027	0.0633	0.1856	69.6	0.25492	0.01332

			F_{is} = 0					F_{is} = 0.1		
Population	**N**	**#loc.**	**PPL**	**H_j**	**S.E.(H_j)**	**I**	**St. dev.(I)**	**PPL**	**H_j**	**S.E.(H_j)**
NEBE	2	191	69.1	0.15765	0.01029	0.0633	0.1856	69.1	0.25338	0.01339
NEGE	2	191	68.1	0.14304	0.01002	0.057	0.1771	68.1	0.24573	0.01325
NELI1	2	191	70.7	0.21238	0.011	0.0887	0.2145	70.7	0.27624	0.01411
NELI2	4	191	12.6	0.11744	0.01017	0.0718	0.1954	70.7	0.19147	0.01101
NEME	3	191	9.4	0.10806	0.00967	0.0556	0.1757	68.1	0.20168	0.01151
NEMI	2	191	68.6	0.19169	0.01088	0.0792	0.2045	68.6	0.26324	0.01406
NEVA2	2	191	9.4	0.14345	0.00998	0.057	0.1771	69.6	0.25033	0.01306
NEWI1	2	191	2.1	0.03384	0.00557	0.0127	0.0868	66	0.2078	0.01118
NEWI2	7	191	77	0.19066	0.01243	0.1689	0.2677	77	0.21112	0.01225
NEWI3	2	191	68.6	0.17828	0.01068	0.0728	0.1973	68.6	0.25868	0.01383
NEWI4	2	191	69.6	0.17184	0.01052	0.0697	0.1936	69.6	0.25948	0.01357

Table 1. 4: Measures of heterozygosity and population differentiation calculated with AFLPsurv 1.0, with FIS = 0 and FIS = 0.1, respectively. N: number of populations; H_t: total gene diversity; H_j: mean gene diversity within populations; H_b: average gene diversity among populations in excess of that observed within populations; F_{ST}: Wright's fixation index.

	F_{is} = 0				F_{is} = 0.1			
N	**H_t**	**H_j**	**H_b**	**F_{ST}**	**H_t**	**H_j**	**H_b**	**F_{ST}**
34	0.1835	0.1568	0.0268	0.1458	0.2236	0.2229	0.0008	0.0036
S.E.		0.008397	0.002568	0.091466		0.005811	0.002552	3.405172
Var		0.000071	0.000007	0.008366		0.000034	0.000007	11.5952

1.2.3. Genetic structure

Using the AMOVA analysis in Genalex 6.4 (Peakall and Smouse 2006) we calculated Φ_{PT}, a measure of population differentiation, as well as its significance by the Monte Carlo procedure (999 permutations). Again, we only included sampling locations with more than 1 sample. 13 % of the genetic variation seemed to be among populations (p = 0.001). In addition, we calculated F_{ST} values with AFLPsurv using the different F_{IS} values as mentioned above. Again, both F_{ST} 's are very different (Table 1.4).

We constructed PCoA plots based on pairwise Nei genetic distances, between individuals as well as between populations. For the latter, we repeated the analysis after excluding populations containing one sample. We computed the plots with Genalex 6.4, using the distance matrix with data standardisation. Fig. 1.3 shows the PCoA based on the individual genetic distances, with the first two axes explaining 28.67 % and 20.65 % of the variation, respectively. Except for a few outliers, all samples seem to cluster together. Only for FRVA23 the majority of the samples are quite distinct from the main cluster. We checked the quality of the AFLP profiles of the outliers again; the concerning samples are: BR5, BR4, KE7, DP3, 06 Hezelaarsbroek, LI1, EGE13, EGE4, he6.2. Some profiles for certain primer combinations showed lower (or sometimes higher) quality compared to the other samples of the same population, but exclusion of the problematic markers resulted in the same PCoA (results not shown). To exclude a possible misclassification of these samples as *U. laevis*, we scored the *U. laevis* samples together with the total dataset of *U. minor-U. glabra* mentioned in section 2. This was done for primer combination EcoRI-ACC(ned)/MseI-CTG, applied in both studies. A PCoA of individual genetic distances showed the *U. laevis* samples to be very distinct from the other species (results not shown), which was again supported by their morphology.

On the population level, Fig. 1.4 shows that the German and Kyrgyzstani locations are differentiated from the other locations. This is also the case for NEUD1, a location in the

Netherlands, situated in a tree nursery. But for all three locations, only one sample was included in the study. Looking again at a PCoA plot of the populations, without one sample locations, NEMI and BEBR stand out (Fig. 1.5).

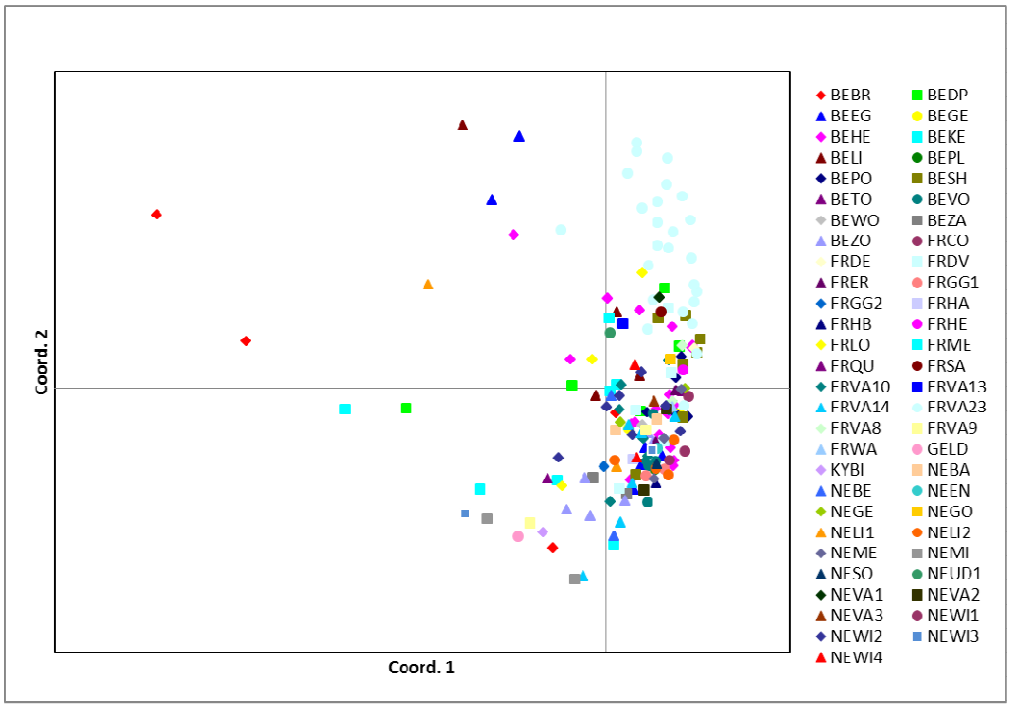

Fig. 1. 3: Principal coordinates analysis of Nei's genetic distances based on 191 polymorphic AFLP markers. This is a plot with the first two axes explaining 28.67% and 20.65% of the variation, respectively.

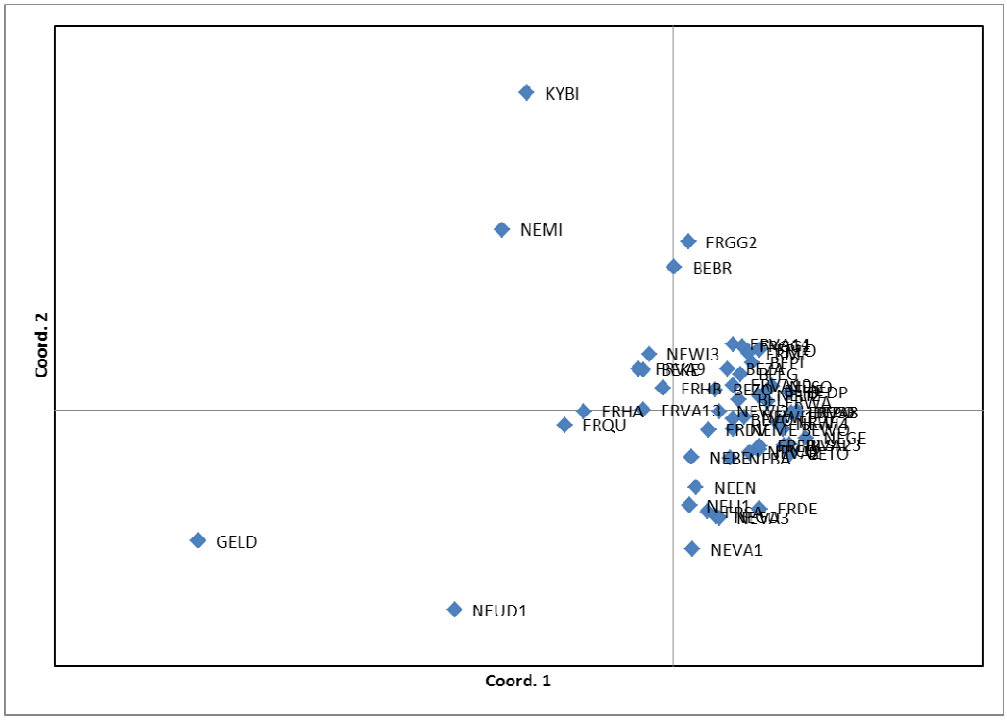

Fig. 1. 4: Principal coordinates analysis of Nei's pairwise population genetic distances based on 191 polymorphic AFLP markers. This is a plot with the first two axes explaining 24.35% and 20.48% of the variation, respectively.

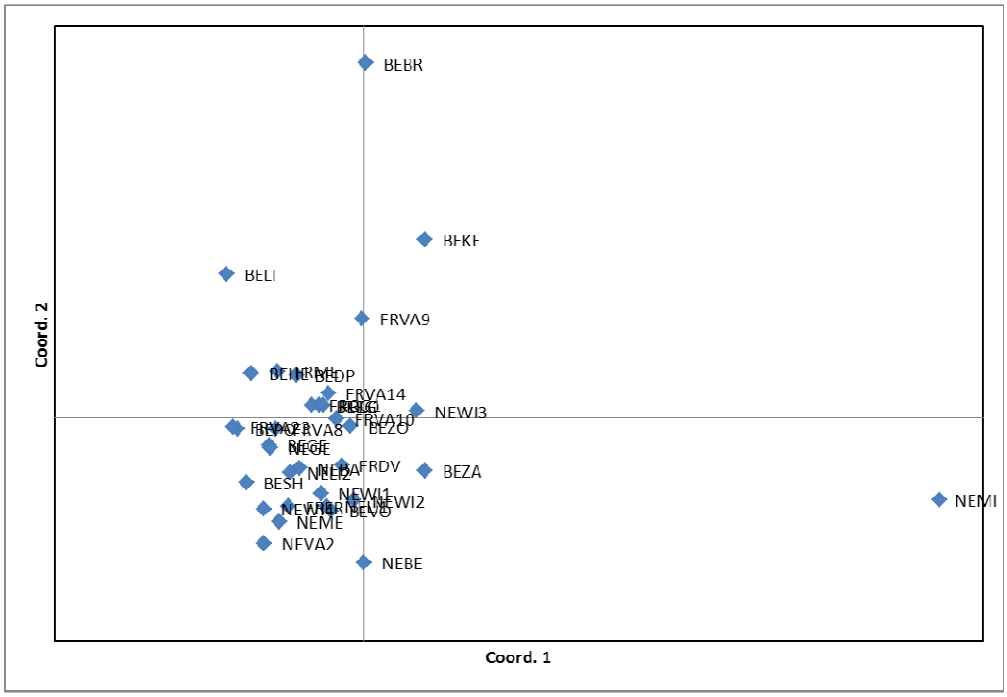

Fig. 1. 5: Principal coordinates analysis of Nei's pairwise population genetic distances based on 191 polymorphic AFLP markers, after excluding populations with one sample. This is a plot with the first two axes explaining 21.04% and 18.56% of the variation, respectively.

With a Mantel test we tried to investigate a possible relationship between pairwise population geographic and genetic distances using Genalex 6.4. However, there was no significant correlation between both matrices, which suggests that there is no isolation-by-distance.

Because most of the sampled populations are small, Hardy-Weinberg may be violated. We therefore used nonhierarchical K-means clustering (Hartigan and Wong 1979), which assigns individuals to K genetic groups in order to maximize the variance among groups, also called the intergroup inertia (Legendre and Legendre 1998). The computations were performed using R (package 'stats'; R Core Development Team, 2009) with a script supplied by Arrigo (2010). This script incorporates the approach of Evanno et al. (2005) to select the most likely number of groups using intergroup inertia as a proxy of clustering accuracy. We performed 50 000 independent runs for each K, ranging from 1 to 10. This resulted in five groups as the most likely number of clusters describing the genetic structure (Fig. 1.6). Groups 2, 4 and 5 contain samples found across the sampling range. Group 1, however only contains the outliers shown in the PCoA plot (Fig. 1.3). Group 3 consists of population FRVA23, except for one sample, and 5 other samples from 5 different populations spread over the sampling area.

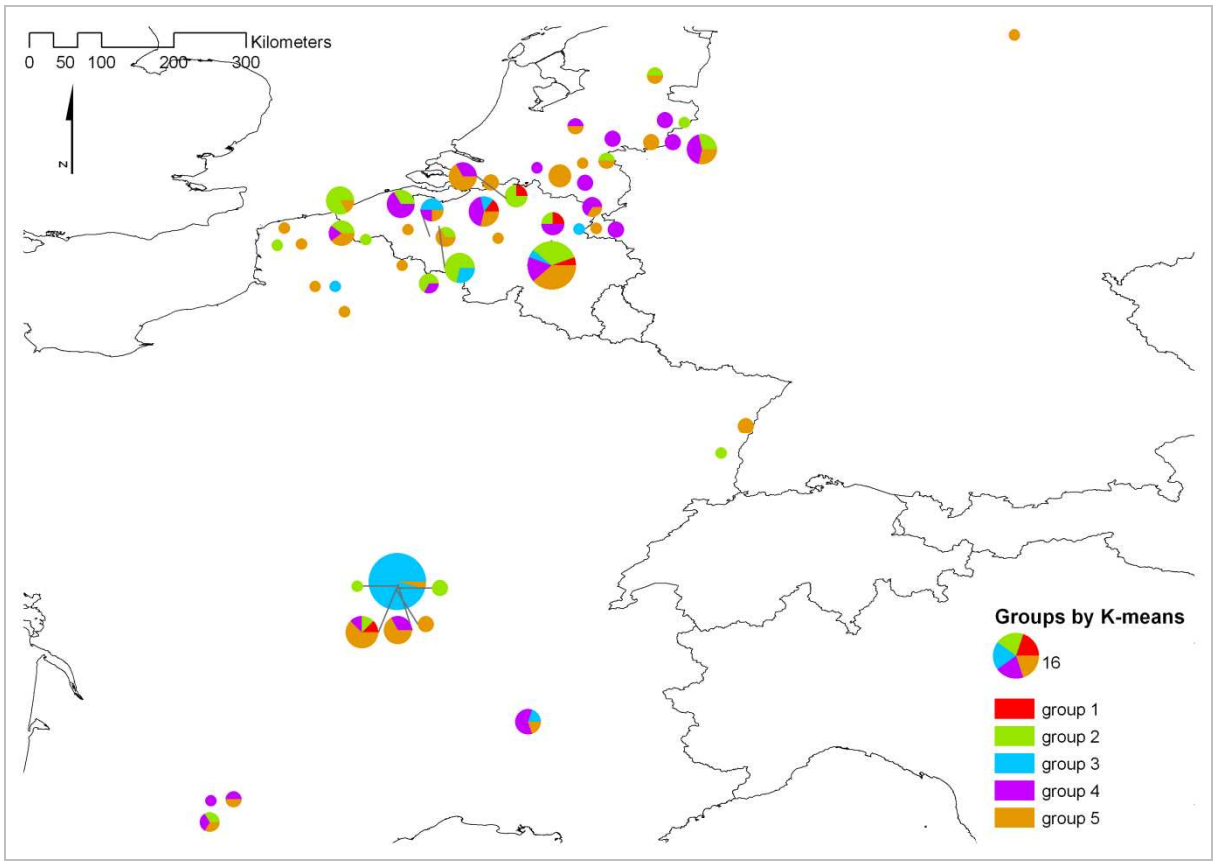

Fig. 1. 6: Geographical mapping of the five groups defined by K-means. The proportions of individuals observed among groups 1–5 are reported for each population with pie charts. The size of the pie charts is in relation to the sum of the sampled individuals. The sample of Kyrgyzstan (not shown) belongs to group 4.

In addition we used BAPS v 5.3 (Corander et al. 2008), a model-based Bayesian clustering approach. Mixture of individuals was computed with four replicates for each value up to K = 25. Clusters found with this procedure were then tested for admixture using 100 iterations. Here, only one cluster was found as most probable.

1.3. Discussion

1.3.1. Clonality

Identifying clones based on AFLP markers is quite arbitrary. Especially when samples are included with lower quality band intensity, it becomes increasingly difficult to define a reliable threshold. For the *U. laevis* samples, the markers did not seem to be very polymorphic.

