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The contribution made by molecular biology to our knowledge of the ecology and silviculture of wild service trees (*Sorbus torminalis* (L.) Crantz)

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Abstract: In European forestry, there is an increased need for a reliable inventory of genetic resources and the use of less traditional tree species is on the rise. An example of this is the wild service tree (*Sorbus torminalis* (L.) Crantz). This review covers the scientific literature that deals with the genetics of the wild service tree, with a specific focus on the contribution made by molecular biology and how they translate to our current knowledge of its biology and future practical needs for silviculture. The highest number of papers on molecular biology were found in France, Poland, Germany and the United Kingdom, with the highest number of publications released in the decade from 2000 to 2010. In phylogenetics, the DNA sequences studied are traditionally limited to plastomes and nuclear ribosomal spacers. When it comes to population diversity studies, microsatellite markers dominate. Research efforts that rely on molecular biology made a significant contribution to the knowledge, preservation and cultivation of the wild service tree. Prior genetic knowledge of the species can be a useful tool for later management and conservation of genetic resources. However, there is still a significant gap between the theory and practice that needs to be closed. Furthermore, nurseries and breeding programs may need to make better informed decisions in the future, which may require the mapping of more sequences of the genome of wild service trees and the development of new DNA markers related to specific traits, which are not currently available.

Keywords: history, geographical distribution, molecular methodologies, practical implications, breeding


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Introduction

S. torminalis is a slow-growing deciduous tree that produces high-quality timber (CABI Compendium, 2019). It is typically found in Central and Southern Europe at altitudes of up to 1000 m in mixed forests (typically with *Fagus sylvatica* and *Quercus* spp.), but can also be found in North Africa, Asia Minor, and the Caucasus and Crimean regions (CABI Compendium, 2019). The wild service tree is distributed (Fig. 1) across Western, Central and Southern Europe, Northwest Africa and Southwest Asia (Maděra et al., 2013; Kurtto et al., 2018).

The wild service tree (*Sorbus torminalis* (L.) Crantz) is a minor scattered species among the broadleaf deciduous trees of Europe and has a role in the stabilization and enrichment of forest and woodland ecosystems. The wild service tree is an accompanying woody plant of forest communities where oak species dominate and there is a high degree of biodiversity (Szymura et al., 2014). The wild service tree is considered to be a tree that might increase biodiversity, supporting other species, for example 88 species of pollinators were counted on its flowers (Werres & Blanke, 2019).

Many authors mention the wild service tree as a prospective woody plant suitable for global climate change (Walentowski et al., 2017; Albrecht & de Avila, 2018; Šeho et al., 2018; Koch et al., 2022; Affi et al., 2023) as it is very drought tolerant (Thomas, 2017; Sułkowska & Mohytych, 2024) and resistant to other environmental stresses such as high temperatures (Paganová, 2007; Maděra et al., 2013).

Coppicing or coppice with standards are considered to be the main management practices that are advantageous for wild service tree growth. Unfortunately, today these forestry techniques have almost been forgotten (Maděra et al., 2017; Slach et al., 2021), which has led to a decline in the occurrence of wild service trees in forest stands, especially at the limits of species distribution (Bednorz et al., 2015; Jankowska-Wroblewska et al., 2016a).

Knowledge of the genetic variation and population structure of forest trees is essential when establishing programs aimed at the preservation of biodiversity and to ensure the security of populations with a high adaptive potential (Belletti et al., 2008). The proper characterization of the biological material that makes up a wild service tree is fundamental to its cultivation, with its genetic information being the major



Fig. 1. The natural range of *Sorbus torminalis* covers two Northwest African countries (Morocco, Algeria), six in Southeast Asia (Turkey, Syria, Iran, Georgia, Armenia, Azerbaijan) and 28 European countries (UK, Portugal, Spain, Germany, Switzerland, France, Italy, Monaco, Austria, Slovenia, Croatia, Bosnia and Herzegovina, Montenegro, Serbia, Albania, Greece, North Macedonia, Bulgaria, Romania, Moldova, Russia, Hungary, Slovakia, Czechia, Ukraine, Poland, Denmark and Belgium).

Source: Demesure-Musch and Oddou-Muratorio (2004).

building block. In the last few decades, rapidly evolving techniques within molecular biology have made significant progress in building the genetic picture of *Sorbus torminalis* and this is likely to be an ongoing process. This review brings together the current state of knowledge and considers future possibilities.

History and geographical distribution of research

The taxon was first described by Carl Linnaeus in 1753 as *Crataegus torminalis* L. In 1763, the taxon was transferred into a new genus, *Sorbus*, by Crantz (1763), as *Sorbus torminalis* (L.) Crantz. According to Govaerts et al. (2021) who accepted the opinion of Sennikov and Kurtto (2017) the current valid name of the taxon is a new combination, *Torminalis glaberrima* (Gand.) Sennikov and Kurtto and *Sorbus torminalis* (L.) Crantz is a synonym. In contrast, Rich et al. (2022) consider *Sorbus torminalis* (L.) Crantz to be valid and *Torminalis glaberrima* is mentioned as a synonym.

Since the time of its first description, the wild service tree has been subject to in-depth research. In the Web of Science (WoS) database, using the simple keyword search, *Sorbus torminalis* (accessed on 5th September 2024), 176 results were found, mostly from the past two decades. It is clear that the level of scientific interest in the wild service tree has accelerated since the '90s (Table 1).

This increase in interest has been linked to the development of new research technologies, especially in molecular biology, and to heightened environmental awareness related to scattered broadleaf tree species in Europe (Nicolescu et al., 2009; Hemery et al., 2010; Albrecht & de Avila, 2018; Afifi et al., 2023). Until 2010, papers on molecular biology were mostly responsible for the boom in scientific papers on *Sorbus torminalis* (Fig. 2). Since 2010, growth in the number of papers on different topics is visible (Fig. 2).

Ignoring genetics, the highest proportion (28.7%) of papers deal with its distribution in individual countries and the ecology and silviculture of communities with *Sorbus torminalis* (including global climate change). The second most common topic is genetic variability and the structure of populations (15.0%). A similar number of articles is devoted to hybridisation of the *Sorbus* genera (11.8%) and the biochemical composition and bioactivity of secondary

metabolites in *Sorbus torminalis* (12.4%). Other topics that include subjects such as pollen grain, seed and leaf morphology (7.8%), gene source conservation including micropropagation (6.5%), taxonomy and phylogeny (5.9%), wood anatomy (5.2%), seed stratification and germination (5.2%) and paleobotany (1.3%) are less common (Fig. 3).

The first genetic study was carried out in south-west England and looked at the genetic variability of populations through isoenzymes, it was published as early as 1989 (Proctor et al., 1989). In total, we found 63 papers that mentioned *Sorbus torminalis* as the subject of genetic research. The highest number of papers were published between 2005 and 2014 (Table 2).

It is interesting to see where the genetic research on *Sorbus torminalis* was conducted. The commonest location is France, followed by Poland, Germany and

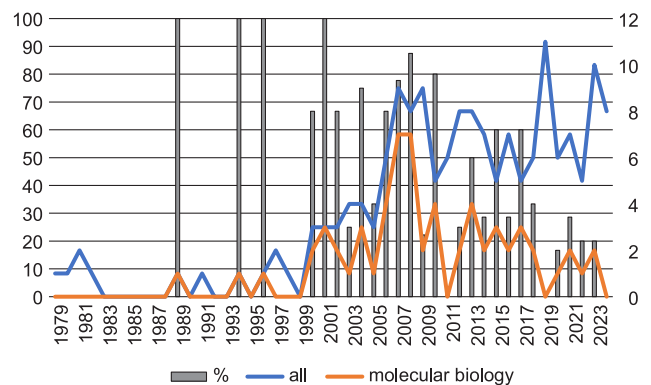


Fig. 2. Number (X axis) and proportion (Y axis in %) of all papers on *Sorbus torminalis* and molecular biology papers related to *Sorbus torminalis*

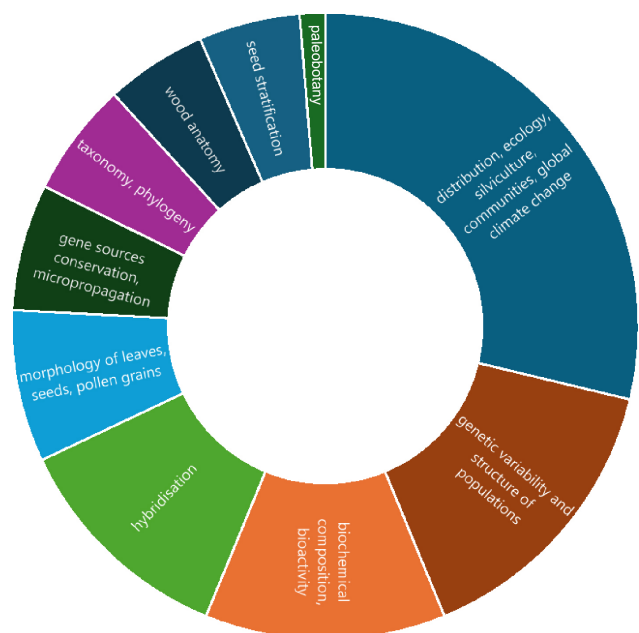


Fig. 3. Frequency of research topics that involve *Sorbus torminalis*

Table 1. Number of papers published on *S. torminalis* found in the WoS database (accessed on 5th September 2024)

Period	1975–1984	1985–1994	1995–2004	2005–2014	2015–2024
No. of articles	6	3	21	74	72

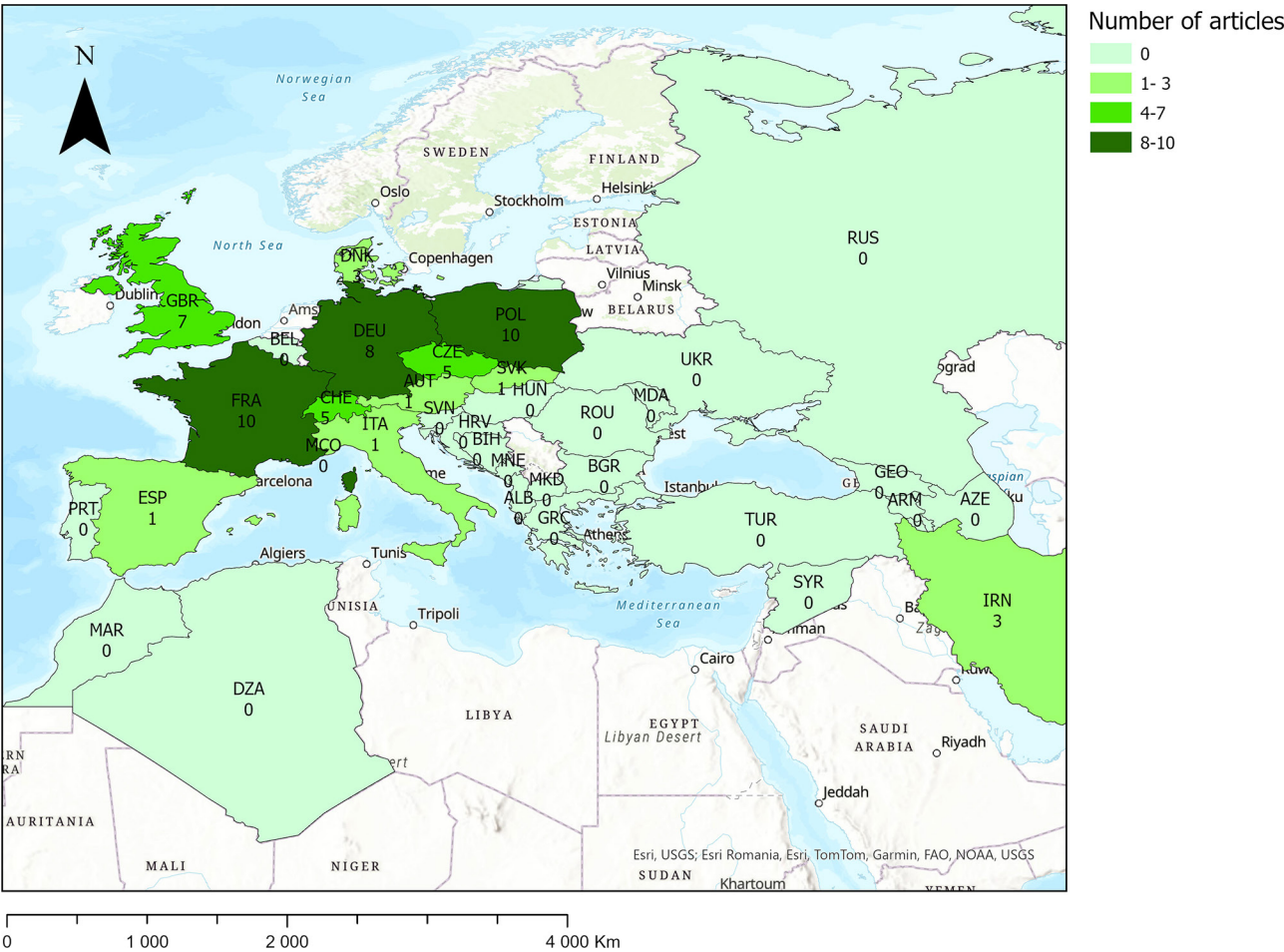


Fig. 4. Number of genetic studies (source: WoS) on *Sorbus torminalis* by country. The green areas are countries where *Sorbus torminalis* naturally occurs

Table 2. Number of molecular biology papers published related to *Sorbus torminalis* (according to the WoS database, accessed on 5th September 2024)

Period	1975–1984	1985–1994	1995–2004	2005–2014	2015–2024
No. of articles	0	2	12	33	16

the United Kingdom (Fig. 4). It is clearly visible in Fig. 4, that genetic research into *Sorbus torminalis* is mostly restricted to the countries of north west Europe with the exception of Iran. This could be due to the natural occurrence of the species at its north-western limit of distribution, local conservation and forestry policies, or funding for research in different countries.

Research relying on molecular biology methodologies

Research into the *Sorbus* genus through molecular biology initially developed in two major areas: i) taxonomical and phylogenetic studies; and ii) studies of genetic diversity and populations.

Taxonomical and phylogenetic studies

The early taxonomical studies relied upon morphological characteristics (Kovanda, 1996), supported by cytogenetic analysis, i.e. counting chromosomes and DAPI (4',6-diamidino-2-phenylindole) flow cytometry (Lepší et al., 2008; 2009; Vít et al., 2012). The main goal of these works was the revision of apomictic triploid whitebeams and a description of several new independent species. In addition to these whitebeam triploids, Hamston et al. (2015) recorded the first triploid *Sorbus torminalis* in Britain. Apart from the triploid representatives of the *Sorbus* genus, Bailey et al. (2008) also recorded the occurrence of diploids ($2n=34$) and tetraploids ($2n=68$) in the British Isles. Later, this was also reported in the Balkans (Siljak-Yakovlev et al., 2010). Pellicer et al. (2012) and Meyer et al. (2014) analysed ploidy levels and interspecific hybridization possibilities within more than 50 taxa (both recognized and hypothesized) from the *Sorbus* genus. On a DNA sequence level, the work of Li et al. (2012) was focused on the analysis of an ITS (*Internal Transcribed Spacer*) region of rDNA in 24 genera of the *Pyrinae* subtribe,

including 21 species of *Sorbus*, and found this group to be monophyletic within the *Maloideae* subfamily. Similarly, Dłużewska et al. (2013) verified the taxonomic status of the *Sorbus* population in the Pieniny Mts. through the use of ITS sequences. Following this, work shifted to a detailed study of plastid DNA. The parentage of 30 polyploid species of *Sorbus* in the British Isles was investigated using plastid DNA microsatellites by Chester et al. (2007). Ulaszewski et al. (2017) provide a detailed description of the whole *Sorbus torminalis* plastid genome and also a comparison with the plastid genomes of other *Maloideae* subfamily members. The highest degree of genetic similarity was found for *Malus prunifolia* and members of the *Pyrus* genus. Further work by Ulaszewski et al. (2021) involved a complete analysis of the plastid genome of several new genera within *Sorbus* L. (*Sorbus aucuparia*, *Aria edulis*, *Chamaemespilus alpina* and *Torminalis glaberrima*). This also included the construction of a phylogenetic tree with an additional 110 *Malae* family members. These results implied the validity of the proposal for the independent genera *Aria*, *Chamaemespilus* and *Torminalis*. Other work that deals with complete plastid genome analysis is Tang et al. (2022) who focused on members of *Sorbus* sensu stricto (*Sorbus* s.s.) with the aim of distinguishing and delineating those members of this group that are challenging to classify by morphological traits alone. This work compared a total of 29 plastid genomes which included 16 that were newly sequenced. *Sorbus* s.s. and other five genera were separated from the *Sorbus* sensu lato genus (*Sorbus* s.l.); *Aria*, *Chamaemespilus*, *Cormus*, *Miromeles* and *Torminalis*. There is strong support for these to be classified as monophyletic, while the *Sorbus* s.l. genus is confirmed to be polyphyletic. Although the existence of the separate genus *Torminalis* is so far supported by phylogenies based on the available DNA sequence data, this classification still does not seem to be widely accepted in classical taxonomy, where the original classification under the *Sorbus* genus is still prevalent (Sennikov & Kurtto, 2017; Rich et al., 2022). A clear classification of some whitebeams and wild service tree individuals, especially putative hybrids, can sometimes still be challenging due to cases of apomixis and polyploidy (Robertson et al., 2010; Leinemann et al., 2010; 2013; Németh et al., 2020). Furthermore, statistical inconsistencies found in a comparison between the genetic data and morphology are sometimes reported (Feulner et al., 2023). Due to the lack of a universal DNA barcode for plants, the definitive taxonomic picture of whitebeams, service trees and rowans is still to be resolved. By far the most common DNA sequences currently relied upon in whitebeam and service tree phylogenetic studies are nuclear ribosomal ITS and partial or entire plastid DNA, with drawbacks such as paralogs and amplification challenges in the former,