Sometimes, *U. laevis* appears to propagate vegetatively. Collin (2003) stated that root suckering may play a role in established stands while stool suckering is thought to be poor. In the Netherlands, identical genotypes were found, but probably due to coppicing (J. Buiteveld, personal communication). Vakkari et al. (2009) found a high proportion of identical genotypes, but because the genetic variation was low, they could as well be reproduced sexually. Also, they used allozyme markers which might be less adequate to detect clones (e.g. Hotz et al. 2008). Except for three individuals found in population FRVA23, no other clones seem to be present among the sampled trees. Although, this is no certainty, considering the difficulties mentioned above. In addition, selfing cannot be excluded (Hans 1981), although Nielsen and Kjaer (2010a) found self-pollination to be absent in a natural Danish population. However, levels of heterozygosity and PPL seem too high for frequent and long-term self-pollination. In addition, higer population differentiation is to be expected in highly selfing species (Siol et al. 2008, Ford et al. 2009).

1.3.2. Genetic diversity and structure

Compared with other outcrossing tree species, genetic diversity is quite low in the *U. laevis* populations. Likewise, Machon et al. (1995) found *U. laevis* to have lower genetic diversity than *U. minor*, *U. glabra* and their hybrids. Similarly, genetic diversity in populations of Southern Finland and Estonia was even lower (Vakkari et al. 2009). However, for many populations in our study sampling effort was low and could give inaccurate estimates of gene diversity. Nevertheless, on numerous sampling locations only a few *U. laevis* trees are present, especially in Flanders (Vander Mijnsbrugge et al. 2005) and the Netherlands (Maes 2006). Due to the small sizes of the populations and the loss of habitat causing increased isolation, genetic diversity is expected to be low as a result of genetic drift and inbreeding. BEBR and BEKE are exceptions, showing higher diversity due to some outliers, although the populations are very small. These and other unexplainable outliers, were not due to errors in species determination, as all *U. laevis* were very distinct from *U. minor*, *U. glabra* and their hybrids based on the results of one primer combination. This is in agreement with the studies of Machon et al. (1995) and of Goodall-Copestake et al. (2005) for all three species, and with the paper of Gehle and Krabel (2002) on *U. minor* and *U. laevis*. Also, FRME (south of France), shows a higher level of genetic diversity. Although FRVA23 is quite a large *U. laevis* population, it has a higher density than usual (E. Collin, personal communication). This may indicate the presence of clones and/or highly related individuals (half sibs), which would explain the population's low genetic diversity.

Comparing all results in the analysis of the genetic structure, FRVA23 seems to be quite distinct, even from neighbouring populations in the same valley, as well as some individuals (i.e. the outliers found in Fig. 1.3). But the other samples could not be divided into logical groups. Population differentiation was moderate for F_{IS} = 0 to low for F_{IS} = 0.01, as opposed to the high differentiation among marginal populations of Southern Finland and Estonia (Vakkari et al. 2009). Furthermore, no IBD pattern was found. This lack of structure could still be a reflection of the tree's colonisation history. Whiteley (2004) only found one haplotype from Russia and Finland to Southern France. Two remaining haplotypes were merely present in Southern France, where we found the genetic diversity of FRME to be higher compared to the other populations. In the second section, we discuss the historical use of elms in landscaping. They were among the most widely planted trees in Europe. But this entails mostly *U. minor* and *U.* x *hollandica*. *U. laevis* on the other hand is never mentioned. It is, however, possible that seeds and other reproductive material were moved around, causing an illogical genetic structure. Knowing that elms have a long history of cultivation for fodder, it is quite conceivable that this also entailed *U. laevis*. A few of the sampled *U. laevis* are actually old pollard or coppiced trees.

1.3.3. Seed orchard in Flanders

Because the number of individuals of *U. laevis* is limited in Flanders, a seed orchard was realised for the whole region, instead of for each of the four major regions of provenance in Flanders. Considering the low genetic diversity of most of the locations sampled in Flanders, this seems to be a good decision. Trees from surrounding regions may also be included to further increase genetic variation. Furthermore, duplicate genotypes do not seem to be present among the investigated trees, or are at least not ubiquitous.

2. *Ulmus minor–U. glabra* complex and cultivars

2.1. Material and methods

2.1.1. Samples and DNA extraction

Between 2007 and 2009 leaves of *Ulmus minor*, *U. glabra*, *U. pumila*, *U. procera*, hybrids and cultivars were collected mainly in Flanders in northern Belgium and France (cultivars mainly collected by H. Heybroek in the Netherlands). They were stored on silica gel. The locations are listed in Table 2.1. Almost all leaves were collected in a seed orchard/ gene bank containing clones of the orginal ortets except for the samples in BESP, FRAU, FRCB, FRLR, FRLV, FRBL. The original ortets in the Belgian populations were at least 3 m apart from each other. All samples are listed in Table B in the Annex. The species identity of the cultivars was obtained from Heybroek et al. (2009). DNA extraction was performed using the same procedure as for *U. laevis* (see 1.1.1).

Table 2. 1: List of sampled locations of Ulmus minor, U. glabra, U. pumila, their hybrids, U. procera and the cultivars included in the study. N: number of sampled individuals; N AFLP: number of samples successfully analysed with AFLP; N pop: total number of individuals present on a location; Type LE: type of landscape element; UM: *U. minor*; UG: *U. glabra*; UH: *U.* x *hollandica*; UPM: *U. pumila*; UL: *U. laevis*; UP: *U. procera*; UJ: *U. japonica*; UW: *U. wallichiana*; UMc: *U. minor* var. *cornubiensis*.

Pop	Country	City	Collection place	Species	Lon	Lat	N	N AFLP	N pop	Type LE
BEBR	Belgium	Brugge (Sint-Pieters)	Zuienkerkstraat - loc BG75	UM	3.1728	51.2387	8	7	20	Old hedge
BEDI	Belgium	Dilbeek	Wolfsputten	UG	4.2530	50.8536	2	2	10	Forest
BEDM1	Belgium	Diksmuide (Woumen)		UM	NA	NA	2	2		
BEDM2	Belgium	Disksmuide (Esen)	Woumenhoek - loc DI27	UM	2.9040	51.0095	4	4	5 - 10	Old hedge
BEEG	Belgium	Heverlee	Egenhovenbos	UG	4.6662	50.8541	8	6	20 - 30	Forest
BEEN	Belgium	Oudenaarde (Ename)	Bos 't Ename, Schuifelbeen - loc 454	UM	3.6593	50.8616	3	3	20 - 30	Wooded banks
BEGE	Belgium	Geraardsber-gen	Raspaillebos - loc GE58, 59, 60, 61, 62	UG, UH	3.9290	50.7700	8	8	20	Forest
BEHE	Belgium	Heusden	loc 205	UM	3.8159	51.0099	2	2	10 - 20	Old hedge
BEHO	Belgium	Houthulst	Heugstraat 8 - loc HU21	UM	2.8720	50.9770	4	4	10 - 20	Old hedge
BELE	Belgium	Lemberge	Church path west of church in Lemberge	UM	3.7693	50.9788	5	5	10 - 20	Old hedge

Pop	Country	City	Collection place	Species	Lon	Lat	N	N AFLP	N pop	Type LE
BEMA	Belgium	Maarkedal	Kapelleberg - loc 434	UM, UG, UH	3.6520	50.8247	7	7	10 - 15	Wooded bank
BEME1	Belgium	Merelbeke	Bruinbos - loc 120	UM, UH	3.7198	50.9519	6	6	10	Forest
BEME2	Belgium	Merelbeke	Gentbos	UH	3.7508	50.9739	3	3	10	Forest
BEOO	Belgium	Oosterzele	Ettingebos - loc 180	UM	3.8065	50.9350	1	1	10	Forest edge
BERI	Belgium	Riemst	Plateau van Kaestert, Kanne	UM, UG, UH	5.6857	50.8058	38	36	50 - 100	Forest
BESC	Belgium	Schorisse	Ganzenberg - loc 251	UM, UG, UH	3.7065	50.8028	7	7	20 - 30	Forest, wooded bank
BESP	Belgium	Sint-Pieters-Kapelle (Herne)	Philipskouter	?	3.9795	50.6930	2	2		
BETO	Belgium	Tongeren	's Herenhelderen	UG	5.4908	50.8035	1	1		
FRAM	France	Amplier		UM	2.4010	50.1352	1	1		
FRAR	France	Orne	Argentan	UM	-0.0187	48.7402	1	1		
FRAU	France	Aunay		UM	0.6307	49.0205	2	2		
FRBB	France	Bourg-Blanc	bordure voie romaine	UM x UPM?	-4.5017	48.5005	1	1		
FRBL	France	Nièvre	Blismes	UM	3.8202	47.1315	1	1		
FRCB	France	La Chapelle Bâton		UM	0.3297	46.4746	3	3		
FRCM	France	Charente-Maritime	Saint-Martin-de Ré	UM	-1.3593	46.2027	1	1		
FRCU	France	Cucq	hameau de Trepied	UM	1.6207	50.4742	1	1		
FRGO	France	Godewaers-velde		UM	2.6380	50.7898	1	1		
FRGS	France	Grande-Synthe	CES Anne Franck	UM	2.2897	51.0087	1	1		
FRIL	France	Illkirch-Graffenstaden	FC. Strasbourg "Neuhof" p 37	UM	7.7185	48.5243	1	1		
FRLR	France	Le Rheu		UM	1.7954	48.1011	2	2		

Pop	Country	City	Collection place	Species	Lon	Lat	N	N AFLP	N pop	Type LE
FRLV	France	Le Vey		UM	0.4701	48.9175	5	5		
FRLW	France	La-Wantzenau	FC. La Wantzenau p 12	UM	7.8222	48.6575	1	1		
FRMA	France	Magnicourt-en-Comt	rue du Château de la Motte	UM	2.4877	50.4018	1	1		
FRME	France	Meteren		UM	2.6880	50.7383	2	2		
FRMQ	France	Mecquignies	Le château	UM	3.7890	50.2738	1	1		
FROS	France	Ostwald	FC. Ostwald p 8	UM	7.7058	48.5403	1	1		
FRSP	France	Saint-Pé-de-Bigorre	forêt domaniale de Saint-Pé-de-Bigorre (Génie Longue)	UG	0.1552	43.0737	3	2		
FRST	France	Strasbourg	FC. Strasbourg "Robertsau" p15	UM	7.7537	48.5845	1	1		
GEGO1	Germany	Göttingen	Rfö Pfaffenstrauch	UG	9.1500	51.3333	3	2		
GEGO2	Germany	Göttingen	Rfö Nörten-Hardenberg	UM	9.9557	51.6502	1	1		
GEKA	Germany	Pfalz	Kallstadt	UP			1	1		
GELD	Germany	Lüchow-Dannenberg	Rfö Carrenzien	UM	10.8833	53.2667	3	3		
GRIR	Greece	Iraklion	Festor	UM	24.8062	35.3878	1	1		
GRTH	Greece	Thessaloniki	Vrasna	UM	23.7340	40.7523	1	1		
ITBC	Italy	Bocchigliero	in the village	UM x UPM	16.7500	39.4167	1	1		
ITBO	Italy	Bolzano	Lana	UG	11.1167	46.6167	1	1		
ITCA	Italy	Catanzaro	SS 106, km 204	UM	16.7500	38.8833	1	1		
ITCV	Italy	Cerro Al Volturno	Castel S.Vincenzo	UPM	14.3667	41.9667	1	1		
ITFV	Italy	Fiume Veneto	locality Vallon	UM	12.6833	45.9167	1	1		
ITLA	Italy	Latina	Iana	UM	13.0000	41.4667	1	1		
ITMO	Italy	Monfalcone	SS 202, km 128 direction Venez	UM	13.5333	45.8000	1	1		
ITNI	Italy	Nimis	locality	UM	13.2500	46.2167	1	1		

Pop	Country	City	Collection place	Species	Lon	Lat	N	N AFLP	N pop	Type LE
			Molmentet							
ITRO	Italy	Rovereto	Borgo Sacco, parck Fedrigotti	UPM	11.1667	45.8833	1	1		
ITSE	Italy	Sesto Al Reghena	in the village	UM	12.7833	45.8667	1	1		
ITTA	Italy	Tamai	Tamai 1, small church	UM	12.5667	45.9333	2	2		
ITTR	Italy	Trieste	SS 14 , km 139,4	UM	13.7000	45.7167	1	1		
NEBU	The Nether-lands	Bunnik	Nieuw-Amelisweerd	UMc	5.1553	52.0710	1	1		
SPMA	Spain	Madrid	Pezuela Torres	UPM	-3.1667	40.4167	1	1		

cultivars	Parents	Species			N	N AFLP		
Lobel	clone 202 (*U. glabra* 'Exoniensis' × *U. wallichiana*) x clone 336 ('Bea Schwarz'*, selfed)	(UG x UW) x UM or UH			3	3		
Clusius	clone 202 (*U. glabra* 'Exoniensis' × *U. wallichiana*) x clone 336 ('Bea Schwarz'*, selfed)	(UG x UW) x UM or UH			1	1		
Sapporo Autumn Gold	U. pumila x U. japonica	UPM x UJ			1	1		
73P	*U. pumila* (mother tree of 'Sapporo Autumn Gold') x ? (open pollinated)	UPM x ?			1	1		
2P	U. japonica	UJ			1	1		
Klemmer	U. glabra x U. minor Or U. minor	UH or UM			1	1		
Dodoens	Selfed seedling of clone 202 (*U. glabra* 'Exoniensis' × *U. wallichiana*)	UG x UW			1	1		
Groeneveld	clone 49 (*U. glabra* or *U.* × *hollandica*) x clone 1 (*U. minor*)	UH			1	1		
Commelin	U. x hollandica 'Vegeta' x U. minor	UH			1	1		
Plantyn	Clone 202 (*U. glabra* 'Exoniensis' × *U. wallichiana*) x clone 302 (*U. minor* '1' × *U. minor* '28')	(UG x UW) x UM			2	2		

cultivars	Parents	Species			N	N AFLP		
Christine Buisman	U. minor (Or U. glabra x U. minor)	UM			1	1		
Vegeta	U. glabra x U. minor	UH			1	1		
Major	U. glabra x U. minor	UH			1	1		
Belgica	U. glabra x U. minor	UH			1	1		
Horizontalis	U. glabra	UG			1	1		
Dampieri	U. glabra x U. minor Or U. minor	UH or UM			1	1		
Den Haag	U. pumila x U. x hollandica 'Belgica'	UPM x UH			1	1		
Columella	Probably selfed seedling of Plantyn	(UG x UW) x UM			1	1		
Sarniensis	U. minor	UM			1	1		

*: 'Bea Schwarz' is an *U. minor* or *U.* x *hollandica*.

2.1.2. AFLP analysis

Amplified Fragment Length Polymorphism (AFLP) fingerprints were generated the same way as for *U. laevis*. Here, 21 primer combinations (EcoRI / MseI) were tested on 16 samples (14 individuals and 2 replicates). The following two primer combinations were selected for the selective amplifications: EcoRI-AGC(ned)/MseI-CTG (PC1) and EcoRI-ACC(ned)/MseI-CTG (PC2). Again, we used the RawGeno v 2.0 R CRAN package (Arrigo et al. 2009) for automated scoring, which resulted in 389 polymorphic loci.

Table 2.2 shows samples with poor quality AFLP electropherograms for one or more primer combinations. To avoid series of missing values, we discarded these samples from further analysis, leaving a total of 182 samples. About 19% of the samples were randomly replicated.

Table 2. 2: Samples with poor quality AFLP profiles.

Field code	PC1	PC2
NFV036	x	x
RIE13/1	x	
RIE13/2	x	
Saint-Pé 7		x
BG4		x
EGE2		x
EGE17		x

2.2. Data analysis and results

2.2.1. Clonality

To identify genets among the samples we used GenoType (Meirmans and Van Tienderen 2004) with a threshold of 0.94 – 0.95 Dice similarity, which is comparable to the mean Dice similarity of 0.95 calculated for the duplicate samples. Table 2.3 shows those samples sharing the same genotype when using a Dice similarity of 0.95 or 0.94. The different ramets of the cultivars Lobel were assigned to the same genet, as expected. This was also the case for both ramets of 'Plantyn'. Clones were detected among *U. minor* as well as among *U. glabra* and their hybrids, and this on almost all of the sampling locations where more than one sample was taken.

Certain multilocus genotypes (MLG) seemed to be present in more than one population: MLG 'D' in BEDI, BEME2 and BESC, MLG 'I' in BEEG and BERI, MLG 'R' in BEMA and BESC (Dice index of 0.95). The latter two locations are in the same area (4.5 km apart from each other). Furthermore, some samples of the same genet were identified as different species. Another interesting matter is that one sample of BEGE and most (Dice index: 0.95-0.94) samples of BEME1 resemble the 'Klemmer' cultivar. Only sample MER2 of the latter location seems different, with a Dice index of 0.92.