and the lower evolutionary rate and resolution in the latter. That is why some phylogenetic studies of *Sorbus* complex have tried an approach that combines the nuclear and plastid datasets. The advent of recent techniques such as genome skimming may help to further resolve the phylogenetic relationships in the *Sorbus* complex (Qiu et al., 2019; Meng et al., 2021). Nevertheless, based on the available molecular data, the existence of a separate genus, *Torminalis*, currently appears to be justified. Outside of phylogenetic studies, the future benefits of sequencing these DNA regions and knowledge of their intra-population and inter-population variability will probably be greatest in studies aimed at studying the origin and identification of valuable genotypes and their possible spread (or hybridization) in the context of climate change, when individuals are exposed to various biotic and abiotic stresses.

Studies into genetic diversity and populations

To study the genetic diversity and population structure of the *Sorbus* genus, the first studies used protein markers (Proctor et al., 1989; Aas et al., 1994). These included isoenzymes in particular, where Demesure et al. (2000) tested the following single- and double-locus systems: AAP, E.C. 3.4.11.1 (alanine aminopeptidase, one locus: *AAP-1*), ACP, E.C. 3.1.3.2 (acid phosphatase, one locus: *ACP-1*), ADH, E.C. 1.1.1.1 (alcohol dehydrogenase, one locus: *ADH-1*), GOT, E.C. 2.6.1.1 (glutamate oxaloacetate transaminase, one locus: *GOT-2*), 6PGD, E.C. 1.1.1.44 (6-phosphogluconate dehydrogenase, one locus: *6PGD-1*), SKDH, E.C. 1.1.1.25 (shikimate dehydrogenase, one locus: *SKDH-1*), ME, E.C. 1.1.1.40 (malic enzyme, one locus: *ME-1*), IDH, E.C. 1.1.1.42 (isocitrate dehydrogenase, two loci: *IDH-1*, *IDH-2*), PRX, E.C. 1.11.1.7 (peroxidase, two loci: *PRX-1*, *PRX-2*), MR, E.C. 1.6.99.2 (menadione reductase, two loci: *MR-1*, *MR-2*) and PGM, E.C. 5.4.2.2 (phosphoglucosmutase, two loci: *PGM-1*, *PGM2*). Their aim was to compare and distinguish between Slovak, Slovenian, Bulgarian and Swiss populations of *Sorbus torminalis*. The coefficient of differentiation (F_{ST}) was between 0.10 and 0.32 for French populations, which was higher than that found in Eastern European populations (0.08). At the same time, they recommend the use of three loci (*ADH*, *6-PDH*, and *IDH-1*). Bednorz and Krzakowa (2002) tested one locus of the PGI (phosphoglucose isomerase) enzyme system in eight Polish populations of *Sorbus torminalis*, while also providing sufficient polymorphism to distinguish populations. Bednorz et al. (2004) investigated 16 isozyme loci to characterise the *S. torminalis* population in the Bytyń Forest (Poland).

Seven loci (*ADH-A*, *6PGD-A*, *GDH-B*, *ME-A*, *SOD-A*, *PGM-A*, *PGM-B*) proved to be polymorphic, whereas the other nine loci (*SDH-A*, *SDH-B*, *DIA-C*, *DIA-D*, *FLE-A*, *FLE-B*, *GOT-B*, *IDH-A*, *IDH-B*) were monomorphic. Bednorz et al. (2006) used 25 isoenzymes to describe the genetic variability of *Sorbus torminalis* populations in Poland. The coefficient of differentiation was relatively high ($F_{ST}=0.17$) and a unique genetic structure (clonal population) was described for the 'Brekenia' population. Consequently Bednorz (2007) and Bednorz et al. (2015), successfully used six enzymatic systems MDH (malate dehydrogenase, E.C. 1.1.1.37), ME, 6PGD, ADH, PGM-1 and PGM-2 to describe the genetic diversity of Polish populations, resulting in a better understanding of the genetic diversity of parental trees and their offspring. The estimate of F_{ST} (0.058) was statistically significant, indicating differentiation between the groups compared. ME and ADH were evaluated and found to be less suitable systems (Bednorz et al., 2015). However, enzymatic systems are translation products and are therefore subject to external influence from the environment or ontogenetic stage, which can be a substantial limitation in practical purposes. In this regard, genomic DNA markers that are not influenced by the environment seem to be much more promising.

The first DNA analyses of the *Sorbus* genus were made using RFLP (Restriction Fragment Length Polymorphism) to evaluate hybridization between species (Nelson-Jones et al., 2002) and RAPD (Random Amplified Polymorphic DNA) to evaluate the genetic diversity of populations in China (Liu et al., 2003). It is clear from the following text that these methodological principles are still used and are suitably supplemented by SSR (Simple Sequence Repeats) markers.

Silfverberg-Dilworth et al. (2006) tested the utility and extrapolation of *Malus* SSR markers from the Apple SSR database (<http://www.hidras.unimi.it>) when applied to the *Maloideae* (*Amygdaloideae*) subfamily, including *Sorbus torminalis*, and found the success rate was only 41 %. Meanwhile Oddou-Muratorio et al. (2001a) described and characterized nine microsatellite markers, from which the six best markers yielded an average of 10.7 alleles per locus and thus made it possible to identify individual *Sorbus* species.

However, thanks to the co-dominant heredity pattern it was also possible to identify hybrids among these species. It can be stated, that within the individual studies dedicated to the *Sorbus* genus, approximately 30 SSR markers have been used to date and the most frequently employed are MSS1, MSS5, MMS6, MMS9, MSS13, and MSS 16, Oddou-Muratorio et al. (2001a) (Table 3). The frequency of use of individual SSR markers depends on the time of publication and the authors of the study. However, in most cases, there is an obvious trend that the most commonly used SSR markers are those that provide the highest degree of variability and thus are the most suitable for practical use. Thanks to SSR markers, it has been possible to successfully characterize chosen populations of *Sorbus torminalis* in Europe (Kučerová et al., 2010; George et al., 2015; Jankowska-Wroblewska et al., 2016a, 2016b; Hamston et al., 2018) and some related species, such as *S. domestica*, in Switzerland (Kamm et al., 2009). Kučerová et al. (2010) described a relatively high level of variability within the analysed populations ($F_{ST}=0.228$) in contrast to Jankowska-Wroblewska et al. (2016a), who stated an F_{ST} of 0.048. This low value is realistic and justified by the clonal structure of populations. Hamston et al. (2018) attributes the lower degree of variability in his study to apomixis in *Sorbus* taxa. Kamm et al. (2009) sees a possible application of SSRs for monitoring seed dispersal. Aside from the above, SSR markers can also be used in the analysis of genetic drift, gene flow or inbreeding studies (Oddou-Muratorio et al., 2004, 2005, 2006; Hoebee et al., 2007; Oddou-Muratorio and Klein, 2008; Klein et al., 2008; Kamm et al., 2009).

In addition to SSR markers, another DNA polymorphism analysis method, based on repetitive sequence variability detection, more specifically ISSR (Inter Simple Sequence Repeat), was used for *Sorbus*. Angelone et al. (2007) used this method to successfully characterize and identify local Swiss populations of *Sorbus torminalis*. They found that molecular variability within populations was not determined by size but by habitat quality (openness), where it had a positive effect on the percentage of fruiting trees and the degree of fecundity per tree, suggesting that more open forests increase sexual reproduction.

Table 3. Summary and frequency of the use of SSR markers in *Sorbus* genus studies (21 in total according to the WoS database)

SSR marker name	Frequency of use in publications	SSR marker name	Frequency of use in publications
MSS5	17	CH02c09 a CH01h01	4
MSS16	16	CH01h01 a Ms6g	3
MSS1	13	BGT23b, CH02D11, CH02d08, Ms14h03, Ms14, SA01, SA02, SA03, SA06, SA09, SA14 a SA19.1	2
MSS6 a MMS9	12	CH01F02, CH01F09, CH02B03b, MSS3, MSS4, SA07 a SA08	1
MSS13	11		

As with SSR markers, co-dominant heredity characteristics are also present when using RFLP. This enables the detection of heterozygous (hybrid) genotypes in populations. Nelson-Jones et al. (2002) had success employing this method, together with SSR markers, to identify individual members of the *Sorbus* genus, while focusing on restriction polymorphism of nuclear DNA (*EcoRI*, *PstI*), rDNA operons from *Brassica oleracea*, ten cpDNA regions from *Lycopersicon esculentum* and two mtDNA regions (*COXI* – cytochrome oxidase subunit I and *atpA* – the α -subunit of the ATP synthase of maize (*Zea mays*). It is the analysis of maternally inherited cytoplasmic genomes in particular, that can reveal the direction of hybridization and the origin of *Sorbus torminalis* seeds. For the analysis of genetic variability in populations and their fragmentation, RAPD was successfully used in Italy by Belletti et al. (2008). Considering the fact that RAPD employs markers characterized by the dominant heredity pattern, it is the only study of this type, despite the positive results obtained and SSR markers are still the current choice for studies.

The next DNA marker in practical use is variability detection in the locus for *S-RNase*, which plays an important role in the investigation of the incompatibility and diversity of the *Sorbus* genus. Oddou-Muratorio et al. (2003) and Jankowska-Wróblewska et al. (2016b) achieved very similar results when comparing SSR markers and *S-RNase* analyses in *Sorbus torminalis*. Of course, at the same time, they highlighted the fact that the primers used for *S-RNase* were originally designed for the *Prunus* genus (Sonneveld et al., 2003) and therefore their results should be treated with due caution. This is because the number of alleles is influenced by the size of the population analysed, that is by genetic drift in small populations (Bush & Schoen, 2008). For example, Raspé and Kohn (2007) found thirty *S*-alleles when comparing two *S. aucuparia* populations in the French Pyrenees and Jankowska-Wróblewska et al. (2016b) found only four and six alleles within two populations of *Sorbus torminalis* in Poland (Jamy and Jarocin). For *S-RNase* allele detection it is possible to use a standard PCR reaction with electrophoretic detection of the amplicon size differences (Oddou-Muratorio et al., 2003) or sequencing of the obtained PCR products (Jankowska-Wróblewska et al., 2016b). Mainly through the use of sequencing techniques it is possible to not only evaluate DNA variability, through insertions and deletions (size differences), but also SNP (*Single Nucleotide Polymorphism*). Thus, this approach is more effective, but more expensive. Aside from genetic diversity assessments, with regards to future preservation of rare and valuable tree species in European ecosystems and their possible use in forestry under climate change, the underlying approach from molecular biology that may prove useful is the

development of DNA markers related to specific phenotypic traits. So far, these types of markers have not been developed for members of the *Sorbus* complex, perhaps due to the current marginal practical demand and economic importance of the genus. However, Feulner et al. (2014) carried out a study with a similar goal. They confirmed the existence of a highly significant correlation between floral chemistry and amplified fragment length polymorphism (AFLP). The AFLP technique (which roughly speaking combines RAPD and RFLP) also proved to be useful in the study of modes of reproduction, hybrid origins and gene flow in the *Sorbus* complex (Feulner et al., 2013).

Practical implications in silviculture

Over the past four decades, most European countries have become interested in the ecology and silviculture of the wild service tree and many studies have been published (Nicolescu et al., 2009). Growing young trees with strong competition and natural pruning will result in the development of good stem form (Wilhelm & Ducos, 1996). The wild service tree is a useful indicator of the existence of ancient woodlands and hedgerows (Roper, 1993).

Vegetative propagation

The distribution and use of the wild service tree has drastically decreased since the conversion from coppice-with-standards to high forest and the replacement of wood by other materials (Zeitlinger, 1990; Kausch-Blecken von Schmeling, 1994). Some authors have stated that *Sorbus torminalis* is unsuitable for coppicing because its capacity for suckering is poor (Camarda & Valsecchi, 1982; Bernetti, 1995; Svoboda, 1942), although others have reported natural regeneration by root suckering (Svoboda, 1942; Maděra et al., 2012; CABI Compendium, 2019). Natural layers from creeping shoots have also been recorded (Bernetti, 1995). Shoots often arise after the trunk or roots are injured during the clearing of wood (Svoboda, 1942). However, it is not easy for them to maintain their growth, because the seedlings of other species are mostly pre-grown and limit their development. Nevertheless, some authors found a high ratio of individuals of vegetative origin in stands (Hoebee et al., 2006), clonal reproduction dominates in peripheral populations under stress (Rasmussen & Kollmann, 2004; Jankowska-Wróblewska et al., 2016a) or in coppice woodlands (Maděra et al., 2012). Clonal offspring are not usually suitable, even when older, for nurseries or transplantation, given that they are nourished by the mother plant for

a relatively long time and only form their own root system late on (Svoboda, 1942). Vegetative propagation can be performed through cuttings, grafting, air layering, sets and tissue cultures (Bernetti, 1995).

Generative propagation

Natural propagation is usually by seed in the spring (CABI Compendium, 2019). However, *Sorbus torminalis* has a poor ability to naturally regenerate as is also the case for both *S. domestica* and *S. aria* (Prudič, 2000). This is not due to a lack of seeds, although some trees are unable to self-propagate (Wojciechowski & Bednorz, 2000), they do not fall from the tree but serve as food for birds. Thus, the seeds can be spread over relatively large distances. However, they also serve as food for mice and many seedlings are destroyed by animals (Prudič, 2000). Therefore, the coppice-with-standards is the most suitable form to encourage natural regeneration, where it is desirable to leave *Sorbus torminalis* as the upper tree species. In this way, it can last for several rotations of the underlying wood species. Seedlings and vegetative shoots must be released early to give them a sufficient head start over other woody plants (Svoboda, 1942). The generative offspring of *Sorbus torminalis* grow faster than the vegetative ones (Bednorz & Nowinska, 2018).

Seed collection is used in the artificial regeneration of trees and stands. Seeds must be collected from a sufficiently high number of mother trees to ensure that the genetic variability of the population is maintained. According to Czech Act No. 149/2003 Coll., relating to trade in the reproductive material of forest trees, seed collection must be carried out from at least 10 or 20 trees in a stand, depending on the wood species and the categorisation of the source of the reproductive material (source-identified or selected). Doran et al. (1983) recommend a minimum of 25 trees for *Acacia* with a spacing of no less than 100 m to minimize any relationship between the mother trees. The authors state that while 25 widely spaced trees are the preferable minimum sample size to represent heterogeneous populations, less populous crops may dictate a much smaller sample size. An arbitrary number of, for example, 5 seed trees may be considered to be the absolute minimum sample size (Doran et al., 1983). However, Biedenkopf et al. (2007) highlighted that seed collection from the wild service tree population for commercial harvest can result in a statistically significant reduction in genetic diversity. They used eight isoenzymes to study genetic variation in 121 mature trees of *Sorbus torminalis* in a natural stand and a subset of 21 high yield seed trees in the same stand. Within the climatic conditions of Central Europe the seeds ripen in September, remain on the trees until the beginning

of winter and then fall (Hofmann et al., 2005). Ripe fruit still on the trees can then be collected. After collection, the seeds must be removed from the pulp by straining and rinsing on sieves (Hofmann et al., 2005). The seed can be sown immediately after collection, and it emerges very well in the spring (Hofmann et al., 2005). After drying, seeds can be stored in jute bags or well perforated crates in cool airy spaces (Hofmann et al., 2005). For long-term storage, it is recommended that the seeds are dried to a moisture content of 6-8% and then they may be stored in hermetically sealed containers at 1-4 °C for up to 8 years (Hofmann et al., 2005). After storage and before sowing, the seeds must be stratified for 2-4 weeks at a temperature of 15 °C and then for 16-30 weeks at a temperature of 4 °C (Tylkowski, 2016). A 1:1 mixture of peat and sand is recommended as the stratification medium, the ratio of stratified seeds to the medium is 1:3 (Hofmann et al., 2005). Without this stratification, seeds sown in the spring will lie dormant in soil or substrate for 1 year (Hofmann et al., 2005).