As expected, the MLG was found among neighbouring French *U. minor* (Table 3.5). Le Vey Q and TUS.027 are the only trees that show a similarity below 0.95 with their neighbours, with a Dice similarity of 0.92 and 0.93, respectively. But they are at least very closely related to the surrounding trees. Furthermore, there is a Dice similarity of 0.95 or higher between some Le Vey trees and the trees from Aunay (14260 A and B). The locations are about 16 km apart from each other according to the available coordinates, which suggests that root suckers might have been translocated from one location to the other, or that ramets of the same ortet were planted on both locations. Since Le Vey holds more than one MLG, the first scenario seems more likely, with a translocation of plant material from Le Vey to Aunay.

Table 2. 3: List of samples of the same genet according to a Dice similarity of 0.95 or 0.94. Samples sharing the same character belong to the same genet. Characters in bold are present in multiple populations. UM: *Ulmus minor*; UG: *U. glabra*; UH: *U.* x *hollandica*.

Pop	**Sample**	**Species**	**Dice similarity**	
			0.95	**0.94**
BEBR	BG1	UM	A	A
	BG2	UM	A	A
	BG3	UM	B	B
	BG5	UM	B	B
	BG6	UM	C	C
	BG7	UM	C	C
	BG8	UM	C	C
BEDI	DIL1	UG	**D**	**D**
BEDM1	Di46	UM	E	E
	Di48	UM	E	E
BEDM2	DIK1	UM	F	**F**
	DIK2	UM	G	**F**
	DIK4	UM	H	**F**
BEEG	EGE6	UG	**I**	**G**
	EGE7	UG	J	**G**
	EGE8	UG	**I**	**G**
BEGE	GE5	UG	K	H

Pop	Sample	Species	Dice similarity	
			0.95	**0.94**
	GE6	UG	L	H
	GE8	UG	**M**	**I**
BEHO	HOU1	UM	N	**F**
	HOU2	UM	N	**F**
	HOU3	UM	N	**F**
BELE	Lem1	UM	P	K
	Lem2	UM	P	K
	Lem3	UM	P	K
	Lem5	UM	P	K
	LEM4	UM	P	K
BEMA	EN7	UG	Q	**L**
	EN8	UG	**R**	**L**
	EN9	UG	**R**	**L**
	EN10	UG	**R**	**L**
	EN13	UH	S	M
	EN14	UM	S	M
BEME1	MER1	UM	**M**	**I**
	MER3	UM	**M**	**I**
	MER4	UH	**M**	**I**
	MER5	UM	T	**I**
	MER6	UM	**M**	**I**
BEME2	MER7	UH	U	N
	MER8	UH	**D**	**D**
	MER9	UH	U	N
BERI	RIE1	UH	Z	S
	RIE2	UH	Z	S
	RIE3	UH	W	P
	Rie9	UG	V	O
	Rie10	UG	V	O
	Rie23	UG	W	P
	RIE32	UG	**I**	**G**
	RIE33	UG	**I**	**G**
	Rie34	UM	**I**	**G**
	RIE35	UM	**I**	**G**
BESC	SCH1	UG	**R**	**L**
	SCH2	UG	**R**	**L**
	SCH3	UG	**R**	**L**
	SCH4	UG	AA	**L**
	SCH6	UH	**D**	**D**
	SCH7	UH	**D**	**D**
FRAU	14260A	UM	**AB**	**T**
	14260B	UM	**AB**	**T**
FRCB	TUS028	UM	AC	U
	TUS029	UM	AC	U
FRLR	TUS008	UM	AD	V
	TUS009	UM	AD	V

Pop	Sample	Species	Dice similarity	
			0.95	0.94
FRLV	LeVeyN	UM	**AB**	**T**
	LeVeyJ	UM	**AB**	**T**
	LeVeyU	UM	**AB**	**T**
	LeVeyR	UM	**AB**	**T**
Cv	Klemmer	UH	**M**	**I**
	Lobel1		AE	W
	LobelB4		AF	W
	Lobel		AF	W
	plantyn		AG	X
	Plantijn		AG	X

Finally, clonality indices were obtained for the Belgian populations using GenoDive (Meirmans and Van Tienderen 2004), shown in Table 2.4. The indices were all obtained based on the number of multilocus genotypes, including the Shannon index.

Table 2. 4: Clonality indices calculated for the Belgian populations. N: sample size; eff: effective number of genotypes; div: Nei's genotypic diversity; eve: eveness; shw: Shannon-Wiener; shc: corrected Shannon-Wiener.

Pop	N	#MLG	eff	div	eve	shw	shc
BEBR	7	3	2.8824	0.7619	0.9608	0.4686	0.5044
BEDI	2	2	2.0000	1.0000	1.0000	0.3010	na
BEDM1	2	1	1.0000	0.0000	1.0000	0.0000	0.0000
BEDM2	4	4	4.0000	1.0000	1.0000	0.6021	na
BEEG	6	5	4.5000	0.9333	0.9000	0.6778	1.1701
BEEN	3	3	3.0000	1.0000	1.0000	0.4771	na
BEGE	8	8	8.0000	1.0000	1.0000	0.9031	na
BEHE	2	2	2.0000	1.0000	1.0000	0.3010	na
BEHO	4	2	1.6000	0.5000	0.8000	0.2442	0.3875
BELE	5	1	1.0000	0.0000	1.0000	0.0000	0.0000
BEMA	7	4	3.2667	0.8095	0.8167	0.5546	0.7294
BEME1	6	4	3.0000	0.8000	0.7500	0.5396	0.8465
BEME2	3	2	1.8000	0.6667	0.9000	0.2764	0.4631
BERI	36	30	24.0000	0.9857	0.8000	1.4392	2.0062
BESC	7	4	3.2667	0.8095	0.8167	0.5546	0.7294
BESP	2	2	2.0000	1.0000	1.0000	0.3010	na

2.2.2. Species determination

In order to validate the species determination based on the morphology, we used the Bayesian method implemented in NewHybrids v 1.1 beta 3 (Anderson and Thompson 2002). We restricted the analyses to samples assigned to *U. minor*, *U. glabra* and their hybrids. The program was run with the default parameters for the six genotype class frequencies (pure *U. minor*, pure *U. glabra*, F1 hybrids and F2 progeny, backcrosses with each parent species), uniform priors and two runs with a burnin phase of 10 000 steps and 100 000 MCMC iterations. For comparison, another run with uninformative Jeffreys priors was performed. It must be noted that the model underlying NewHybrids relies on the assumption that the genetic markers in the dataset are unlinked

(Anderson 2008). This assumption is likely to be partly violated when many markers are used, as is the case here.

For comparison purposes, we repeated the analysis using BAPS v 5.4 (Corander et al. 2008) on the same dataset. Mixture of individuals was computed with 10 replicates for each value up to K = 6. Clusters found with this procedure were then tested for admixture using 100 iterations. In addition, the same steps were taken for the total dataset, but with 15 as the maximum value of K.

The results from both analyses are presented in Table C in the Annex. BAPS obtained the highest posterior probabilities for the *U. minor–U. glabra* complex when K=3. Only one cluster was added when we added the AFLP profiles of the other species and hybrids. Of the 106 samples taken in Flanders, only 29 samples seemed to be from pure *U. glabra* and 29 samples from pure *U. minor*. Only one in each group was misclassified as an hybrid based on their morphology. So, 45 % of the Belgian samples seemed to be hybrids between both species or backcrosses, of which 77 % was identified as one of both pure species. No F2 hybrids were found, based on the NewHybrids results. Since no further generations of backcrosses were implemented in NewHybrids, they cannot be identified and can therefore be assigned to any of the other genotype classes. Because BAPS gave only three clusters, it is difficult to identify hybrids as F1 progeny or as backcrosses with one of the pure species. Hybrids are assigned to the third group or as admixed individuals with significant coefficients in two or three groups. Fig.2.1 shows the distribution of the different species and their hybrids in the Belgian populations. Pure species do not seem to occur together in a population. The species of the samples of France, Italy, Greece and Germany seemed to be correctly identified. For just one sample (CEM330) there is no consensus between methods: according to BAPS this is a pure *U. minor*, but according to NewHybrids it might me a backcross with *U. minor*.

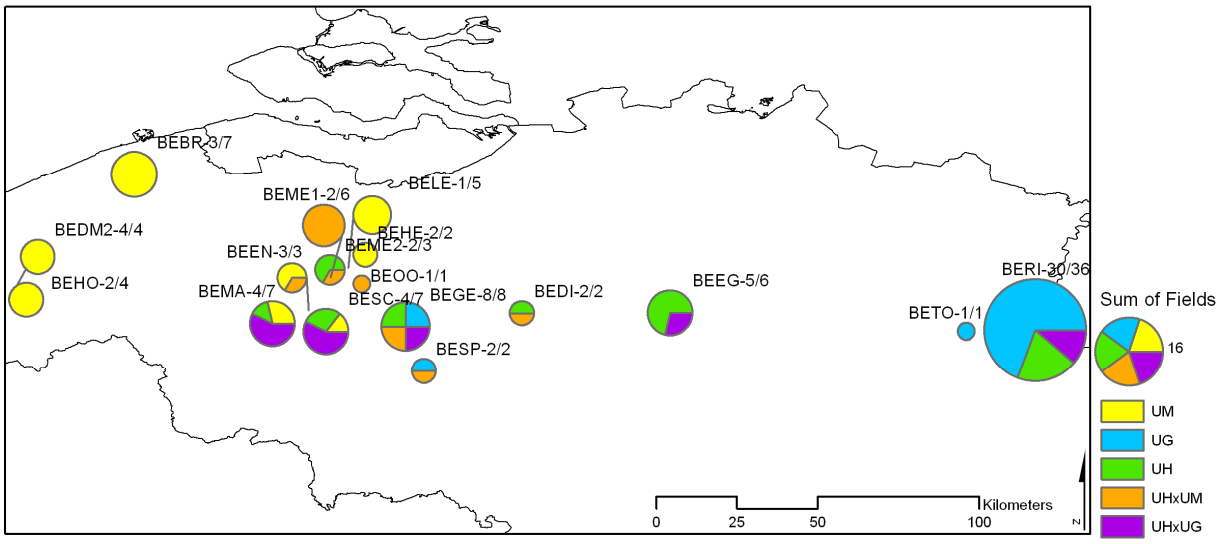

Fig. 2. 1: Distribution of *U. minor*, *U. glabra* and their hybrids in the Belgian populations. The size of the pie charts is proportional to the number of samples. Labels contain the population code and the ratio #MLG/N (i.e. ratio of number of multilocus genotypes and number of samples). UM: *Ulmus minor*; UG: *U. glabra*; UH: F1 *U.* x *hollandica*; UHxUM: backcross with *U. minor*; UHxUG: backcross with *U. glabra*.

Looking back at Table 2.3, we can now adjust the species identity of certain samples (Table D in the Annex), especially the *U. glabra* samples. Almost all of the *U. glabra* samples that showed evidence of clonality, appeared to be misidentified: they should have been coded as F1 hybrids or as backcrosses. RIE9, RIE10 and RIE23 are exceptions. The first two seemed to be ramets of the same genet, situated next to each other, and RIE23 shared the same genet with RIE3, which was identified as an *U. glabra* instead of *U.* x *hollandica*.

The sample of *U. procera* was grouped together with *U. minor* according to the BAPS results. CNR069 might be an *U.minor* instead of *U. pumila*. Whereas UPM111 could be a hybrid of *U. pumila* and *U. minor*. Also, *U. minor* var. *cornubiensis* was according to our results a backcross with *U. glabra* instead of a pure *U. minor*. As for the cultivars, the analyses confirmed that 'Groeneveld' is probably a backcross with *U. minor* and not a F1 hybrid and that 'Dampieri' is an *U. minor* instead of a hybrid. Furthermore, 'Vegeta' and 'Klemmer' were identified as backcrosses with *U. minor*. Finally, 'Major' seemed to be a pure *U. minor*, but was claimed to be a hybrid. Though, results for 'Major' from NewHybrids based on Jeffreys priors are slightly different from the results based on uniform priors, which could indicate some uncertainty. The other cultivars involving solely *U. minor* and *U. glabra* were assigned to their predetermined group, including 'Crist. Buisman'. Although the latter has a very distinct morphology compared to *U. minor*, our analysis confirms that it is an *U. minor*. The influence of *U. wallichiana* in certain cultivars cannot be determined based on these four groups. Also, *U. japonica* and *U. pumila* cannot be kept apart on the basis of the BAPS analysis and the few samples available.

Consequently, a Neighbour Joining tree was constructed using Treecon v1.3b (Van de Peer and De Wachter 1994) based on genetic distances according to Nei and Li (1979) (100 bootstraps). We only included a few samples of each of the following species next to the cultivars with genes of *U. wallichiana*: *U. minor*, *U. glabra* and *U.* x *hollandica* (F1 hybrids). The tree was rooted with sample UPM111 which is an *U. pumila* or possibly a hybrid with *U. minor* as mentioned above. Only bootstrap values above 50 are shown in Fig. 2.2. As expected, cultivars 'Clusius' and 'Lobel' form their own clade, because they are full sibs (Table 2.1). Half sibs 'Plantyn' and 'Dodoens' also cluster together, and are positioned near their half sibs Clusius and Lobel in the tree. In contrast, 'Columella' which is believed to be a product of selfing of 'Plantyn', does not seem to be closely related with the latter. Possibly, 'Columella' was not a selfed seedling of 'Plantyn'.

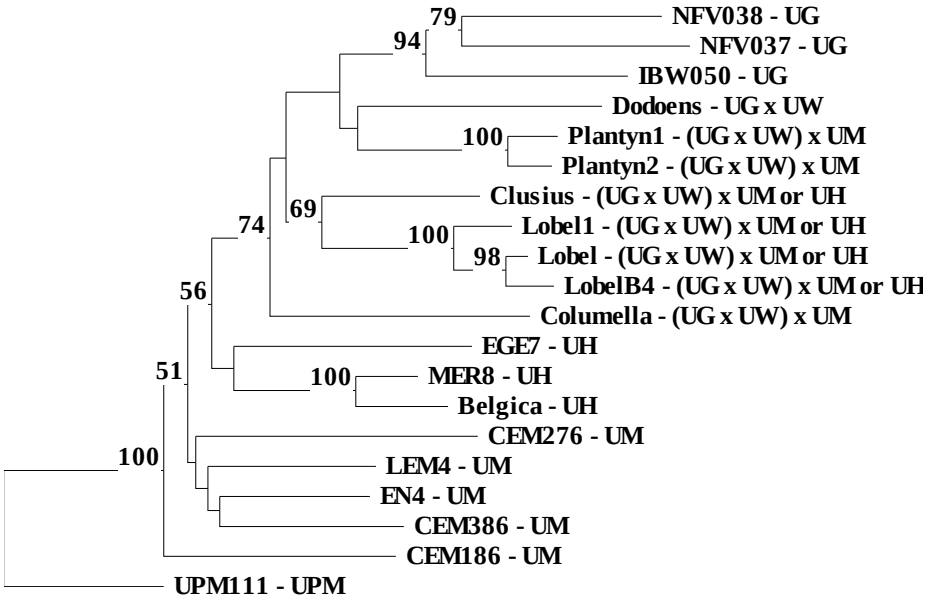

Fig. 2. 2: Neighbour Joining tree of a selection of *Ulmus minor*, *U. glabra* and *U.* x *hollandica* (F1) samples with samples of cultivar hybrids with *U. wallichiana*.

Finally, we constructed a PCoA plot using Nei genetic distance matrix with data standardisation with Genalex 6.4 (Fig. 2.3). We adjusted the species determination of the samples according to the results of NewHybrids and BAPS, except for *U. procera* and the species and hybrids outside the *U. minor–U. glabra* complex. Also in the PCoA the *U. procera* clusters together with *U. minor*. Two samples of *U. pumila* are positioned within (CNR069) or near (UPM111) the *U. minor* cluster. Looking at the position of clone 'Plantyn', it is located closer to the *U. glabra* cluster and 'Dodoens'

(UG x UW), while 'Columella' seems to be closer related with *U. minor*. The other hybrids with *U. wallichiana* (green triangles in Fig. 2.3) have a more intermediate position, but without reference samples of *U. wallichiana*, it is not possible to determine if the father was a *U.* x *hollandica* or a *U. minor* (i.e. if 'Bea Schwarz' was a hybrid or a pure *U. minor*).

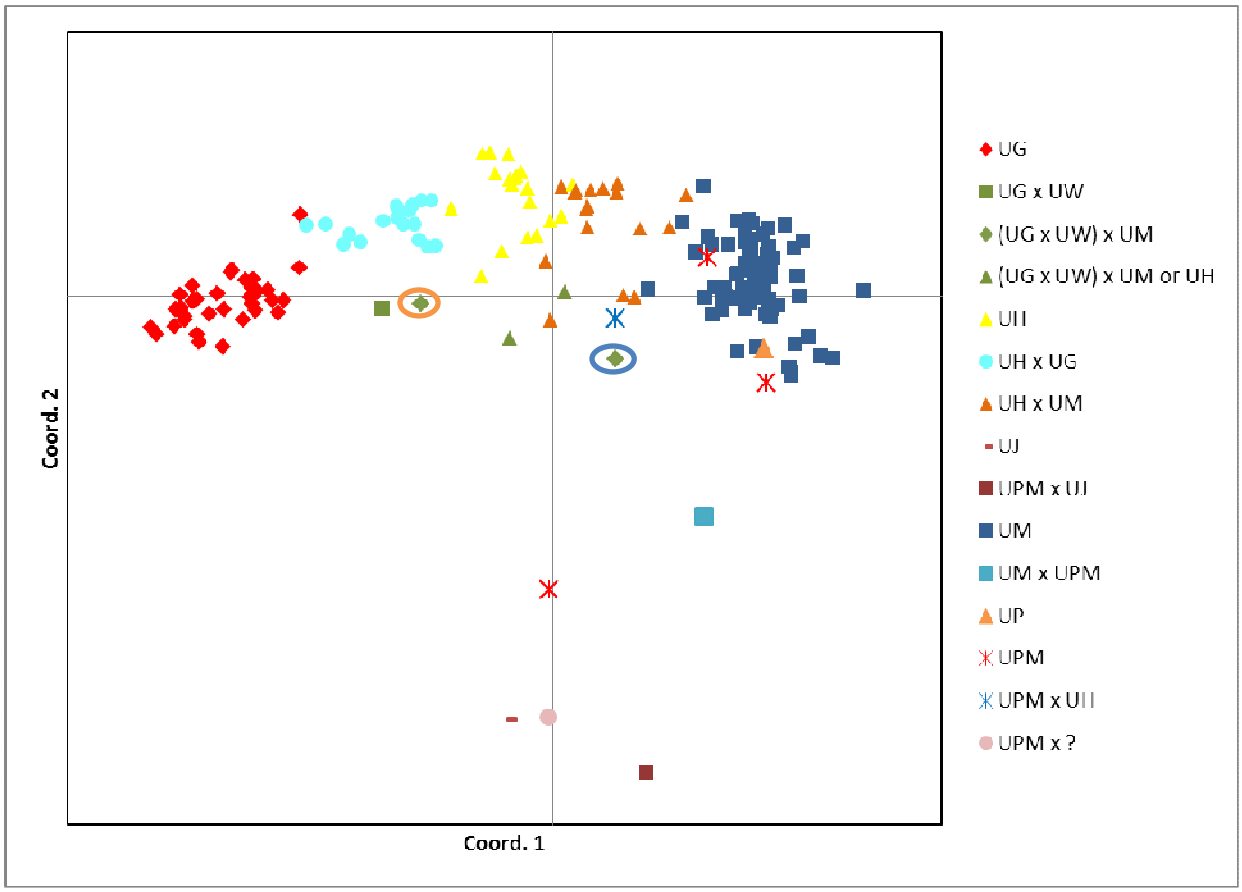

Fig. 2. 3: PCoA plot using Nei genetic distance matrix with data standardisation. 53 % and 19.7 % of the variation is explained by the first and second axis, respectively. The diamond circled in orange is the clone 'Plantyn', the other diamond circled in blue is 'Columella'.

2.2.3. Genetic diversity

Because the Belgian populations have a high degree of mixture of pure species with hybrids, we decided not to separate populations based on species composition to determine and compare their genetic diversity.

We calculated the populations' genetic diversity using AFLPsurv (Vekemans et al. 2002) and the Shannon Information Index with Popgene (Yeh et al. 1997) the same way as we did for *U. laevis*. Here, different values for F_{IS} did not seem to have a great effect on the estimates. We therefore continue with the values under Hardy-Weinberg equilibrium (Table 2.5). To evaluate the effect of the clonal propagation we performed the analyses with and without potential clones within populations according to a Dice similarity of 0.95. Nei's gene diversity increases after exclusion of potential clones. The Shannon information index does not change much. The only exception is BEME1 where both values decrease. This is not surprising, because the two remaining MLGs are very similar (Dice of 0.94; Table 2.3). Fig. 2.4 visualizes the values of the Shannon information index for the Belgian populations. Comparing figures 2.1 and 2.4, it seems that populations that contain a mixture of species/hybrids, tend to have a higher genetic diversity, especially when *U. glabra* is involved, either as a pure species or as a backcross.

Table 2. 5 : Genetic diversity measures for the Belgian populations. N: number of individuals; #loc: number of loci; PPL: proportion of polymorphic loci with allelic frequencies within the range of 0.05–0.95; H_j: Nei's gene diversity; S.E.(H_j): standard error of H_j; I: Shannon's information index; St. dev. (I): standard deviation of I.

	Total dataset (number of loci: 307)						Excl. potential clones (number of loci: 300)					
Pop	**N**	**PPL**	**H_j**	**S.E.(H_j)**	**I**	**St. dev. (I)**	**N**	**PPL**	**H_j**	**S.E.(H_j)**	**I**	**St. dev. (I)**
BEBR	7	47.9	0.10564	0.00768	0.1118	0.2283	3	39.3	0.16272	0.01047	0.1008	0.2197
BEDI	2	45.6	0.15201	0.00898	0.0906	0.2162	2	38.3	0.18496	0.01115	0.0907	0.2163
BEDM1	2	2.6	0.03197	0.00399	0.0158	0.0965	1					
BEDM2	4	43.0	0.07629	0.00676	0.0624	0.1863	4	36	0.09752	0.00868	0.0638	0.1882
BEEG	6	55.7	0.13952	0.0085	0.156	0.2455	5	47.7	0.18749	0.01091	0.1633	0.2536
BEEN	3	51.1	0.16956	0.00923	0.1367	0.2436	3	44.3	0.20706	0.01129	0.1398	0.2456
BEGE	8	63.2	0.1691	0.00922	0.2202	0.2706	8	56.3	0.20663	0.0111	0.2245	0.2719
BEHE	2	48.9	0.19567	0.01008	0.128	0.2475	2	42	0.23665	0.01218	0.131	0.2495
BEHO	4	48.9	0.12027	0.00806	0.1073	0.2234	2	39.3	0.19704	0.01142	0.0988	0.2239
BELE	5	5.5	0.03303	0.00423	0.0284	0.123	1					
BEMA	7	56.7	0.15131	0.00906	0.1791	0.2651	4	48.7	0.21595	0.01149	0.1791	0.2652
BEME1	6	13.7	0.07187	0.00656	0.0727	0.1926	2	2.3	0.0367	0.00487	0.0141	0.0914
BEME2	3	48.2	0.13856	0.00853	0.1052	0.2249	2	40.3	0.20629	0.01157	0.1048	0.2293
BERI	3	60.3	0.14747	0.00857	0.2577	0.2548	3	56	0.18423	0.01033	0.2578	0.2547
BESC	7	54.1	0.12992	0.00861	0.1568	0.2543	4	46.3	0.20142	0.0115	0.1627	0.2619
BESP	2	51.8	0.21596	0.01035	0.1458	0.2591	2	44.7	0.25755	0.01227	0.1471	0.2599

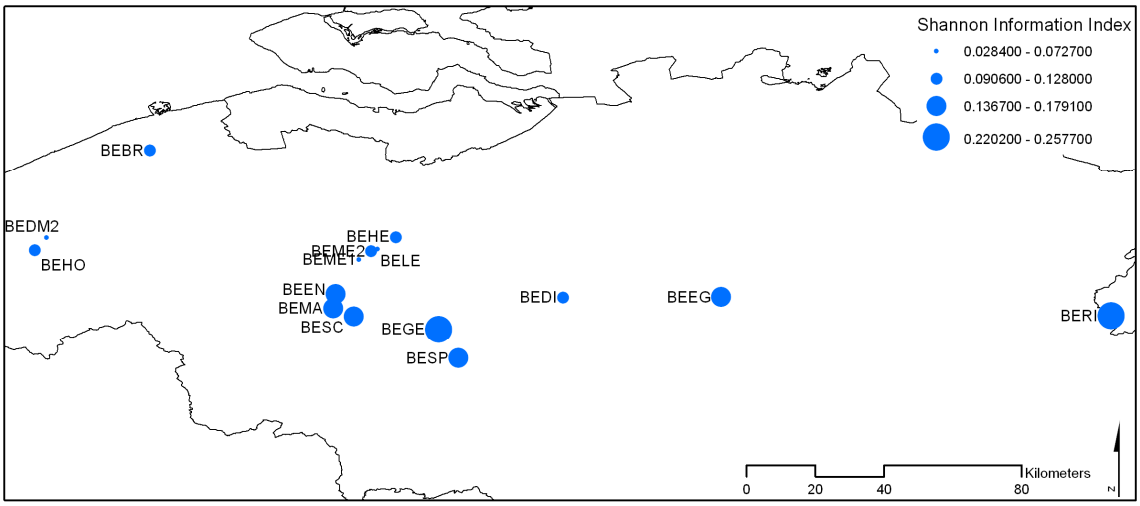

Fig. 2. 4: Shannon information index for the Belgian populations.

To determine if cultivars of *Ulmus* have had an influence on the supposedly autochthonous populations, we conducted a sibship and parentage analysis with Colony v2.0.1.9 (Jones and Wang 2009). In this program, a maximum likelihood method is used, based on the individual MLG. Offspring are clustered into paternal families and maternal families using a simulated annealing approach to maximize the group likelihood value. Then, Candidate parents are assigned to the clusters at a 95% confidence level. If no candidate parents seem available, the program reconstructs parental genotypes. It can also incorporate scoring errors.

For these analyses, we included the Flemish samples and 'Den Haag' as offspring, resulting in 35 individuals. All available cultivars in our dataset, including 'Den Haag', were listed as potential

parents. We excluded monomorphic loci which resulted in a set of 355 polymorphic markers. Many of the samples were found to be full sibs or half sibs (Fig. A in the Annex). This is in agreement with the results of GenoType. Therefore, full sibs could be in fact clones. An exception is BERI, which holds many individuals that were not identified as ramets of the same genet, but as full sibs. Still, a few of the full sibs in BERI were identified as backcrosses, while the majority seemed to be pure *U. glabra*. Also, a few peculiar full and half sib combinations could be detected between samples of distant locations, such as BERI and BEGE, BERI and BEEG.

None of the candidate fathers were assigned to the offspring. But as for the potential mothers, 'Klemmer', 'Belgica' and 'Major' came up several times (Table 2.6). Off course, this could also be the other way around, since there is no way to make a distinction between potential mothers and fathers. For the sake of clarity, we keep calling 'Klemmer', 'Belgica' and 'Major' potential mothers, as described in Colony's results. As shown before, GE8 and MER1 until MER6 probably have an identical genotype as 'Klemmer'. Although the high Dice similarity of 0.92 (15 differences) between OOS1 and 'Major' is lower than the clonality threshold used above, it is still quite high. In other words, OOS1 might also be the same clone as 'Major'. This is also the case for 'Belgica' and DIL1, MER8, SCH6 and SCH7 (Dice similarity = 0.92, 17 differences). For the other offspring, this seems less likely, since Dice similarity indices were below 0.88. Dice similarity between 'Klemmer', 'Major' and 'Belgica' is 0.86, which is also quite high. Because of the high probabilities for the inferred mothers of GE3, HEU1 and HOU4, the mothers are likely to be 'Klemmer' for the first and 'Major' for the latter two. However, we expected 'Belgica' to be assigned as a parent of 'Den Haag', which did not happen. For comparison, we added 'Columella' as offspring and the following prior information: 'Belgica' is father of 'Den Haag', 'Plantyn' is mother of 'Columella'. This adjusted the outcome only slightly. 'Horizontalis' was assigned as father to GE4 (probability = 0.841), 'Crist. Buisman' as mother to GE3 (probability = 1) and 'Plantyn' as mother to HEU2 (probability = 1). Also, the probability of 'Major' being the mother tree of HEU1 decreased to 0.177, while the probability of the same cultivar being mother of SPK Philipskouter 684/1306 and DIL2 increased to 0.961 and 0.983, respectively. Finally, 'Belgica' was now identified as father instead of mother of DIL1, MER8, SCH6 and SCH7.

Table 2. 6: Maternity of each offspring inferred by Colony. On each line, the ID of the offspring is shown on the 1st column, followed by the ID and probability of the 1st inferred mother, the ID and probability of the 2nd inferred mother, etc., when the probability > 0.001.

Offspring ID	**Inferred Mum1**	**Prob Mum1**	**Inferred Mum2**	**Prob Mum2**	**Inferred Mum3**	**Prob Mum3**
DIL1	Belgica	1				
EN12	Belgica	0.51				
MER8	Belgica	1				
SCH6	Belgica	1				
SCH7	Belgica	1				
EGE11	Klemmer	0.003				
SPK Philipskouter 684/1306	Major	0.049	Klemmer	0.048		
DIL2	Major	0.058				
GE8	Klemmer	1				
GE3	Klemmer	0.692	Crist. Buisman	0.183	Major	0.001
MER4	Klemmer	1				
EN6	Major	0.131				
MER1	Klemmer	1				
MER2	Klemmer	1				
MER3	Klemmer	1				
MER5	Klemmer	1				
MER6	Klemmer	1				
OOS1	Major	1				
HEU1	Major	0.999	Crist. Buisman	0.001		
HOU4	Major	1				

2.2.4. Genetic structure

As a measure of population differentiation for the Belgian populations, we calculated F_{ST} using AFLPsurv with 500 permutations. In addition, general and pairwise population Φ_{PT} values were estimated using AMOVA of Genalex 6.4 with 999 Monte Carlo permutations. The population differentiation estimates were 0.2524 for F_{ST} ($P < 0.0001$) and 0.33 for Φ_{PT} ($P= 0.001$), which are quite high values for outcrossing, wind-pollinated tree species, though not surprising, since two different species and interspecific hybrids are involved. The pairwise Φ_{PT} values show that BEME1 is highly differentiated from the other populations (Table 2.7). This is probably because this population mainly consists of 'Klemmer' hybrids, unlike the other populations (Table 2.3). However, BEME1 is least differentiated from BEGE ($\Phi_{PT} = 0.280$), because of the potential clones and half sibs found in both locations (see above). Actually, the findings of the clonal en sib ship assignments in general explain certain low differentiation values. Furthermore, BELE seems genetically very different from the other populations. Populations that frequently show insignificant Φ_{PT} values are populations with very small sample sizes (2 to 3 samples).

Table 2. 7: Pairwise population Φ_{PT} values calculated with Genalex 6.4 of the Belgian populations with *U. minor*, *U. glabra* and their hybrids. Φ_{PT} values below diagonal; probability values based on 999 permutations are shown above diagonal. Φ_{PT} values with probabilities below 0.05 are indicated in red.

	BEBR	BEDI	BEDM1	BEDM2	BEEG	BEEN	BEGE	BEHE	BEHO	BELE	BEMA	BEME1	BEME2	BERI	BESC	BESP
BEBR	0	0.059	0.001	0.005	0.001	0.157	0.002	0.035	0.004	0.004	0.002	0.001	0.014	0.001	0.001	0.001
BEDI	0.335	0	0.327	0.065	0.227	0.361	0.422	0.34	0.079	0.062	0.305	0.028	0.302	0.024	0.357	0.321
BEDM1	0.486	0.546	0	0.081	0.038	0.109	0.021	0.345	0.06	0.036	0.016	0.001	0.151	0.001	0.001	0.333
BEDM2	0.429	0.546	0.733	0	0.003	0.028	0.001	0.054	0.093	0.014	0.004	0.006	0.034	0.001	0.003	0.064
BEEG	0.4	0.06	0.524	0.506	0	0.001	0.011	0.038	0.009	0.007	0.004	0.004	0.293	0.001	0.002	0.179
BEEN	0.131	0.089	0.368	0.363	0.221	0	0.043	0.364	0.145	0.024	0.112	0.001	0.284	0.003	0.048	0.357
BEGE	0.295	0.001	0.361	0.374	0.123	0.122	0	0.106	0.002	0.001	0.022	0.002	0.12	0.001	0.008	0.322
BEHE	0.213	0.083	0.402	0.475	0.279	0	0.124	0	0.142	0.031	0.045	0.043	0.166	0.004	0.046	0.665
BEHO	0.337	0.387	0.559	0.1	0.437	0.212	0.311	0.279	0	0.001	0.001	0.005	0.052	0.001	0.001	0.058
BELE	0.494	0.684	0.858	0.745	0.598	0.5	0.456	0.573	0.617	0	0.002	0.001	0.024	0.001	0.002	0.05
BEMA	0.336	0.049	0.432	0.447	0.204	0.154	0.117	0.22	0.364	0.507	0	0.001	0.115	0.001	0.301	0.001
BEME1	0.514	0.43	0.744	0.703	0.431	0.447	0.28	0.519	0.603	0.756	0.37	0	0.02	0.001	0.001	0.04
BEME2	0.359	0	0.574	0.452	0.023	0.121	0.091	0.208	0.331	0.655	0.135	0.472	0	0.005	0.08	0.42
BERI	0.405	0.171	0.465	0.447	0.21	0.287	0.098	0.31	0.415	0.492	0.21	0.367	0.193	0	0.001	0.091
BESC	0.414	0.075	0.557	0.537	0.233	0.273	0.165	0.348	0.451	0.615	0	0.405	0.19	0.216	0	0.046
BESP	0.369	0	0.45	0.498	0.143	0.097	0	0.048	0.38	0.66	0.143	0.462	0.096	0.075	0.215	0

2.3. Discussion

2.3.1. Clonality

We found evidence of clonality, especially among *U. minor* and F1 hybrids. Clones among backcrosses with *U. glabra* were also detected, but less frequent: one common genotype in two populations, BEMA and BESC, merely 4.5 km away from each other. Considering this small distance, translocation of planting material from one location to the other could have taken place. Only two cases of clones among backcrosses with *U. minor* were found (in BEME1 and BEGE) and seemed to be the cultivar 'Klemmer'.