Conservation of genetic resources

Approaches to the selection and conservation of genetic resources for wild service tree vary between European countries, but proper guidelines are still often given a low priority, overlooked or are simply entirely lacking, despite the knowledge that information about the genetic structure of natural populations should form the basis for the selection and protection of forest genetic resources (Kavaliauskas et al., 2021). However, there are technical guidelines for genetic conservation of *Sorbus torminalis* issued by the European Forest Genetic Resources Programme (EUFORGEN), which, for example, mention the importance of maintaining gene flow and a dynamic ecosystem during *in situ* conservation efforts, while stressing that this should be carried out on a wider landscape or even regional scale, rather than just locally. The long-term, genetic diversity of this species seems to be significantly affected by rare long-distance seed and pollen dispersal events, which should be accounted for in management units. Conserving this long-distance gene flow is therefore of highest importance, rather than the establishment of precisely defined spatially constrained conservation units. For *ex situ* measures it is recommended to collect seeds from many trees that grow at least 200 meters apart (Demesure-Musch & Oddou-Muratorio, 2004). The first genetic survey using isozymes for *Sorbus torminalis* discovered an astonishingly high degree of genetic diversity comparable to abundant species such as beech or oak (Rotach, 2000). According to Bednorz (2007), both *in situ* and *ex situ* methods should be applied to the conservation of the

genetic resources of *Sorbus torminalis*. Conservation efforts should first focus on forest management practises that favour the wild service tree, for example, logging intervention, competition control, preparation of favourable sites for the establishment of new areas. Further, *in situ* measures should include the selection of conservation areas (natural gene reserves) and the preservation of trees of the highest quality (protected genotypes). This would provide seeds for the establishment of new areas and to seed small populations. The genotypes of trees selected for preservation (about 250-300) would be protected in *ex situ* conservation areas, seedling and clonal seed orchards (Bednorz, 2007; Bednorz, 2009). Benedíková (2007) also confirmed that seed sets are often established to preserve the *Sorbus torminalis* gene pool. Rotach (2000) demonstrated that a phenotypic selection of 80 to 90 plus trees for a seed orchard may be an excellent tool to conserve a regional gene pool and to produce offspring with high genetic diversity. Thus, plus trees at one of the sites may be used for clonal seed orchard establishment (Espahbodi et al., 2008). Aside from seed banks and clonal seed orchards, the micropropagation of wild service trees *in vitro* has also been employed as a method for the long term conservation of genetic resources (Máchová et al., 2009; Marques et al., 2013; Bilous & Matashuk, 2021; Šedivá et al., 2023).

According to the General Declaration of the Third Ministerial Conference on the Protection of Forest in Europe, that took place in Lisbon (Collective of authors, 1998), native species and those with local provenance that are well adapted to site conditions should be preferred for reforestation and afforestation. Research into forestry has shown that if forests are to be of increased value, including their stability, adaptation, resistance, productivity and diversity, it is necessary to use reproductive material which is genetically and phenotypically suited to the site and of high quality, therefore the Member States of European Union shall ensure that only basic material that is approved will be used in the production of forest reproductive material intended to marketed (Council Directive 105/1999/ES). In forestry, selected sources (stands) are most often used, which are judged with respect to the specific stated purpose for which the reproductive material is intended and due weight shall be given to requirements 1-10 when considering the specific purpose, origin, degree of isolation, effective size of the population, age and development, uniformity, how well it is adapted, health and disease resistance, volume of production, wood quality, form or growth habitat. The selection criteria shall be determined by the Member State and the purpose entered into the National Register (Council Directive 105/1999/ES).

During phenotypic selection, many tree characteristics are assessed. As a rule, these are height, diameter at breast height, wood volume, trunk quality, and furthermore crown diameter, height under the branches, leaf area index, branch angles, number and diameter of branches (Liao et al., 2022; Liu et al., 2022; Saravi et al., 2008 etc.). Saravi et al. (2022) concluded that at the selection stage, if genotypes with greater collar diameters and height but with less branch angles are selected as the *Sorbus torminalis* parent trees, then seedlings (progenies) with higher survival rates and better growth would result. However, selection can lead to the elimination of alleles from the population, thereby reducing genetic variability. However, the effects of selection depend on the intensity and the initial variability of genes (Collective of authors, 2023).

Provenance research

In Germany, *Sorbus torminalis* has been the subject of provenance research for more than 20 years (Šeho et al., 2018), and provenances from all over Europe are tested here (Prudič, 2000). The results from Šeho et al. (2018) underscore the importance of collecting seeds from as many mother trees as possible to ensure an optimal degree of genetic variability and growth characteristics in individual provenances, although significant differences in phenotype between provenances were sometimes observed. Benedíková and Kyseláková (2005) state that over recent years in Austria, within forests with a predominance of oak, other broadleaf trees have been supported, especially *Sorbus torminalis*. Kotar (1998) also recommends this measure in Slovenia. In Italy, Piagnani et al. (2018) emphasize that the current production of timber only covers 20 % of the national demand. Their work shows, for the first time, results for the phenotypic characterizations of *Sorbus torminalis*. The annual diameter and height increase was recorded for twenty-five seedlings from a single mother tree, from the Northern Apennines (Italy). Research conducted by Tabandeh et al. (2007) and Saravi et al. (2008) aimed to determine the heritability of some characteristics of *Sorbus torminalis* seedlings through a half-sib progeny test in the north of Iran. Analyses indicated that the heritability of the largest branch ($h^2 = 0.003$) and branch number ($h^2 = 0.007$) was lower than those of the other characteristics measured. The heritability of collar diameter, vitality and total height was $h^2 = 0.22$, $h^2 = 0.20$ and $h^2 = 0.17$, respectively. From 20 parent trees the genotypes of five of them can be introduced as plus trees to provide seeds and for seedling production. It can be deduced that for seedling production of *Sorbus torminalis* in this particular nursery, the parent trees should be those that have the greatest collar diameter, best

vitality and total height in order to increase the possibility of high-quality progeny. Molecular biology work done on wild service trees is usually consistent and reports much higher levels of genetic diversity within individual populations than would be expected given its scattered distribution, however, there is less consensus about the clear spatial genetic structure in relation to geography and it usually depends on the sample size and studied area (Oddou-Muratario et al., 2001b; Kučerová et al., 2010). Interestingly, Kavaliauskas et al. (2021) report higher allelic richness in plus trees and seed orchards than in wild populations of wild service trees, which only highlights the importance of management practices that help maintain gene flow.

Summary & Future perspectives

Up to this point, molecular biology has made a major contribution to the description of the genetic background of the wild service tree, especially when it comes to the phylogenetic standing of the species among other taxa in *Sorbus* complexes and an assessment of genetic diversity within and between populations, with the use of non-coding portions of the genome as a criterion found to be sufficient for the latter. These studies are of significant practical importance, mainly when it comes to the conservation of wild service tree genetic resources, understanding the reproduction strategies required to maintain genetic fitness or identification of possible threats to genetic diversity. However, if this species is eventually more involved in silviculture, not only from ecological standpoint (to increase forest diversity and resilience) but especially for timber production or biologically active compounds (Ak et al., 2024), it may lead to an increase in the need for genome wide association studies (GWAS). That is a focus on markers that confer the important traits of wild service trees, for example its resistance to abiotic and biotic stress. More investment in next generation sequencing approaches coupled with robust bioinformatic analysis might be required to achieve this goal or at the very least to broaden the basis for the possible development of new informative markers (Amiteye, 2021). This would provide another useful globally available tool that could be applied, together with progeny and provenance tests, to take local conditions into consideration.

More specifically, with regards to the selection criteria for tree genetic resources, as stated in Council Directive 105/1999/ES, the following possible future applications of molecular biology in wild service tree research can be suggested:

Origin: Approaches based on the polymorphism of repetitive sequences, such as microsatellite mark-

ers on one hand and barcoding of selected plastid and nuclear DNA sequences on the other, will continue to further populate substitute by expand the database and play a role in the approval of origin, hybrid status or provenance of wild service tree reproductive material. An increased focus on the discovery and screening of single nucleotide polymorphism (SNP) in the *Sorbus torminalis* genome would be particularly helpful here (Cronn et al., 2021).