As mentioned before, it is difficult to infer an exact threshold to determine which of the samples belong to the same clone. Consequently, the results should be interpreted with caution, as you also could be dealing with closely related trees. For instance, a few samples of *U. glabra*, of BERI, were among the clonality results. Two of them were located next to each other, two others were not. Since the sib ship analysis pointed out that most of the samples of BERI could be full sibs, the supposed clones could just as well be highly related individuals. Furthermore, selfing might be another possible explanation for producing nearly identical genotypes. Hans (1981) performed controlled crosses and found *U. glabra* to be self-compatible. Furthermore, *U. glabra* is not able to regenerate through sprouting, except on trunks of young trees, nor through root suckering, so selfing could explain the occurrence of a few highly resembling genotypes among this species within BERI. However, one would expect more evidence of selfing among the 36 samples that were taken in this population. Moreover, Nielsen and Kjaer (2010b) did not find evidence of self-pollination in isolated trees in Denmark. Another explanation for the two closest clones in BERI could be that they are remnants of an old coppice tree. However, more detailed information on these samples is missing to be able to support this hypothesis.

On the other hand, *U. minor* is known for its capability to form suckers or sprouts. Subsequently, hybrids of *U. minor* and *U. glabra* inherit this ability. Hans (1981) did not investigate selfing for *U. minor*, but for *U. procera*, which our analysis confirms to be an *U. minor*. *U. procera* seemed self-compatible. In addition, López-Almansa (2002) found *U. minor* to be self-compatible based on series of controlled crosses. In contrast, López-Almansa et al. (2003) learned self-fertilisation to be rare in natural populations in Spain, suggesting self-incompatibility. Moreover, a lot of trees they investigated seemed female-sterile and *U. minor* is known to produce a high proportion of empty seeds (López-Almansa and Gil 2003). Additionally, high clonality was found in Dutch populations of *U. minor* based on microsatellites (http://www.kennisonline.wur.nl/Project/Abstract/project-baps-10886#linkblockbookmark). Several individuals with the same MLG on different locations were found in Flanders, with distances sometimes exceeding 13 km. So, some planting with root suckers could have happened in the past. Furthermore, many elms in Flanders were found in old hedges, indicating past human activity.

2.3.2. Species determination within *U. minor-U.glabra* complex

Based on the results obtained with BAPS and NewHybrids, many Belgian samples seemed to be misclassified as pure species using morphological criteria. This is not surprising, as the genus elm is known for its taxonomic difficulties and the elm taxonomy has been a topic of debate for a long time (e.g. Coleman et al. 2000). Because of multiple backcrosses, it becomes increasingly difficult to differentiate pure species from hybrids. In addition, it seems that in Flanders and the Netherlands, the full spectrum of the *U. minor-U. glabra* complex is present (e.g. Touw 1963), whereas in the other countries it appears at least more feasible to identify the pure species. This could mean that in those countries there are less hybrids

present and/or that both species only co-occur on specific locations (e.g. Richens and Jeffers 1986). This is hard to say, since we lack background information on these populations. Although, Machon et al. (1997) found that in the plains regions of Northern France and Normandy *U. glabra* was difficult to distinguish from *U. minor* because of the presence of hybrids, while this seemed less of a problem in the east. Also, the samples received from Cemagref were already genetically screened by Goodall-Copestake et al. (2005). So, less confusion about the species of these samples is to be expected. Nevertheless, in that same study, several samples were misidentified and were mainly from Belgium (A. Vanden Broeck, personal communication).

Certain Belgian populations appear to consist solely of pure *U. minor* trees. This might be linked with the fact that these samples are elements in hedgerows, pointing out that they were planted there at one point. Also, both species do not co-occur as pure species on the same location, although backcrosses with one of the pure species were found together with the other species. Besides, *U. minor* and backcrosses with this species seemed more or less restricted to the sandy region of Flanders within our sampling area, whereas *U. glabra*, F1 hybrids and backcrosses with *U. glabra* appear to grow more in Southern Flanders with its richer soils. However, our sampling effort was very limited within populations and we did not take any samples from potential surrounding elms. Consequently, we could have missed the presence of *U. minor* near *U. glabra*. The reverse seems less probable, since the inventory of autochthonous trees and shrubs of Flanders shows no records of *U. glabra* in Northern Flanders (Maes 2006).

2.3.3. Other *Ulmus* species and cultivars

As expected, *U. procera* is likely an *U. minor*. One *U. pumila*, *U. japonica* and their hybrid were well differentiated from the other species. Another *U. pumila* sample (CNR069) seemed to be rather an *U. minor*, while the third *U. pumila* (UPM111) could well be a hybrid with *U. minor*. More samples from these species are, however, needed for confirmation.

Our analysis sheds more light on the taxonomy of many old *Ulmus* cultivars. Nonetheless, everything depends on the reliability of the reference samples for each of the pure species. Moreover, we needed (more) duplicates for most of the cultivars to give a consistent result, to exclude scoring or technical errors. For instance, *U. minor* var. *cornubiensis* was classified as a backcross with *U. glabra*, but seems a classic *U. minor* morphologically. Also, the cultivar 'Major' has characteristics of both *U. minor* and *U. glabra* (Heybroek et al. 2009), though our analysis identified the cultivar as a pure *U. minor*. In addition, because no sample of *U. wallichiana* was at hand, it was only possible to give a descriptive and inconclusive answer on the contribution of each species in the final hybrid cultivar.

To our knowledge, information on the influence of cultivated elms on wild populations through hybridisation is missing. However, this kind of knowledge is essential to obtain efficient conservation guidelines for the remaining natural populations. Besides the samples with the same MLG as of 'Klemmer' found in BEME1 and BEGE, the cultivar could also be the parent of one other sample. Even 'Belgica' and 'Major' were found as potential parents, but for a number of individuals this was questionable as they were very similar to the cultivars in question. Nonetheless, these cultivars seemed to have influenced the natural elm populations, either through planting and possibly clonal reproduction, or through hybridisation. Another consideration to be made is that the starting material for these three cultivars could have originated from the same region in Belgium. All three cultivars are very old. 'Major' is probably the oldest and dates from around 1600 or even before that (Heybroek et al. 2009). It was planted a lot in the Netherlands until 'Belgica' became more popular mid-19th century. The latter was thought to originate from Belgium in the 18th century. It was planted exceedingly starting from 1850. Almost all elm plantings in Belgium

and the Netherlands existed out of this cultivar until 1928. In addition, for a long time, 'Belgica' was used as rootstock. Also from Belgium, is 'Klemmer'. It dates back from 1877 or maybe 1789. It was always rare in the Netherlands and common in Belgium and the north of France in the beginning of the 20th century. However, it is now considered to be rare in general (Heybroek et al. 2009).

2.3.4. Genetic diversity and structure of Belgian populations

In general, the populations we investigated in Flanders showed low to moderate values of genetic diversity. Especially, the locations with *U. glabra* and/or backcrosses with the species seemed to have slightly higher values. Collada et al. (2004) also found lower levels of genetic diversity in Spanish *U. minor* populations compared to *U. glabra* populations. The explanation Gil et al. (2004) gave, was that these *U. minor* populations were greatly influenced through pollination from and backcrosses with the widely distributed clone of *U. procera*. However, genetic diversity values of the Belgian populations with a different species composition (and different sample size) cannot simply be compared.

Likewise, the high value for population differentiation (F_{ST} = 0.25) might be caused by DED causing many populations across Europe and North-America to go through a genetic bottleneck, but is probably influenced by the different proportions of pure species and hybrids in the sampled populations as well. Based on allozymes, Machon et al. (1997) discovered only a moderate differentiation between French regions with *U. minor*. In the Netherlands, populations of *U. minor* were not strongly differentiated (http://www.kennisonline.wur.nl/Project/Abstract/project-baps-10886#linkblockbookmark). Considering the pairwise population Φ_{PT} values between pure U. minor populations BEBR, BEDM1, BEDM2, BEHO, BEHE, BELE and BEEN (with a few backcrosses with U. minor), most of them were insignificant, except for comparisons with BEBR and BELE. These results seem to confirm the Dutch findings, but the number of *U. minor* populations and samples are too small to make such general conclusions. Nonetheless, it seems quite possible that, compared to *U. glabra*, *U. minor* could have maintained better its genetic variation, because its ability to rejuvenate vegetatively helped the species survive DED through root suckering on surviving roots. Additionally, the *Scolytus* beetles seem to have a preference for older twigs (Pajares et al. 2004). Established hedgerows kept low by clipping thus escaped the disease. At the same time, *U. glabra* is less preferred than *U. minor* by the beetles due to certain triterpenes and sterols in the bark (Martin-Benito et al. 2005). On the other hand, *U. minor* was probably propagated and planted more than *U. glabra* because of the ability to regenerate asexually (López de Heredia et al. 2005). Although, our results showed that the latter could also have been planted in Belgium, due to the similar genotypes found in BERI, BEGE and BEEG. This is very plausible as cultivation of the species in Flanders has occurred since the 17th century (Maes 2006).

Nevertheless, genetic diversity within *U. minor* populations is low and their population sizes are small. This is also the case for *U. glabra*. The population of BERI might have the highest number of trees, but they are highly related. Given the fact that infections with DED still occur and that sexual propagation seems rare, population differentiation might increase as a result of genetic drift and actual losses of genotypes due to DED. Finally, the spread of cultivars has had its influence on the remaining genetic recourses of *U. minor* and *U. glabra* (see above), which could have further altered the genetic variation. Consequently, the autochthonous status of certain populations becomes questionable.

Since the 16th century, the elm was one of the most planted tree species in the city and the surrounding countryside. Also, *Ulmus* x *hollandica* was well known since the 17th century, followed later by 'Belgica' (Heybroek et al. 2009). Consequently, it is quite possible that reproductive material has been moved around a lot, obscuring the genetic structure of the

populations. Moreover, this could explain the species mix present in the studied populations and the abundance of hybrids.

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4. Annex

Table A: List of samples of *Ulmus laevis*

Pop	N	Sample_ID	Country	city	Collection place
BEBR	5	BR1	Belgium	Brakel	
		BR2	Belgium	Brakel	
		BR3	Belgium	Brakel	
		BR4	Belgium	Brakel	
		BR5	Belgium	Brakel	
BEDP	6	DP3	Belgium	De Panne	Oosthoek
		DP4	Belgium	De Panne	Oosthoek
		DP6	Belgium	De Panne	Oosthoek
		DP7	Belgium	De Panne	Oosthoek
		DP7	Belgium	De Panne	Oosthoek
		DP11	Belgium	De Panne	Oosthoek
		DP12	Belgium	De Panne	Oosthoek
BEEG	7	EGE1	Belgium	Egenhoven	Egenhovenbos
		EGE3	Belgium	Egenhoven	Egenhovenbos
		EGE4	Belgium	Egenhoven	Egenhovenbos
		EGE9	Belgium	Egenhoven	Egenhovenbos
		EGE12	Belgium	Egenhoven	Egenhovenbos
		EGE13	Belgium	Egenhoven	Egenhovenbos
		EGE14	Belgium	Egenhoven	Egenhovenbos
BEGE	3	MO1	Belgium	Geraardsbergen	Moerbekebos
		MO2	Belgium	Geraardsbergen	Moerbekebos
		GE7	Belgium	Geraardsbergen	Moerbekebos
BEHE	22 + 11*	HE30	Belgium	Heers	loc HE08, horneveld
		HE31	Belgium	Heers	loc HE08, horneveld
		HE32	Belgium	Heers	loc HE08, horneveld
		HE33	Belgium	Heers	loc HE08, horneveld
		HE38	Belgium	Heers	loc HE08, horneveld
		HE39	Belgium	Heers	loc HE08, horneveld
		HE43	Belgium	Heers	loc HE08, horneveld
		HE44	Belgium	Heers	loc HE08, horneveld
		HE45	Belgium	Heers	loc HE08, horneveld
		HE46	Belgium	Heers	loc HE08, horneveld
		HE50	Belgium	Heers	loc HE08, horneveld
		RU1	Belgium	Heers	Rukkelingen-Loon
		RU2	Belgium	Heers	Rukkelingen-Loon
		RU3	Belgium	Heers	Rukkelingen-Loon
		RU4	Belgium	Heers	Rukkelingen-Loon
		RU5	Belgium	Heers	Rukkelingen-Loon
		he6.1	Belgium	Heers	langs bospad
		he6.2	Belgium	Heers	langs bospad
		he6.3	Belgium	Heers	langs bospad
		he6.4	Belgium	Heers	langs bospad
		he6.5	Belgium	Heers	langs bospad

Pop	N	Sample_ID	Country	city	Collection place
		he6.6	Belgium	Heers	langs bospad
		he6.9	Belgium	Heers	langs bospad
		he6.10	Belgium	Heers	langs bospad
		he6.12	Belgium	Heers	langs bospad
		he8.1	Belgium	Heers	holle weg
		he8.2	Belgium	Heers	holle weg
		he8.3	Belgium	Heers	holle weg
		he8.4	Belgium	Heers	holle weg
		he8.8	Belgium	Heers	holle weg
		he8.9	Belgium	Heers	holle weg
		he8.10	Belgium	Heers	holle weg
		he8.11	Belgium	Heers	Holle weg
BEKE	5	KE7	Belgium	Kermt	
		KE8	Belgium	Kermt	
		ker 10	Belgium	Kermt	
		ker 11	Belgium	Kermt	
		KER15	Belgium	Kermt	
BELI	4	LI1	Belgium	Lille	loc 140
		LI2	Belgium	Lille	loc 140
		LI3	Belgium	Lille	loc 140
		LI6	Belgium	Lille	loc 140
BEPL	1	PL1	Belgium	Ploegsteert	615 Bois de la Hutte
BEPO	6	POP1	Belgium	Poperingen	420 Herberg Au Nouveau St. Eloi
		POP2	Belgium	Poperingen	420 Herberg Au Nouveau St. Eloi
		POP3	Belgium	Poperingen	420 Herberg Au Nouveau St. Eloi
		POP4	Belgium	Poperingen	420 Herberg Au Nouveau St. Eloi
		POP5	Belgium	Poperingen	420 Herberg Au Nouveau St. Eloi
		POP6	Belgium	Poperingen	420 Herberg Au Nouveau St. Eloi
BESH	8	SH1	Belgium	Sint-Lievens-Houtem	Kottem
		SH2	Belgium	Sint-Lievens-Houtem	Kottem
		SH3	Belgium	Sint-Lievens-Houtem	Kottem, locatie Hugo, naast baantje
		SH4	Belgium	Sint-Lievens-Houtem	Kottem, locatie Hugo
		SH7	Belgium	Sint-Lievens-Houtem	Kottem, locatie Hugo
		SH8	Belgium	Sint-Lievens-Houtem	Kottem, locatie Hugo
		SH9	Belgium	Sint-Lievens-Houtem	Kottem, locatie Hugo
		SH10	Belgium	Sint-Lievens-Houtem	Kottem, locatie Hugo
BETO	2	TOM1	Belgium	Tombeek	
		TOM2	Belgium	Tombeek	
BEVO	5	VO1	Belgium	Ruiselede	Vortebossen
		VO2	Belgium	Ruiselede	Vortebossen
		VO3	Belgium	Ruiselede	Vortebossen
		VO4	Belgium	Ruiselede	Vortebossen
		VO5	Belgium	Ruiselede	Vortebossen
BEWO	1	WOR1	Belgium	Wortegem-Petegem	
BEZA	2	ZO5	Belgium	Zandhoven	328 Pulderbos
		ZO6/7	Belgium	Zandhoven	328 Pulderbos
BEZO	4	ZOE1	Belgium	Zoersel	Zoerselbos, langs baantje

Pop	N	Sample_ID	Country	city	Collection place
	+	ZOE2	Belgium	Zoersel	Zoerselbos, in houtkant
	1	ZOE3	Belgium	Zoersel	Zoerselbos, nieuwe locatie conservator
		ZOE4	Belgium	Zoersel	Zoerselbos, nieuwe locatie conservator
	**	ZO1	Belgium	Zoersel	317 Zoerselbos
		ZO2	Belgium	Zoersel	317 Zoerselbos
		IBW100	Belgium	Zoersel	
FRCO	1	CEM199	France	Colmar	privé en limite de FRONHOL. p
FRDE	1	CEM279	France	DESVRES	Stade
FRDV	5	Chabrillan N°1	France	Chabrillan	Drôme-valley
		Chabrillan N°2	France	Chabrillan	Drôme-valley
		Chabrillan N°3	France	Chabrillan	Drôme-valley
		Chabrillan N°4	France	Chabrillan	Drôme-valley
		Chabrillan N°5	France	Chabrillan	Drôme-valley
FRER	2	CEM193	France	Erstein	FC. ERSTEIN p 13
	+	CEM194	France	Erstein	FD. DAUBENSAND p 2
		FRA.US.0193	France	Erstein	FC. ERSTEIN p 13
FRGG1	2	CEM407	France	Grenade-sur-Garonne	
		CEM409	France	Grenade-sur-Garonne	
FRGG2	1	CEM423	France	Grenade-sur-Garonne	GRE13 = CAP DUP 03
FRHA	1	CEM284	France	Hasnon	FD. de Saint-Amand
FRHB	1	CEM314	France	Harbonnières	
FRHE	1	CEM265	France	Hem-Hardinval	bord de D 925
FRLO	4	CEM335	France	Locquignol	de Mormal "le Triolin" p. 10.4
		CEM334	France	Locquignol	de Mormal "le Triolin" p. 10.4
		CEM336	France	Locquignol	de Mormal "le Triolin" p. 10.4
		CEM011	France	Locquignol	de Mormal "le Triolin" p. 10.4
FRME	3	CEM420	France	Merville	MER01
		CEM424	France	Merville	MER08 = ARBRE N°5
		CEM422	France	Merville	MER11 = MER PARK
FRQU	1	CEM282	France	QUERCAMPS	village
FRSA	1	CEM382	France	SAINT-AMAND	
FRVA10	8	S10N5	France	Chatêl-de-Neuvre	'Réserve Naturelle du Val d'Allier'
		S10N4	France	Chatêl-de-Neuvre	'Réserve Naturelle du Val d'Allier'
		S10N6	France	Chatêl-de-Neuvre	'Réserve Naturelle du Val d'Allier'
		S10N8	France	Chatêl-de-Neuvre	'Réserve Naturelle du Val d'Allier'
		S10N12	France	Chatêl-de-Neuvre	'Réserve Naturelle du Val d'Allier'
		S10N13	France	Chatêl-de-Neuvre	'Réserve Naturelle du Val d'Allier'
		S10N16	France	Chatêl-de-Neuvre	'Réserve Naturelle du Val d'Allier'
		S10N19	France	Chatêl-de-Neuvre	'Réserve Naturelle du Val d'Allier'
FRVA13	1	S13N8,1	France	Tilly	'Réserve Naturelle du Val d'Allier'
FRVA14	4	S14N6	France	Bessay-sur-Allier	'Réserve Naturelle du Val d'Allier'
		S14N5	France	Bessay-sur-Allier	'Réserve Naturelle du Val d'Allier'
		S14N7	France	Bessay-sur-Allier	'Réserve Naturelle du Val d'Allier'
		S14N9	France	Bessay-sur-Allier	'Réserve Naturelle du Val d'Allier'
		S14N11	France	Bessay-sur-Allier	'Réserve Naturelle du Val d'Allier'
		S14N12	France	Bessay-sur-Allier	'Réserve Naturelle du Val d'Allier'
FRVA23	26	S23N1	France	Chemilly	'Réserve Naturelle du Val d'Allier'

Pop	N	Sample_ID	Country	city	Collection place
		S23N3	France	Chemilly	'Réserve Naturelle du Val d'Allier'
		S23N4	France	Chemilly	'Réserve Naturelle du Val d'Allier'
		S23N8	France	Chemilly	'Réserve Naturelle du Val d'Allier'
		S23N9	France	Chemilly	'Réserve Naturelle du Val d'Allier'
		S23N11	France	Chemilly	'Réserve Naturelle du Val d'Allier'
		S23N12	France	Chemilly	'Réserve Naturelle du Val d'Allier'
		S23N13	France	Chemilly	'Réserve Naturelle du Val d'Allier'
		S23N14	France	Chemilly	'Réserve Naturelle du Val d'Allier'
		S23N18	France	Chemilly	'Réserve Naturelle du Val d'Allier'
		S23N22	France	Chemilly	'Réserve Naturelle du Val d'Allier'
		S23N23	France	Chemilly	'Réserve Naturelle du Val d'Allier'
		S23N25	France	Chemilly	'Réserve Naturelle du Val d'Allier'
		S23N26	France	Chemilly	'Réserve Naturelle du Val d'Allier'
		S23N27	France	Chemilly	'Réserve Naturelle du Val d'Allier'
		S23N28	France	Chemilly	'Réserve Naturelle du Val d'Allier'
		S23N29	France	Chemilly	'Réserve Naturelle du Val d'Allier'
		S23N30	France	Chemilly	'Réserve Naturelle du Val d'Allier'
		S23N31	France	Chemilly	'Réserve Naturelle du Val d'Allier'
		S23N32	France	Chemilly	'Réserve Naturelle du Val d'Allier'
		S23N34	France	Chemilly	'Réserve Naturelle du Val d'Allier'
		S23N35	France	Chemilly	'Réserve Naturelle du Val d'Allier'
		S23N36	France	Chemilly	'Réserve Naturelle du Val d'Allier'
		S23N37	France	Chemilly	'Réserve Naturelle du Val d'Allier'
		S23N38	France	Chemilly	'Réserve Naturelle du Val d'Allier'
		S23N39	France	Chemilly	'Réserve Naturelle du Val d'Allier'
FRVA8	2	S8N2	France	Chatêl-de-Neuvre	'Réserve Naturelle du Val d'Allier'
		S8N3	France	Chatêl-de-Neuvre	'Réserve Naturelle du Val d'Allier'
FRVA9	2	S9N1	France	Monténay-sur-Allier	'Réserve Naturelle du Val d'Allier'
		S9N7	France	Monténay-sur-Allier	'Réserve Naturelle du Val d'Allier'
FRWA	1	CEM285	France	Wavrans-sur-l'Aa	Vallée-sous-les-Monts
GELD	1	NFV034	Germany	Lüchow-Dannenberg	Rfö Bohldamm
KYBI	2	Kyrgyzstan1	Kyrgystan	Bishkek	
		Kyrgyzstan2	Kyrgystan	Bishkek	
NEBA	2	6302	Netherlands	Barneveld	Kl. Barneveldse beek langs Kallenbroek
		6306	Netherlands	Barneveld	Kl. Barneveldse beek langs Kallenbroek
NEBE	2	5102	Netherlands	Beilen	76 Hulzedink
		5101	Netherlands	Beilen	76 Hulzedink
NEEN	1	7101	Netherlands	Enschede	Smalenbroek/'t Spik
NEGE	2	8102	Netherlands	Gennep	De Gebrande Kamp
		8101	Netherlands	Gennep	De Gebrande Kamp
NEGO	1	12205	Netherlands	Geulle en Elsloo	5 Bunderbos, Kruisbos?
NELI1	3	02 Hezelaar UL	Netherlands	Liempde	Hezelaar
		05 Hezelaar, Liempde	Netherlands	Liempde	Hezelaarsbroek
		06 Hezelaarsbroek, Liempde	Netherlands	Liempde	Hezelaarsbroek
NELI2	4	03 de hut bij Schooringen	Netherlands	Liempde	Hut bij Schooringen
		04 Schooringe knotboom	Netherlands	Liempde	Schooringen
		07 Schoevingen kleine boom?	Netherlands	Liempde	Schooringen

Pop	N	Sample_ID	Country	city	Collection place
		08 Liempdse Duik, Liempde	Netherlands	Liempde	Achterste Elzinge, Liempdse Dijk
NEME	4	12216	Netherlands	Meersen	Bunderbos zuid
		12202	Netherlands	Meersen	Bunderbos zuid
		12203	Netherlands	Meersen	Bunderbos zuid
		12201	Netherlands	Meersen	Bunderbos zuid spoorwegoverg.
NEMI	2	8302	Netherlands	Millingen a/s Rijn	25 Millingerwaard, Colenbrandersbos
		8301	Netherlands	Millingen a/s Rijn	25 Millingerwaard, Colenbrandersbos
NESO	1	11206	Netherlands	Sint-Oedenrode	103 Boschkant
NEUD1	1	11201	Netherlands	Udenhout	86 Hoornmanken Tiend
NEUD2	1	01 Kuilpad Udenhout	Netherlands	Udenhout	Kuilpad
NEVA1	1	12220	Netherlands	Valkenburg a.d. Geul	43 Schansweg
NEVA2	2	12217	Netherlands	Valkenburg a.d. Geul	12 Schaelsberg, noordelijke uitloper
		12212	Netherlands	Valkenburg a.d. Geul	12 Schaelsberg, noordelijke uitloper
NEVA3	1	12207	Netherlands	Valkenburg a.d. Geul	8 Kloosterbos, oostelijke gedeelte
NEWI1	2	7202	Netherlands	Winterswijk	54 Ratumse beek bij Lutgenkossink
		7225	Netherlands	Winterswijk	54 Ratumse beek bij Lutgenkossink
NEWI2	7	7208	Netherlands	Winterswijk	43 Willinkbeek nabij Willink
		7218	Netherlands	Winterswijk	49 Ratumse beek bij Revendink
		7230	Netherlands	Winterswijk	43 Willinkbbek nabij Willink
		7226	Netherlands	Winterswijk	43 Willinkbeek nabij Willink
		7229	Netherlands	Winterswijk	43 Willinkbeek nabij Willink
		7216	Netherlands	Winterswijk	48 Ratumse beek bij Revendink
		7211	Netherlands	Winterswijk	43 Willinkbeek nabij Willink
NEWI3	2	7223	Netherlands	Winterswijk	64 Het Bonnink, Ratumse beek
		7224	Netherlands	Winterswijk	64 Het Bonnink, Ratumse beek
NEWI4	2	7220	Netherlands	Winterswijk	26 Bovenslinge bij Rietbrug
		7222	Netherlands	Winterswijk	28 Buskersbos

*: samples with code 'HE' were independently collected from samples with code 'he'. To avoid possible replicates, the sample with code 'HE' were discarded.

**: IBW100 is a ramet of ZOE2 and was discarded.

$: FRA.US.0193 is a ramet of CEM193 and was discarded in the population genetics analysis. Both samples were however compared with each other at the request of Cemagref.

Table B: list of samples of *U. minor*, *U. glabra*, *U. pumila*, *U. procera*, hybrids and cultivars.

Pop	Sample	Species	Name cultivar	Country	City	Collection place
BEBR	BG1	U. minor		Belgium	Brugge (Sint-Pieters)	Zuienkerkstraat - loc BG75
	BG2	U. minor		Belgium	Brugge (Sint-Pieters)	Zuienkerkstraat - loc BG75
	BG3	U. minor		Belgium	Brugge (Sint-Pieters)	Zuienkerkstraat - loc BG75
	BG4	U. minor		Belgium	Brugge (Sint-Pieters)	Zuienkerkstraat - loc BG75
	BG5	U. minor		Belgium	Brugge (Sint-Pieters)	Zuienkerkstraat - loc BG75
	BG6	U. minor		Belgium	Brugge (Sint-Pieters)	Zuienkerkstraat - loc BG75
	BG7	U. minor		Belgium	Brugge (Sint-Pieters)	Zuienkerkstraat - loc BG75
	BG8	U. minor		Belgium	Brugge (Sint-Pieters)	Zuienkerkstraat - loc BG75
BEDI	DIL1	U. glabra		Belgium	Dilbeek	Wolfsputten
	DIL2	U. glabra		Belgium	Dilbeek	Wolfsputten
BEDM1	DIK46	U. minor		Belgium	Diksmuide (Woumen)	
	DIK48	U. minor		Belgium	Diksmuide (Woumen)	
BEDM2	DIK1	U. minor		Belgium	Disksmuide (Esen)	Woumenhoek - loc DI27
	DIK2	U. minor		Belgium	Disksmuide (Esen)	Woumenhoek - loc DI27
	DIK4	U. minor		Belgium	Disksmuide (Esen)	Woumenhoek - loc DI27
	DIK3	U. minor		Belgium	Disksmuide (Esen)	Woumenhoek - loc DI27
BEEG	EGE2	U. glabra		Belgium	Heverlee	Egenhovenbos
	EGE5	U. glabra		Belgium	Heverlee	Egenhovenbos
	EGE6	U. glabra		Belgium	Heverlee	Egenhovenbos
	EGE7	U. glabra		Belgium	Heverlee	Egenhovenbos
	EGE8	U. glabra		Belgium	Heverlee	Egenhovenbos
	EGE11	U. glabra		Belgium	Heverlee	Egenhovenbos
	EGE16	U. glabra		Belgium	Heverlee	Egenhovenbos
	EGE17	U. glabra		Belgium	Heverlee	Egenhovenbos
BEEN	EN4	U. minor		Belgium	Oudenaarde (Ename)	Bos 't Ename, Schuifelbeen - loc 454
	EN5	U. minor		Belgium	Oudenaarde (Ename)	Bos 't Ename, Schuifelbeen - loc 454
	EN6	U. minor		Belgium	Oudenaarde (Ename)	Bos 't Ename, Schuifelbeen - loc 454
BEGE	GE2	U. glabra		Belgium	Geraardsbergen	Raspaillebos - loc GE58, 59, 60, 61, 62
	GE3	U. x hollandica		Belgium	Geraardsbergen	Raspaillebos - loc GE58, 59, 60, 61, 62
	MO3	U. glabra		Belgium	Geraardsbergen	Moerbekebos, raspaillebos Geraardsbergen
	GE4	U. glabra		Belgium	Geraardsbergen	Moerbekebos, raspaillebos Geraardsbergen
	GE5	U. glabra		Belgium	Geraardsbergen	Moerbekebos, raspaillebos Geraardsbergen
	GE6	U. glabra		Belgium	Geraardsbergen	Moerbekebos, raspaillebos Geraardsbergen
	GE8	U. glabra		Belgium	Geraardsbergen	Moerbekebos, raspaillebos Geraardsbergen
	GE9	U. glabra		Belgium	Geraardsbergen	Moerbekebos, raspaillebos Geraardsbergen

Pop	Sample	Species	Name cultivar	Country	City	Collection place
BEHE	HEU1	U. minor		Belgium	Heusden	loc 205
	HEU2	U. minor		Belgium	Heusden	loc 205
BEHO	HOU1	U. minor		Belgium	Houthulst	Heugstraat 8 - loc HU21
	HOU2	U. minor		Belgium	Houthulst	Heugstraat 8 - loc HU21
	HOU3	U. minor		Belgium	Houthulst	Heugstraat 8 - loc HU21
	HOU4	U. minor		Belgium	Houthulst	Heugstraat 8 - loc HU21
BELE	LEM1	U. minor		Belgium	Lemberge	Church path west of chuch in Lemberge
	LEM2	U. minor		Belgium	Lemberge	Church path west of chuch in Lemberge
	LEM3	U. minor		Belgium	Lemberge	Church path west of chuch in Lemberge
	LEM5	U. minor		Belgium	Lemberge	Church path west of chuch in Lemberge
	LEM4	U. minor		Belgium	Lemberge	Church path west of chuch in Lemberge
BEMA	EN7	U. glabra		Belgium	Maarkedal	Kapelleberg - loc 434
	EN8	U. glabra		Belgium	Maarkedal	Kapelleberg - loc 434
	EN9	U. glabra		Belgium	Maarkedal	Kapelleberg - loc 434
	EN10	U. glabra		Belgium	Maarkedal	Kapelleberg - loc 434
	EN12	U. glabra		Belgium	Maarkedal	Kapelleberg - loc 434
	EN13	U. x hollandica		Belgium	Maarkedal	Kapelleberg - loc 434
	EN14	U. minor		Belgium	Maarkedal	Kapelleberg - loc 434
BEME1	MER4	U. x hollandica		Belgium	Merelbeke	Bruinbos - loc 120
	MER1	U. minor		Belgium	Merelbeke	Bruinbos - loc 120
	MER2	U. minor		Belgium	Merelbeke	Bruinbos - loc 120
	MER3	U. minor		Belgium	Merelbeke	Bruinbos - loc 120
	MER5	U. minor		Belgium	Merelbeke	Bruinbos - loc 120
	MER6	U. minor		Belgium	Merelbeke	Bruinbos - loc 120
BEME2	MER7	U. x hollandica		Belgium	Merelbeke	Gentbos - loc 134
	MER8	U. x hollandica		Belgium	Merelbeke	Gentbos - loc 134
	MER9	U. x hollandica		Belgium	Merelbeke	Gentbos - loc 134
BEOO	OOS1	U. minor		Belgium	Oosterzele	Ettingebos - loc 180
BERI	RIE6	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE9	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE10	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE13	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE18	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE20	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE22	U. minor		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE23	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE25	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE26	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE27	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE28	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE30	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne

Pop	Sample	Species	Name cultivar	Country	City	Collection place
	RIE31	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE34	U. minor		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE35	U. minor		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE37	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE38	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE41	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE1	U. x hollandica		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE2	U. x hollandica		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE3	U. x hollandica		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE4	U. minor		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE5	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE8	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE11	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE12	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE13/1	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE13/2	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE14	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE15	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE17	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE19	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE24	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE32	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE33	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE36	U. x hollandica		Belgium	Riemst	Plateau van Kaestert, Kanne
	RIE39	U. glabra		Belgium	Riemst	Plateau van Kaestert, Kanne
BESC	SCH1	U. glabra		Belgium	Schorisse	Gazenberg - loc 251
	SCH2	U. glabra		Belgium	Schorisse	Gazenberg - loc 251
	SCH3	U. glabra		Belgium	Schorisse	Gazenberg - loc 251
	SCH4	U. glabra		Belgium	Schorisse	Gazenberg - loc 251
	SCH5	U. minor		Belgium	Schorisse	Gazenberg - loc 251
	SCH6	U. x hollandica		Belgium	Schorisse	Gazenberg - loc 251
	SCH7	U. x hollandica		Belgium	Schorisse	Gazenberg - loc 251
BESP	SPK Philipskouter 684/1306			Belgium	Sint-Pieters-Kapelle (Herne)	Phiipskouter
	SPK Philipskouter 683/1304			Belgium	Sint-Pieters-Kapelle (Herne)	Phiipskouter
BETO	IBW050	U. glabra		Belgium	Tongeren	‘s Herenhelderen
FRAM	CEM275	U. minor		France	Amplier	
FRAR	CEM052	U. minor		France	Orne	Argentan
FRAU	Aunay 14260 A	U. minor		France	Aunay	
	Aunay 14260 B	U. minor		France	Aunay	
FRBB	CEM350	? U. minor x U. pumila		France	Bourg-Blanc	bordure voie romaine

Pop	Sample	Species	Name cultivar	Country	City	Collection place
FRBL	Blismes	U. minor		France	Nièvre	Blismes
FRCB	TUS.027	U. minor		France	La Chapelle Bâton	
	TUS.028	U. minor		France	La Chapelle Bâton	
	TUS.029	U. minor		France	La Chapelle Bâton	
FRCM	CEM140	U. minor		France	Charente-Maritime	Saint-Martin-de Ré
FRCU	CEM280	U. minor		France	Cucq	hameau de Trepied
FRGO	CEM328	U. minor		France	Godewaersvelde	
FRGS	CEM330	U. minor		France	Grande-Synthe	CES Anne Franck
FRIL	CEM190	U. minor		France	Illkirch-Graffenstaden	FC. STRASBOURG "NEUHOF"
FRLR	TUS.008	U. minor		France	Le Rheu	
	TUS.009	U. minor		France	Le Rheu	
FRLV	Le Vey Q	U. minor		France	Le Vey	
	Le Vey N	U. minor		France	Le Vey	
	Le Vey J	U. minor		France	Le Vey	
	Le Vey U	U. minor		France	Le Vey	
	Le Vey R	U. minor		France	Le Vey	
FRLW	CEM186	U. minor		France	La-Wantzenau	FC. LA WANTZENAU p 12
FRMA	CEM276	U. minor		France	Magnicourt-en-Comt	rue du Château de la Motte
FRME	CEM386	U. minor		France	Meteren	
	CEM340	U. minor		France	Meteren	
FRMQ	CEM339	U. minor		France	MECQUIGNIES	Le château
FROS	CEM196	U. minor		France	Ostwald	FC. OSTWALD p 8
FRSP	Saint-Pé 7	U. glabra		France	Saint-Pé-de-Bigorre	forêt domaniale de Saint-Pé-de-Bigorre (Génie Longue)
	Saint-Pé 11	U. glabra		France	Saint-Pé-de-Bigorre	forêt domaniale de Saint-Pé-de-Bigorre (Génie Longue)
	Saint-Pé 18	U. glabra		France	Saint-Pé-de-Bigorre	forêt domaniale de Saint-Pé-de-Bigorre (Génie Braque)
FRST	CEM188	U. minor		France	Strasbourg	FC. STRASBOURG "ROBERTSAU" p15
GEGO1	NFV036	U. glabra		Germany	Göttingen	Rfö Pfaffenstrauch
	NFV037	U. glabra		Germany	Göttingen	Rfö Pfaffenstrauch
	NFV038	U. glabra		Germany	Göttingen	Rfö Pfaffenstrauch
GEGO2	NFV010	U. minor		Germany	Göttingen	Rfö Nörten-Hardenberg
GEKA	Kallstadt	U. procera		Germany	Pfalz	Kallstadt
GELD	NFV028	U. minor		Germany	Lüchow-Dannenberg	Rfö Carrenzien
	NFV029	U. minor		Germany	Lüchow-Dannenberg	Rfö Carrenzien
	NFV030	U. minor		Germany	Lüchow-Dannenberg	Rfö Carrenzien
GRIR	FRI956	U. minor		Greece	Iraklion	Festor
GRTH	FRI943	U. minor		Greece	Thessaloniki	Vrasna
ITBC	CNR212	U. minor x U. pumila		Italy	Bocchigliero	in the village
ITBO	CNR055	U. glabra		Italy	Bolzano	Lana
ITCA	CNR218	U. minor		Italy	Catanzaro	SS 106, km 204
ITCV	CNR181	U. pumila		Italy	Cerro Al Volturno	CASTEL S.VINCENZO
ITFV	CNR094	U. minor		Italy	Fiume Veneto	locality VALLON

Pop	Sample	Species	Name cultivar	Country	City	Collection place
ITLA	CNR170	U. minor		Italy	Latina	Iana
ITMO	CNR088	U. minor		Italy	Monfalcone	SS 202, km 128 direction VENEZ
ITNI	CNR100	U. minor		Italy	Nimis	locality MOLMENTET
ITRO	CNR069	U. pumila		Italy	Rovereto	Borgo Sacco, parck Fedrigotti
ITSE	CNR091	U. minor		Italy	Sesto Al Reghena	in the village
ITTA	CNR093	U. minor		Italy	Tamai	TAMAI 1, small church
	CNR089	U. minor		Italy	Tamai	locality BRUGNERA
ITTR	CNR099	U. minor		Italy	Trieste	SS 14 , km 139,4
NA	Klemmer	U. x hollandica or U. minor	Klemmer	cultivar		
NA	Sapporo	U. pumila x U. japonica	Sapporo Autumn Gold	cultivar		
NA	Lobel	Lobel	Lobel	cultivar		3 ramets collected at three locations
NA	Clusius	Clusius	Clusius	cultivar		
NA	73P	U. pumila x ?	73P	cultivar		Offspring of open pollinated mother tree of 'Sapporo Autumn Gold' in Sapporo Botanical Garden
NA	2P	U. japonica	2P	cultivar		Offspring from U. japonica from Kyushu, near Akagi village.
NA	Dodoens	Dodoens	Dodoens	cultivar		
NA	Groeneveld	U. x hollandica	Groeneveld	cultivar		
NA	Commelin	U. x hollandica	Commelin	cultivar		
NA	Plantyn	Plantyn	Plantyn	cultivar		2 ramets collected at two locations
NA	Crist. Buisman	U. minor	Crist. Buisman	cultivar		
NA	Vegeta	U. x hollandica	Vegeta	cultivar		
NA	Major	U. x hollandica	Major	cultivar		
NA	Belgica	U. x hollandica	Belgica	cultivar		
NA	Horizontalis	U. glabra	Horizontalis	cultivar		
NA	Dampieri	U. x hollandica/ U. minor	Dampieri	cultivar		
NA	Den Haag	*U. pumila* x 'Belgica'	Den Haag	cultivar		
NA	Columella	Plantyn selfed	Columella	cultivar		
NA	Sarniensis	U. minor	Sarniensis	cultivar		
NEBU	U. minor 'cornubiensis ' Nieuw-Amelisweerd	U. minor var. cornubiensis		Netherlands	Bunnik	Nieuw-Amelisweerd
SPMA	UPM111	U. pumila		Spain	Madrid	Pezuela Torres

Table C: Results from the analyses using NewHybrids v 1.1 beta 3 on samples of the species complex *U. minor-U. glabra* (with uniform and Jeffreys' priors, and using BAPS again on all samples. All individuals showing admixture using BAPS have significant admixture ($p \leq 0.03$). For the species codes I refer to Table x; UH1: *U. minor* x *U. glabra*. Samples in yellow appear to be pure *U. minor* and samples in blue are identified as pure *U. glabra*. Discrepancies between results from both programs are denoted in italic.

Pop	Sample	Species based on morphol.	BAPS all studied species				NewHybrids uniform priors						NewHybrids Jeffreys' priors					
			1	2	3	4	UM	UG	UH1	UH1 x UH1	UH1 x UM	UH1 x UG	UM	UG	UH1	UH1 x UH1	UH1 x UM	UH1 x UG
BEBR	BG1	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
BEBR	BG2	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
BEBR	BG3	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
BEBR	BG5	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
BEBR	BG6	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
BEBR	BG7	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
BEBR	BG8	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
BEDI	DIL1	UG	0.00	0.00	1.00	0.00	0.00	0.00	0.98	0.01	0.00	0.02	0.00	0.00	0.99	0.00	0.00	0.01
BEDI	DIL2	UG	0.50	0.00	0.50	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
BEDM1	Di46	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
BEDM1	Di48	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
BEDM2	DIK1	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
BEDM2	DIK2	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
BEDM2	DIK4	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
BEDM2	DIK3	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
BEEG	EGE5	UG	0.00	0.00	1.00	0.00	0.00	0.00	0.87	0.08	0.04	0.01	0.00	0.00	0.95	0.01	0.03	0.01
BEEG	EGE6	UG	0.00	0.00	1.00	0.00	0.00	0.00	0.96	0.02	0.02	0.00	0.00	0.00	0.98	0.00	0.01	0.00
BEEG	EGE7	UG	0.00	0.00	1.00	0.00	0.00	0.00	0.97	0.02	0.01	0.00	0.00	0.00	0.99	0.00	0.01	0.00
BEEG	EGE8	UG	0.00	0.00	1.00	0.00	0.00	0.00	0.72	0.01	0.27	0.00	0.00	0.00	0.79	0.00	0.21	0.00
BEEG	EGE11	UG	0.00	0.00	1.00	0.00	0.00	0.00	0.02	0.03	0.00	0.95	0.00	0.00	0.03	0.01	0.00	0.97
BEEG	EGE16	UG	0.00	0.58	0.42	0.00	0.00	0.50	0.00	0.00	0.00	0.50	0.00	0.13	0.00	0.00	0.00	0.87

Pop	Sample	Species based on morphol.	BAPS all studied species				NewHybrids uniform priors						NewHybrids Jeffreys' priors					
			1	2	3	4	UM	UG	UH1	UH1 x UH1	UH1 x UM	UH1 x UG	UM	UG	UH1	UH1 x UH1	UH1 x UM	UH1 x UG
BEGE	GE2	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.01
BEGE	GE4	UG	0.00	1.00	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.01	0.00	0.96	0.00	0.00	0.00	0.04
BEGE	GE5	UG	0.62	0.38	0.00	0.00	0.00	0.00	0.86	0.03	0.10	0.00	0.00	0.00	0.88	0.01	0.12	0.00
BEGE	GE6	UG	0.49	0.45	0.06	0.00	0.00	0.00	0.92	0.06	0.01	0.01	0.00	0.00	0.98	0.01	0.01	0.01
BEGE	GE8	UG	0.00	0.00	1.00	0.00	0.00	0.00	0.01	0.00	0.99	0.00	0.00	0.00	0.00	0.00	0.99	0.00
BEGE	GE9	UG	0.25	0.73	0.02	0.00	0.00	0.00	0.04	0.02	0.00	0.95	0.00	0.00	0.02	0.00	0.00	0.97
BEGE	GE3	UH	0.57	0.00	0.43	0.00	*0.52*	*0.00*	*0.00*	*0.00*	*0.48*	*0.00*	0.23	0.00	0.00	0.00	0.77	0.00
BEGE	MO3	UG	0.13	0.53	0.34	0.00	0.00	0.00	0.21	0.01	0.00	0.78	0.00	0.00	0.22	0.00	0.00	0.77
BEHE	HEU1	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
BEHE	HEU2	UM	1.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.00	1.00	0.00
BEHO	HOU1	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
BEHO	HOU2	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
BEHO	HOU3	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
BEHO	HOU4	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
BELE	LEM1	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
BELE	LEM2	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
BELE	LEM3	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
BELE	LEM5	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
BELE	LEM4	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
BEMA	EN7	UG	0.00	0.00	1.00	0.00	0.00	0.07	0.00	0.00	0.00	0.93	0.00	0.01	0.00	0.00	0.00	0.99
BEMA	EN8	UG	0.00	0.00	1.00	0.00	0.00	0.03	0.00	0.00	0.00	0.97	0.00	0.00	0.00	0.00	0.00	1.00
BEMA	EN9	UG	0.00	0.00	1.00	0.00	0.00	0.00	0.02	0.00	0.00	0.98	0.00	0.00	0.01	0.00	0.00	0.99
BEMA	EN10	UG	0.00	0.00	1.00	0.00	0.00	0.01	0.02	0.00	0.00	0.97	0.00	0.00	0.02	0.00	0.00	0.98
BEMA	EN12	UG	0.00	0.00	1.00	0.00	0.00	0.00	0.49	0.05	0.00	0.46	0.00	0.00	0.62	0.01	0.00	0.37
BEMA	EN13	UH	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00

Pop	Sample	Species based on morphol.	BAPS all studied species				NewHybrids uniform priors						NewHybrids Jeffreys' priors					
			1	2	3	4	UM	UG	UH1	UH1 x UH1	UH1 x UM	UH1 x UG	UM	UG	UH1	UH1 x UH1	UH1 x UM	UH1 x UG
BEMA	EN14	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
BEEN	EN4	UM	1.00	0.00	0.00	0.00	0.97	0.00	0.00	0.00	0.03	0.00	0.95	0.00	0.00	0.00	0.05	0.00
BEEN	EN5	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
BEEN	EN6	UM	0.62	0.31	0.07	0.00	0.00	0.00	0.20	0.09	0.71	0.00	0.00	0.00	0.14	0.02	0.84	0.00
BEME1	MER4	UH	0.00	0.00	1.00	0.00	0.00	0.00	0.38	0.02	0.59	0.00	0.00	0.00	0.38	0.00	0.61	0.00
BEME1	MER1	UM	0.00	0.00	1.00	0.00	0.00	0.00	0.07	0.01	0.92	0.00	0.00	0.00	0.07	0.00	0.93	0.00
BEME1	MER2	UM	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.00	1.00	0.00
BEME1	MER3	UM	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
BEME1	MER5	UM	0.00	0.00	1.00	0.00	0.00	0.00	0.01	0.00	0.99	0.00	0.00	0.00	0.00	0.00	1.00	0.00
BEME1	MER6	UM	0.00	0.00	1.00	0.00	0.00	0.00	0.03	0.01	0.96	0.00	0.00	0.00	0.01	0.00	0.98	0.00
BEME2	MER7	UH	0.30	0.00	0.70	0.00	0.00	0.00	0.12	0.01	0.88	0.00	0.00	0.00	0.13	0.00	0.87	0.00
BEME2	MER8	UH	0.00	0.00	1.00	0.00	0.00	0.00	0.98	0.01	0.00	0.01	0.00	0.00	0.99	0.00	0.00	0.00
BEME2	MER9	UH	0.00	0.00	1.00	0.00	0.00	0.00	0.44	0.01	0.55	0.00	0.00	0.00	0.51	0.00	0.49	0.00
BEOO	OOS1	UM	0.67	0.00	0.33	0.00	0.45	0.00	0.00	0.00	0.55	0.00	0.14	0.00	0.00	0.00	0.86	0.00
BERI	RIE6	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
BERI	RIE9	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
BERI	RIE10	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
BERI	RIE13	UG	0.00	1.00	0.00	0.00	0.00	0.63	0.00	0.00	0.00	0.37	*0.00*	*0.15*	*0.00*	*0.00*	*0.00*	*0.85*
BERI	RIE18	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
BERI	RIE20	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
BERI	RIE23	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
BERI	RIE25	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
BERI	RIE26	UG	0.00	1.00	0.00	0.00	0.00	0.92	0.00	0.00	0.00	0.08	0.00	0.65	0.00	0.00	0.00	0.35
BERI	RIE27	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
BERI	RIE28	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00