Isolation, effective population size: While there should be an emphasis on choosing the genetic material that is best suited to local conditions, it is also desirable to introduce the wild service tree into new sites, using material from various sources to increase gene flow between stands and prevent population fragmentation. The question of whether the wild service tree will also be utilised in monospecific planted stands outside of nurseries still remains. In such cases, allozymes, SSR or ISSR markers should be able to identify the genets and ramets in a given stand. Alternatively, when the wild service tree is introduced sparingly, as part of a diverse forest ecosystem, microsatellite markers (SSR) are currently the most reliable method and can also serve as a proxy for diversity in adaptive genetic markers. Again, here the development of SNP panels could be beneficial (Kučerová et al., 2010; Kavaliauskas et al., 2021).

Health and resistance, adaptedness: The wild service tree appears, in general, to be a resilient and prospective species in response to the projected climate change, but biotic stressors such as fungal diseases or abiotic factors such as heat or drought can nevertheless become a concern, at least over some of its native range, which would require a shift to breeding for resistance (Thomas, 2017). That would require a more thorough study of host-pathogen interactions on a molecular physiology level, but also more thorough genetic screening of wild service tree populations to identify resistant individuals. Here, together with the established genetic profiling, based on a variable number of tandem repeats (SSR) and single nucleotide polymorphism, sequencing of more genomic regions and subsequent new marker development might be useful (i.e. genome wide association studies, bulk segregant analysis etc.).

These applications of DNA analysis are only suggestions and there is always room for improvement, but their usefulness will ultimately depend on the goals and strategies chosen in the establishment of wild service tree genetic conservation units and willingness to reintroduce the species into silviculture. The recent approaches that have used DNA based methods for inventory and conservation also vary between countries, which perhaps partly reflects

the silvicultural traditions and natural distribution frequency. To name but a few instances: in France, the wild service tree is relatively abundant and of long-term economic interest and the first successful attempt to develop microsatellite markers to study the genetic structure of populations took place there (Lanier et al., 1990; Oddou-Muratorio et al., 2001a). The results of extensive population screening with SSR markers was used to propose an overall strategy for the management of genetic conservation units over the whole of southern Germany (Kavaliauskas et al., 2021). The substantial application of DNA based methods can also be seen in Poland, where the species has its limit of distribution and is rare and protected (Jankowska-Wróblewska et al., 2016b; Ulaszewski et al., 2017). Valuable research into the inheritance of wild service tree phenotypic traits was done in Iran, despite the lack of a molecular genetic background (Tabandeh et al., 2007; Espahbodi et al., 2008). The situation is also interesting in the Czech Republic, where detailed research into *Sorbus torminalis* distribution on a national scale was carried out (Maděra et al., 2013) and several seed orchards have been established as genetic resources (The Ministry of Agriculture of the Czech Republic, 2024). There has even been the development of a certified methodology for *in vitro* micropropagation of whitebeams, rowans and wild service trees (Malá et al., 2014). Despite this, DNA based analysis has mostly been reserved for karyological studies to resolve phylogenies, ploidy and population dynamics in other related rare or endemic taxa in the *Sorbus* complex although sometimes it has also been used for the results of hybridization with *Sorbus torminalis* (Lepší et al., 2009; Velebil, 2012). In some cases, microsatellite marker analysis was also used (Lepší et al., 2008; Vít et al., 2012; Lepší, 2017), but the precise and informative mapping of the population structure and genetic diversity specifically of *Sorbus torminalis* as a genetic resource is, to date, still missing.

There is no doubt that current wild service tree populations, at the core of their natural range, are affected by fragmentation due to the historical shift of forestry practice from coppicing and more open forests to high forest and closed canopies. But even though their protection status varies in individual European countries, it is not listed as a globally threatened species by the IUCN. Awareness of the importance of rare and noble hardwoods in forestry and nature conservation is hardly new and as early as the 1990s conservation projects for *Sorbus torminalis* were launched in France, Germany, Austria, Switzerland and Slovakia. Despite this there is still a gap between theory and practice and they still only receive minor attention compared to the more traditional and commercially significant forest tree species (Turok et al., 1998). This could also

partially explain the current state of the molecular biology methodologies available and the development of DNA markers for the wild service tree. The total number of papers published that focus on the genetics of the wild service tree in a given country does not always directly translate to actual conservation efforts or forest management practices and what is often missing are case studies (Afifi et al., 2023). The general prevalence of microsatellite markers is also understandable due to their high level of polymorphism and reproducibility. But aside from the development of new DNA markers, more attention should be paid to genetic screening, using methods that are already available, of isolated or peripheral populations on a regional scale, to make sure there is no risk of inbreeding depression, despite the generally high inter-population diversity reported for the species (Hoebee et al., 2007; Rasmussen & Kollmann, 2007, 2008; Jankowska-Wróblewska et al., 2016a). On the other hand, genetic studies focused on mapping haplotypes across countries could also provide valuable information and are still quite rare (Oddou-Muratorio et al., 2001b; Kučerová et al., 2010). These measures would at least partly mitigate the scenario where the selection of forest reproductive material is taken from a limited gene pool. There is undoubtedly an increased need to develop a more connected network between the scientific community (wild service tree genetic diversity and population structure) and forestry practitioners (selection of genetic conservation units and forest reproductive material) to ensure the optimal delineation of provenances and reliable genetic resources for this noble hardwood species both on a national and pan-European scale.

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References

- Aas G, Maier J, Baltisberger M & Metzger S (1994) Morphology, isozyme variation, cytology, and reproduction of hybrids between *Sorbus aria* (L.) Crantz and *S. torminalis* (L.) Crantz. *Botanica Helvetica* 104: 195–214.
- Act on trade in reproductive material of forest trees No. 149/2003 Coll. Law of the Czech Republic. <https://www.zakonyprolidi.cz/cs/2003-149>.
- Afifi L, Lapin K, Tremetsberger K & Konrad H (2023) A systematic review of threats, conservation, and