Pop	Sample	Species based on morphol.	BAPS all studied species				NewHybrids uniform priors						NewHybrids Jeffreys' priors					
			1	2	3	4	UM	UG	UH1	UH1 x UH1	UH1 x UM	UH1 x UG	UM	UG	UH1	UH1 x UH1	UH1 x UM	UH1 x UG
BERI	RIE30	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
BERI	RIE31	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
BERI	RIE34	UM	0.00	0.00	1.00	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
BERI	RIE35	UM	0.00	0.00	1.00	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
BERI	RIE37	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
BERI	RIE38	UG	0.00	1.00	0.00	0.00	0.00	0.97	0.00	0.00	0.00	0.03	0.00	0.71	0.00	0.00	0.00	0.29
BERI	RIE41	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
BERI	RIE5	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
BERI	RIE8	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
BERI	RIE11	UG	0.01	0.65	0.34	0.00	0.00	0.02	0.00	0.00	0.00	0.98	0.00	0.00	0.00	0.00	0.00	1.00
BERI	RIE12	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
BERI	RIE14	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
BERI	RIE15	UG	0.00	0.68	0.32	0.00	0.00	0.40	0.00	0.00	0.00	0.60	0.00	0.05	0.00	0.00	0.00	0.95
BERI	RIE17	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
BERI	RIE19	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
BERI	RIE24	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
BERI	RIE32	UG	0.00	0.00	1.00	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
BERI	RIE33	UG	0.00	0.00	1.00	0.00	0.00	0.00	0.99	0.00	0.01	0.00	0.00	0.00	1.00	0.00	0.00	0.00
BERI	RIE39	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
BERI	RIE1	UH	0.00	0.00	1.00	0.00	0.00	0.00	0.53	0.06	0.41	0.00	0.00	0.00	0.50	0.01	0.49	0.00
BERI	RIE2	UH	0.00	0.00	1.00	0.00	0.00	0.00	0.56	0.06	0.38	0.00	0.00	0.00	0.55	0.01	0.44	0.00
BERI	RIE3	UH	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
BERI	RIE36	UH	0.00	0.70	0.30	0.00	0.00	0.67	0.00	0.00	0.00	0.33	*0.00*	*0.20*	*0.00*	*0.00*	*0.00*	*0.80*
BERI	RIE22	UM	0.42	0.58	0.00	0.00	0.00	0.00	0.94	0.05	0.00	0.01	0.00	0.00	0.98	0.01	0.00	0.01
BERI	RIE4*	UM	*0.00*	*1.00*	*0.00*	*0.00*	0.00	0.29	0.00	0.00	0.00	0.71	0.00	0.04	0.00	0.00	0.00	0.96

Pop	Sample	Species based on morphol.	BAPS all studied species				NewHybrids uniform priors						NewHybrids Jeffreys' priors					
			1	2	3	4	UM	UG	UH1	UH1 x UH1	UH1 x UM	UH1 x UG	UM	UG	UH1	UH1 x UH1	UH1 x UM	UH1 x UG
BESC	SCH1	UG	0.00	0.00	1.00	0.00	0.00	0.04	0.00	0.00	0.00	0.96	0.00	0.00	0.00	0.00	0.00	1.00
BESC	SCH2	UG	0.00	0.00	1.00	0.00	0.00	0.01	0.01	0.00	0.00	0.98	0.00	0.00	0.01	0.00	0.00	0.99
BESC	SCH3	UG	0.00	0.00	1.00	0.00	0.00	0.05	0.00	0.00	0.00	0.95	0.00	0.00	0.00	0.00	0.00	1.00
BESC	SCH4	UG	0.00	0.00	1.00	0.00	0.00	0.01	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.00	1.00
BESC	SCH6	UH	0.00	0.00	1.00	0.00	0.00	0.00	0.99	0.00	0.00	0.01	0.00	0.00	1.00	0.00	0.00	0.00
BESC	SCH7	UH	0.00	0.00	1.00	0.00	0.00	0.00	0.98	0.01	0.00	0.02	0.00	0.00	0.99	0.00	0.00	0.01
BESC	SCH5	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
BESP	SPK Philipskouter 684/1306	NA	0.65	0.01	0.34	0.00	0.01	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.00	1.00	0.00
BESP	SPK Philipskouter 683/1304	NA	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
BETO	IBW050	UG	0.00	1.00	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.01	0.00	0.98	0.00	0.00	0.00	0.02
cultivar	Klemmer	UH	0.00	0.00	1.00	0.00	0.00	0.00	0.02	0.00	0.98	0.00	0.00	0.00	0.02	0.00	0.98	0.00
cultivar	Groeneveld	UH	0.79	0.17	0.04	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
cultivar	Commelin	UH	*1.00*	*0.00*	*0.00*	*0.00*	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
cultivar	Buisman	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
cultivar	Vegeta	UH	0.67	0.33	0.00	0.00	0.00	0.00	0.01	0.23	0.76	0.00	0.00	0.00	0.01	0.05	0.94	0.00
cultivar	Major	UH	1.00	0.00	0.00	0.00	0.95	0.00	0.00	0.00	0.05	0.00	0.77	0.00	0.00	0.00	0.23	0.00
cultivar	Belgica	UH	0.00	0.00	1.00	0.00	0.00	0.00	0.99	0.00	0.00	0.01	0.00	0.00	1.00	0.00	0.00	0.00
cultivar	Dampieri	UH	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
cultivar	Sarniensis	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
FRAM	CEM275	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
FRAR	CEM052	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00

Pop	Sample	Species based on morphol.	BAPS all studied species				NewHybrids uniform priors						NewHybrids Jeffreys' priors					
			1	2	3	4	UM	UG	UH1	UH1 x UH1	UH1 x UM	UH1 x UG	UM	UG	UH1	UH1 x UH1	UH1 x UM	UH1 x UG
FRAU	Aunay 14260	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
FRAU	Aunay 14260	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
FRBL	Blismes	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
FRCB	TUS027	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
FRCB	TUS028	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
FRCB	TUS029	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
FRCM	CEM140	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
FRCU	CEM280	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
FRGO	CEM328	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
FRGS	CEM330	UM	*1.00*	*0.00*	*0.00*	*0.00*	0.47	0.00	0.00	0.00	0.53	0.00	0.28	0.00	0.00	0.00	0.72	0.00
FRIL	CEM190	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
FRLR	TUS008	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
FRLR	TUS009	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
FRLV	Le Vey Q	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
FRLV	Le Vey N	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
FRLV	Le Vey J	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
FRLV	Le Vey U	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
FRLV	Le Vey R	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
FRLW	CEM186	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
FRMA	CEM276	UM	1.00	0.00	0.00	0.00	0.95	0.00	0.00	0.00	0.05	0.00	0.94	0.00	0.00	0.00	0.06	0.00
FRME	CEM386	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
FRME	CEM340	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
FRMQ	CEM339	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
FROS	CEM196	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
FRSP	Saint-Pé11	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00

Pop	Sample	Species based on morphol.	BAPS all studied species				NewHybrids uniform priors						NewHybrids Jeffreys' priors					
			1	2	3	4	UM	UG	UH1	UH1 x UH1	UH1 x UM	UH1 x UG	UM	UG	UH1	UH1 x UH1	UH1 x UM	UH1 x UG
FRSP	Saint-Pé18	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
FRST	CEM188	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.01	0.00
GEGO1	NFV037	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
GEGO1	NFV038	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
GEGO2	NFV010	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
GELD	NFV028	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
GELD	NFV029	UM	1.00	0.00	0.00	0.00	0.47	0.00	0.00	0.00	0.53	0.00	0.33	0.00	0.00	0.00	0.67	0.00
GELD	NFV030	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
GRIR	FRI956	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
GRTH	FRI943	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
ITBO	CNR055	UG	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
ITCA	CNR218	UM	1.00	0.00	0.00	0.00	0.98	0.00	0.00	0.00	0.02	0.00	0.95	0.00	0.00	0.00	0.05	0.00
ITFV	CNR094	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
ITLA	CNR170	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
ITMO	CNR088	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
ITNI	CNR100	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
ITSE	CNR091	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
ITTA	CNR093	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
ITTA	CNR089	UM	1.00	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.01	0.00	0.99	0.00	0.00	0.00	0.01	0.00
ITTR	CNR099	UM	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
NA	Horizontalis	UG	0.00	1.00	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.01	0.00	0.98	0.00	0.00	0.00	0.02
NEBU	*U. minor* 'cornubiensis'	UM	0.00	0.31	0.69	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00
cultivar	Clusius	(UG x UW) x UM or UH	0.65	0.30	0.03	0.02												

Pop	Sample	Species based on morphol.	BAPS all studied species				NewHybrids uniform priors						NewHybrids Jeffreys' priors					
			1	2	3	4	UM	UG	UH1	UH1 x UH1	UH1 x UM	UH1 x UG	UM	UG	UH1	UH1 x UH1	UH1 x UM	UH1 x UG
cultivar	Dodoens	UG x UW	0.28	0.72	0.00	0.00												
cultivar	Lobel	(UG x UW) x UM or UH	0.55	0.45	0.00	0.00												
cultivar	Plantyn	(UG x UW) x UM	0.30	0.70	0.00	0.00												
cultivar	Columella	(UG x UW) x UM	0.73	0.22	0.02	0.03												
cultivar	2P	UJ	0.00	0.00	0.00	1.00												
cultivar	Sapporo	UPM x UJ	0.00	0.00	0.00	1.00												
cultivar	73P	UPM x ?	0.00	0.00	0.00	1.00												
cultivar	Den Haag	UPM x UH	0.14	0.00	0.65	0.21												
FRBB	CEM350	UM x UPM?	1.00	0.00	0.00	0.00												
GEKA	Kallstadt	UP	1.00	0.00	0.00	0.00												
ITBC	CNR212	UM x UPM	0.38	0.00	0.01	0.61												
ITCV	CNR181	UPM	0.00	0.00	0.00	1.00												
ITRO	CNR069	UPM	1.00	0.00	0.00	0.00												
SPMA	UPM111	UPM	0.80	0.00	0.00	0.20												

*: results for RIE4 changed when using BAPS on the samples of the *U. minor-U. glabra* complex. Here, the admixture coefficients were 0, 0.70 and 0.30 for the thee clusters, respectively

Table D: List of samples of the same genet according to a Dice similarity of 0.96 or 0.95. Samples sharing the same character belong to the same genet. Characters in bold are present in multiple populations. Species A: species determination based on morphology; Species B: species determination based on NewHybrids results. UM: *Ulmus minor*; UG: *U. glabra*; UH: *U.* x *hollandica* (F1 hybrid under Species B); UHxUM: backcross with *U. minor*; UHxUG: backcross with *U. glabra*.

Pop	Sample	Species A	Dice similarity		Species B
			0.96	0.95	
BEBR	BG1	UM	A	A	UM
	BG2	UM	A	A	UM
	BG3	UM	B	B	UM
	BG5	UM	B	B	UM
	BG6	UM	C	C	UM
	BG7	UM	C	C	UM
	BG8	UM	C	C	UM
BEDI	DIL1	UG	**D**	**D**	UH
BEDM1	Di46	UM	E	E	UM
	Di48	UM	E	E	UM
BEDM2	DIK1	UM	F	**F**	UM
	DIK2	UM	G	**F**	UM
	DIK4	UM	H	**F**	UM
BEEG	EGE6	UG	**I**	**G**	UH
	EGE7	UG	J	**G**	UH
	EGE8	UG	**I**	**G**	UH
BEGE	GE5	UG	K	H	UH
	GE6	UG	L	H	UH
	GE8	UG	**M**	**I**	UHxUM
BEHO	HOU1	UM	N	**F**	UM
	HOU2	UM	N	**F**	UM
	HOU3	UM	N	**F**	UM
BELE	Lem1	UM	P	K	UM
	Lem2	UM	P	K	UM
	Lem3	UM	P	K	UM
	Lem5	UM	P	K	UM
	LEM4	UM	P	K	UM
BEMA	EN7	UG	Q	**L**	UHxUG
	EN8	UG	**R**	**L**	UHxUG
	EN9	UG	**R**	**L**	UHxUG
	EN10	UG	**R**	**L**	UHxUG
	EN13	UH	S	M	UM
	EN14	UM	S	M	UM
BEME1	MER1	UM	**M**	**I**	UHxUM
	MER3	UM	**M**	**I**	UHxUM
	MER4	UH	**M**	**I**	UHxUM
	MER5	UM	T	**I**	UHxUM

Pop	Sample	Species A	Dice similarity		Species B
			0.96	0.95	
	MER6	UM	**M**	**I**	UHxUM
BEME2	MER7	UH	U	N	UH
	MER8	UH	**D**	**D**	UH
	MER9	UH	U	N	UH
BERI	RIE1	UH	Z	S	UH
	RIE2	UH	Z	S	UH
	RIE3	UH	W	P	UG
	Rie9	UG	V	O	UG
	Rie10	UG	V	O	UG
	Rie23	UG	W	P	UG
	RIE32	UG	**I**	**G**	UH
	RIE33	UG	**I**	**G**	UH
	Rie34	UM	**I**	**G**	UH
	RIE35	UM	**I**	**G**	UH
BESC	SCH1	UG	**R**	**L**	UHxUG
	SCH2	UG	**R**	**L**	UHxUG
	SCH3	UG	**R**	**L**	UHxUG
	SCH4	UG	AA	**L**	UHxUG
	SCH6	UH	**D**	**D**	UH
	SCH7	UH	**D**	**D**	UH
FRAU	14260A	UM	**AB**	**T**	UM
	14260B	UM	**AB**	**T**	UM
FRCB	TUS028	UM	AC	U	UM
	TUS029	UM	AC	U	UM
FRLR	TUS008	UM	AD	V	UM
	TUS009	UM	AD	V	UM
FRLV	LeVeyN	UM	**AB**	**T**	UM
	LeVeyJ	UM	**AB**	**T**	UM
	LeVeyU	UM	**AB**	**T**	UM
	LeVeyR	UM	**AB**	**T**	UM
Cv	Klemmer	UH	**M**	**I**	UHxUM
	Lobel1		AE	W	
	LobelB4		AF	W	
	Lobel		AF	W	
	plantyn		AG	X	
	Plantijn		AG	X	

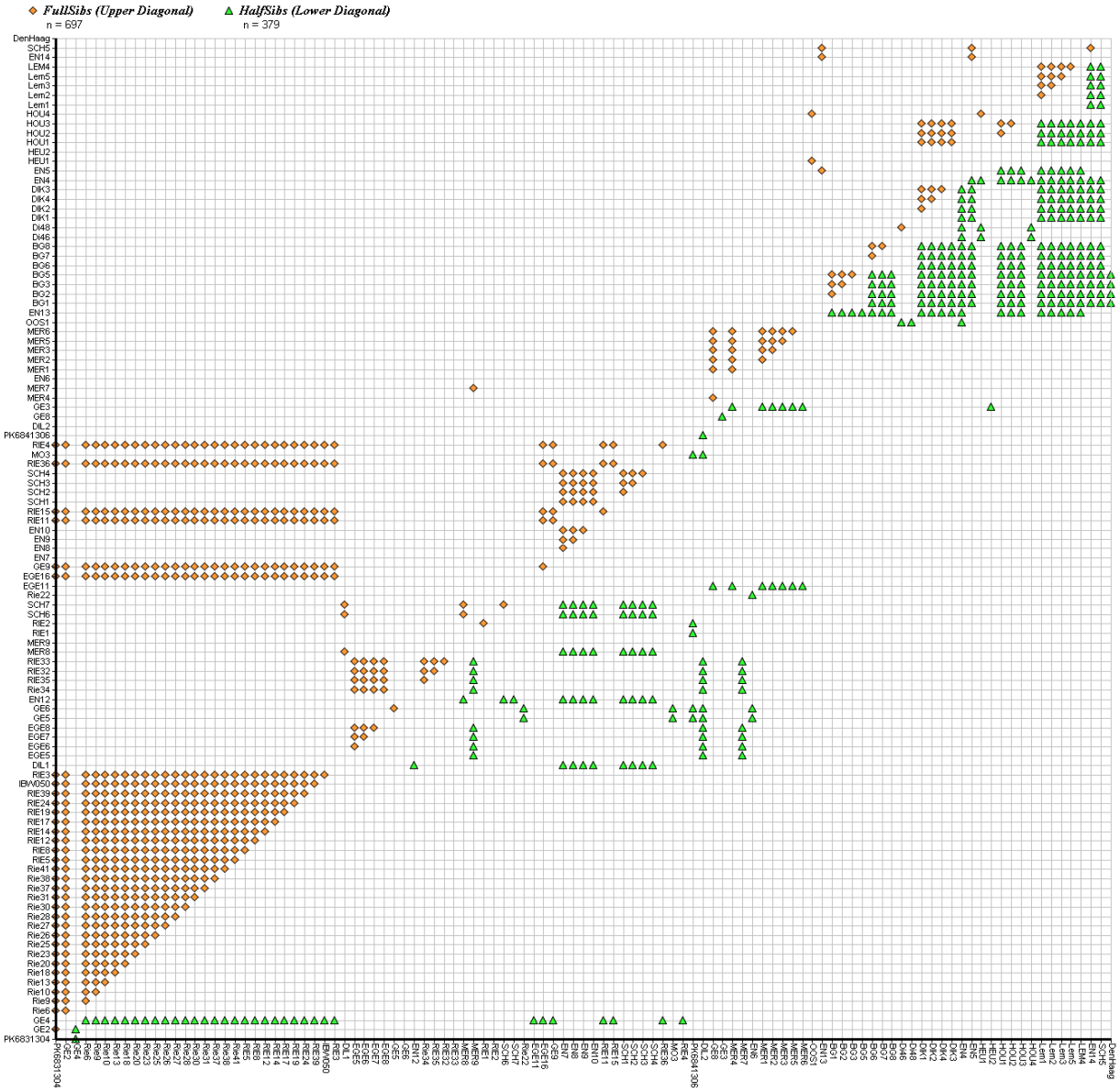

Fig. A: Best Maximum Likelihood Sibship Assignment plot of the sibship structure for the samples of *U. minor-U. glabra* and cultivar 'Den Haag', obtained with Colony v2.0.1.9.