- management measures for tree species of the family Rosaceae in Europe. *Flora* 301: 152244. doi:10.1016/j.flora.2023.152244.
- Ak G, Tüfekci EF, Mustafa AM, Caprioli G, Altunoglu YC, Baloglu MC, Cakılcıoğlu U, Polat R, Darendelioglu E & Zengin G (2024) Exploring *Sorbus torminalis* leaves: unveiling a promising natural resource for diverse chemical and biological applications. *Chemistry & Biodiversity* 21: e202301596. doi:10.1002/cbdv.202301596.
- Albrecht AT & de Avila AL (2018) A proposal how to identify potential alternative tree species under climate change based on a literature review in Southwest Germany. *Allgemeine Forst und Jagdzeitung* 189: 129–143. doi:10.23765/afjz0002025.
- Amiteye S (2021) Basic concepts and methodologies of DNA marker systems in plant molecular breeding. *Heliyon* 7: e08093. doi:10.1016/j.heliyon.2021.e08093.
- Angelone S, Hilfiker K, Holderegger R, Bergamini A & Hoebee SE (2007) Regional population dynamics define the local genetic structure in *Sorbus torminalis*. *Molecular Ecology* 16: 1291–1301. doi:10.1111/j.0962-1083.2006.03202.x.
- Bailey JP, Kay QON, McAllister H & Rich TCG (2008) Chromosome numbers in *Sorbus* L. (Rosaceae) in British Isles. *Watsonia* 27: 69–72.
- Bednorz L (2007) Conservation of genetic resources of *Sorbus torminalis* in Poland. *Dendrobiology* 58: 3–7.
- Bednorz L (2009) Jak chronić jarzab brekinię (*Sorbus torminalis*) w polskich lasach? *Sylwan* 153: 354–360.
- Bednorz L & Krzakowa M (2002) Phosphoglucose isomerase (PGI) polymorphism in *Sorbus torminalis* (L.) Crantz. *Acta Societatis Botanicorum Poloniae* 71: 121–124. doi:10.5586/asbp.2002.013.
- Bednorz L, Myczko Ł & Kosinski P (2004) Isozyme polymorphism and genetic structure of the population of *Sorbus torminalis* (L.) Crantz from the Bytyń Forest (Poland). *Journal of Applied Genetics* 45: 321–324.
- Bednorz L, Myczko Ł & Kosiński P (2006) Genetic variability and structure of the wild service tree (*Sorbus torminalis* (L.) crantz) in Poland. *Silvae Genetica* 55: 197–202. doi:10.1515/sg-2006-0027.
- Bednorz L, Myczko Ł & Kosiński P (2015) An assessment of genetic diversity following natural regeneration of *Sorbus torminalis* in the Forest District of Jamy (northern Poland). *Dendrobiology* 73: 111–116. doi:10.12657/denbio.073.011.
- Bednorz L & Nowinska R (2018) Analysis of growth of recruits of natural regeneration of *Sorbus torminalis* (L.) Crantz - a rare European forest tree species. *iForest* 11: 72–78. doi:10.3832/for2347-010.
- Belletti P, Monteleone I & Ferrazzini D (2008) A population genetic study in a scattered forest species, wild service tree [*Sorbus torminalis* (L.) Crantz], using RAPD markers. *European Journal of Forest Research* 127: 103–114. doi:10.1007/s10342-007-0187-1.
- Benedíková M (2007) Metody zachování a reprodukce genových zdrojů *Sorbus torminalis* Crantz a *Sorbus domestica* L.: Ohrožené dřeviny České republiky (ed. by J Dreslerová & P Packová) Mendel University, Brno, Czech Republic, pp. 15–19.
- Benedíková M & Kyseláková J (2005) Záchrana genofondu jeřábu břeku a jeřábu oskeruše na jihovýchodní Moravě. *Lesnická Práce* 9: 15–17.
- Bernetti G (1995) *Selvicultura speciale*. UTET, Torino, Italy.
- Biedenkopf S, Ammer C & Müller-Starck G (2007) Genetic aspects of seed harvests for the artificial regeneration of wild service tree (*Sorbus torminalis* [L.] Crantz). *New Forests* 33: 1–12. doi:10.1007/s11056-006-9009-4.
- Bilous S & Matashuk R (2021) Primary morphogenesis of *Sorbus Torminalis* (L.) grantz in in vitro culture. *Ukrainian Journal of Forest and Wood Science* 12: 64–71. doi:10.31548/forest2021.04.006.
- Bush JW & Schoen DJ (2008) The evolution of self-incompatibility when mates are limiting. *Trends in Plant Science* 13: 128–136. doi:10.1016/j.tplants.2008.01.002.
- Camarda I & Valsecchi F (1982) Alberi e arbusti spontanei della Sardegna. Regione Autonoma della Sardegna - Assessorato difesa Ambiente, Italy.
- Chester M, Cowan RS, Fay MF & Rich TCG (2007) Parentage of endemic *Sorbus* L. (Rosaceae) species in the British Isles: Evidence from plastid DNA. *Botanical Journal of the Linnean Society* 154: 291–304. doi:10.1111/j.1095-8339.2007.00669.x.
- Collective of authors (1998) General declaration. Third Ministerial Conference on the Protection of Forests in Europe, Lisboa. https://www.forestportal.sk/wp-content/uploads/2021/12/lisabon_general.pdf
- Collective of authors (2019) *Sorbus torminalis* (Rowan). CABI Compendium. <https://www.cabi-digitallibrary.org/doi/10.1079/cabicompendium.50761#tab-contributors>.
- Collective of authors (2023) Population genetics – selection as the main evolutionary force. Mendel University in Brno. <https://user.mendelu.cz/urban/vsg3/popdynam/popul8.html>.
- Council Directive 105/1999/ES on the marketing of forest reproductive material. <https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A31999L0105&qid=1721048022566>
- Crantz HJN (1763) *Sorbus torminalis* (L.) Crantz. *Stirpium Austriarum Fasciculus* 2: 45.

- Cronn RC, Finch KN, Hauck LL, Parker-Forney M, Milligan BG & Dowling J (2021) Range-wide assessment of a SNP panel for individualization and geolocalization of bigleaf maple (*Acer macrophyllum* Pursh). *Forensic Science International: Animals and Environments* 1: 100033. doi:10.1016/j.fsiae.2021.100033.
- Demesure B, Le Guerroué B, Lucchi G, Prat D & Petit RJ (2000) Genetic variability of a scattered temperate forest tree: *Sorbus torminalis* L. (Crantz). *Annals of Forest Science* 57: 63–71. doi:10.1051/forest:2000101.
- Demesure-Musch B & Oddou-Muratorio S (2004) EUFORGEN Technical Guidelines for genetic conservation and use for wild service tree (*Sorbus torminalis*). International Plant Genetic Resources Institute, Rome, Italy.
- Dłuzewska J, Ślesak I & Kruk J (2013) Molecular analysis of *Sorbus* sp. from the Pieniny Mts. and its relation to other *Sorbus* species. *Acta Biologica Cracoviensia Series Botanicae* 55: 86–92. doi:10.2478/abcsb-2013-0009.
- Doran JC, Turnbull JW, Boland DJ & Gunn BV (1983) Handbook on seeds of dry-zone acacias. FAO. <https://www.fao.org/4/q2190E/Q2190E00.htm>.
- Espahbodi K, Mirzaie-Nodoushan H, Tabari M, Akbarinia M, Dehghan-Shuraki Y & Jalali SG (2008) Genetic variation in early growth characteristics of two populations of wild service tree (*Sorbus torminalis* (L.) Crantz) and their interrelationship. *Silvae Genetica* 57: 340–348. doi:10.1515/sg-2008-0050.
- Feulner M, Aas G, Urbon T, Caré O, Kuchma O, Hosi-us B, Kahlert K & Leinemann L (2023) Low rates of apomixis and polyploidy in progeny of Thuringian *Sorbus* subgenus *Tormaria*. *Plant Systematics and Evolution* 309: 16. doi:10.1007/s00606-023-01850-6.
- Feulner M, Pointner S, Heuss L, Aas G, Paule J & Dötterl S (2014) Floral scent and its correlation with AFLP data in *Sorbus*. *Organisms Diversity and Evolution* 14: 339–348. doi:10.1007/s13127-014-0180-8.
- Feulner M, Liede-Schumann S, Meve U, Weig A & Aas G (2013) Genetic structure of three *Sorbus latifolia* (Lam.) Pers. taxa endemic to northern Bavaria. *Plant Systematics and Evolution* 299: 1065–1074. doi:10.1007/s00606-013-0778-x.
- George JP, Konrad H, Collin E, Thevenet J, Ballian D, Idzajtich M, Kamm U, Zhelev P & Geburek T (2015) High molecular diversity in the true service tree (*Sorbus domestica*) despite rareness: data from Europe with special reference to the Austrian occurrence. *Annals of Botany* 115: 1105–1115. doi:10.1093/aob/mcv047.
- Govaerts R, Nic Lughadha E, Black N, Turner R & Paton A (2021) The World Checklist of Vascular Plants, a continuously updated resource for exploring global plant diversity. *Scientific Data* 8: 215. doi:10.1038/s41597-021-00997-6.
- Hamston TJ, de Vere N, King RA, Pellicer J, Fay MF, Cresswell JE & Stevens JR (2018) Apomixis and hybridization drives reticulate evolution and phylogenetic differentiation in *Sorbus* L.: Implications for conservation. *Frontiers in Plant Science* 9: 1796. doi:10.3389/fpls.2018.01796.
- Hamston TJ, Pellicer J & Fay MF (2015) Polyploid wild service tree: First record of a triploid *Sorbus torminalis* (Rosaceae) in Britain. *New Journal of Botany* 5: 34–36. doi:10.1179/2042349715Y.0000000006.
- Hemery GE, Clark JR, Aldinger E, Claessens H, Malvoti ME, O'Connor E, Raftoyannis Y, Savill PS & Brus R (2010) Growing scattered broadleaved tree species in Europe in a changing climate: a review of risks and opportunities. *Forestry* 83: 65–81. doi:10.1093/forestry/cpp034.
- Hochbichler E (2003) Die Elsbeere (*Sorbus torminalis* Crantz) im Weinviertel (Niederösterreich). *Forst und Holz* 58: 647–653.
- Hoebbe SE, Arnold U, Düggelin C, Gugerli F, Brodbeck S, Rotach P & Holderegger R (2007) Mating patterns and contemporary gene flow by pollen in a large continuous and a small isolated population of the scattered forest tree *Sorbus torminalis*. *Heredity* 99: 47–55. doi:10.1038/sj.hdy.6800962.
- Hoebbe SE, Menn C, Rotach P, Finkeldey R & Holderegger R (2006) Spatial genetic structure of *Sorbus torminalis*: The extent of clonal reproduction in natural stands of a rare tree species with a scattered distribution. *Forest Ecology and Management* 226: 1–8. doi:10.1016/j.foreco.2005.12.024.
- Hofmann J, Chválová K & Palátová E (2005) Lesné semenárstvo na Slovensku. Lesmedium, k.s., Bratislava. Slovak Republic.
- Jankowska-Wróblewska S, Meyza K, Sztupecka E, Kubera L & Burczyk J (2016a) Clonal structure and high genetic diversity at peripheral populations of *Sorbus torminalis* (L.) Crantz. *iForest* 9: 892–900. doi:10.3832/for1885-009.
- Jankowska-Wróblewska S, Warmbier J & Burczyk J (2016b) Spatial genetic structure within populations of *Sorbus torminalis* (L.) Crantz: comparative analysis of the self-incompatibility locus and nuclear microsatellites. *Acta Biologica Cracoviensia. Series Botanica* 58: 7–17. doi:10.1515/abcsb-2016-0011.
- Kantor P, Vrška T, Dobrovolný L & Novák J (2014) Pěstění lesů. Mendel university in Brno.
- Kamm U, Rotach P, Gugerli F, Siroky M, Edwards P & Holderegger R (2009) Frequent long-distance gene flow in a rare temperate forest tree (*Sorbus domestica*) at the landscape scale. *Heredity* 103: 476–482. doi:10.1038/hdy.2009.70.

- Kausch-Blecken von Schmelling W (1994) Die Elsbeere (*Sorbus torminalis* (L.) Crantz.). Verlag Kausch, Bovenden, Germany.
- Kavaliauskas D, Šeho M, Baier R & Fussi B (2021) Genetic variability to assist in the delineation of provenance regions and selection of seed stands and gene conservation units of wild service tree (*Sorbus torminalis* (L.) Crantz) in southern Germany. *European Journal of Forest Research* 140: 551–565. doi:10.1007/s10342-020-01352-x.
- Klein EK, Desassis N & Oddou-Muratorio S (2008) Pollen flow in the wild service tree, *Sorbus torminalis* (L.) Crantz. IV. Whole interindividual variance of male fecundity estimated jointly with the dispersal kernel. *Molecular Ecology* 17: 3323–3336. doi:10.1111/j.1365-294X.2008.03809.x.
- Koch O, de Avila AL, Heinen H & Albrecht AT (2022) Retreat of major European tree species distribution under climate change - minor natives to the rescue? *Sustainability* 14: 5213. doi:10.3390/su14095213.
- Kotar M (1998) Razširjenost in rastne značilnosti breka (*Sorbus torminalis* Crantz) v Sloveniji. *Gozdarski Vestnik* 56: 258–278.
- Kovanda M (1996) New taxa of *Sorbus* from Bohemia (Czech Republic). *Verhandlungen der Zoologisch Botanischen Gesellschaft in Österreich* 133: 319–345.
- Kučerová V, Honec M, Paule L, Zhelav P & Gömöry D (2010) Genetic differentiation of *Sorbus torminalis* in Eastern Europe as determined by microsatellite markers. *Biologia* 65: 817–821. doi:10.2478/s11756-010-0082-y.
- Kunz J, Löffler G & Bauhus J (2018) Minor European broadleaved tree species are more drought-tolerant than *Fagus sylvatica* but not more tolerant than *Quercus petraea*. *Forest Ecology and Management* 414: 15–27. doi:10.1016/j.foreco.2018.02.016.
- Kunz J, Räder A & Bauhus J (2016) Effects of drought and rewetting on growth and gas exchange of minor European broadleaved tree species. *Forests* 7: 239. doi:10.3390/f7100239.
- Kurtto A, Sennikov AN & Lampinen R (2018) *Atlas Florae Europaeae*. Distribution of vascular plants in Europe, vol. 17. Rosaceae (*Sorbus* s.l.). The Committee for Mapping the Flora of Europe & Societas Biologica Fennica Vanamo, Helsinki.
- Lanier L, Rameau JC, Keller R, Joly HI, Drapier N & Sevrin E (1990) L'Alisier torminal (*Sorbus torminalis* (L.) Crantz). *Revue Forestière Française* 42: 13–34. doi:10.4267/2042/26038.
- Leinemann L, Hosius B, Kahlert K, Kuchma O, Czernikar H, Arenhövel W & Helmecke K (2013) Gene marker analysis concerning hybrid formation and natural regeneration of *Sorbus latifolia* agg. in Thuringia. *Allgemeine Forst und Jagdzeitung* 184: 204–213.
- Leinemann L, Kahlert K, Arenhövel W, Voth W & Hosius B (2010) Insights into genetic variation patterns in the genus *Sorbus* in Thuringia. *Allgemeine Forst und Jagdzeitung* 181: 169–174.
- Lepší M, Vít P, Lepší P, Boublík K & Suda J (2008) *Sorbus milensis*, a new hybridogenous species from northwestern Bohemia. *Preslia* 80: 229–244.
- Lepší M, Vít P, Lepší P, Boublík K & Kolař F (2009) *Sorbus portae-bohemicae* and *Sorbus albensis*, two new endemic apomictic species recognized based on a revision of *Sorbus bohemica*. *Preslia* 81: 63–89.
- Lepší M (2017) Taxonomy and variability of selected *Sorbus* taxa. Doctoral thesis, University of South Bohemia in České Budějovice, Czech Republic.
- Li QY, Guo W, Liao WB, Macklin JA & Li JH (2012) Generic limits of *Pyrinae*: Insights from nuclear ribosomal DNA sequences. *Botanical Studies* 53: 151–164.
- Liao L, Cao L, Xie Y, Luo J & Wang G (2022) Phenotypic traits extraction and genetic characteristics assessment of *Eucalyptus* trials based on UAV-Borne LiDAR and RGB images. *Remote Sensing* 14: 765. doi:10.3390/rs14030765.
- Linnaeus C (1753) *Species Plantarum*. 1st ed. Volume 1.
- Liu DG, Shen H, Yang YH & Zhang J (2003) Genetic diversity of rare and endangered plant *Sorbus amabilis*. *Ying Yong Sheng Tai Xue Bao* 14: 2141–2144.
- Liu Z, Gao C, Li J, Miao Y & Cui K (2022) Phenotypic diversity analysis and superior family selection of industrial raw material forest species-*Pinus yunnanensis* Franch. *Forests* 13: 618. doi:10.3390/f13040618.
- Maděra P, Kohoutek M, Šenfěldr M & Řepka R (2012) The population structure and regeneration of Wild Service Tree in Hádecká planinka National Nature Reserve (Czech Republic). *Dendrobiology* 68: 63–68.
- Maděra P, Machala M, Slach T, Friedl M, Černušáková L, Volařík D & Buček A (2017) Predicted occurrence of ancient coppice woodlands in the Czech Republic. *iForest* 10: 788–795. doi:10.3832/ifer2295-010.
- Maděra P, Tichá S & Řepka R (2013) Distribution and ecological requirements of *Sorbus torminalis* (L.) Crantz in the Czech Republic. *Dendrobiology* 69: 59–68. doi:10.12657/denbio.069.007.
- Máchová P, Malá J, Cvrčková H & Dostál J (2009) Optimization of wild service tree micropropagation. *Zprávy Lesnického Výzkumu* 54: 218–222.
- Malá J, Cvrčková H, Máchová P & Buriánek V (2014) Mikropropagace endemitních jeřábů (*Sorbus* spp.). Jíloviště (Czech Republic): Forestry and Game Management Research Institute. Certified methodology. https://www.vulhm.cz/files/uploads/2019/03/LP_4_2014-1.pdf.

- Marques SL, Canhoto J, Gonçalves JC & Diogo MG (2013) Micropropagation of *Sorbus torminalis* (L.) Crantz: Hormonal effects during multiplication and rooting phases. *Acta Horticulturae* 990: 397–404. doi:10.17660/ActaHortic.2013.990.50.
- Meng KK, Chen SF, Xu KW, Zhou RC, Li MW, Dharmala MK, Liao WB & Fan Q (2021) Phylogenomic analyses based on genome-skimming data reveal cyto-nuclear discordance in the evolutionary history of *Cotoneaster* (Rosaceae). *Molecular Phylogenetics and Evolution* 158: 107083. doi:10.1016/j.ympev.2021.107083.
- Meyer N, Gregor T, Meierott L & Paule J (2014) Diploidy suggests hybrid origin and sexuality in *Sorbus* subgen. *Tormaria* from Thuringia, Central Germany. *Plant Systematics and Evolution* 300: 2169–2175. doi:10.1007/s00606-014-1043-7.
- Müller SV, Ammer C & Nüsslein S (2000) Analyses of stand structure as a tool for silvicultural decisions – a case study in a *Quercus petraea*-*Sorbus torminalis* stand. *Forstwissenschaftliches Centralblatt* 119: 32–42.
- Nelson-Jones EB, Briggs D & Smith AG (2002) The origin of intermediate species of the genus *Sorbus*. *Theoretical and Applied Genetics* 105: 953–963. doi:10.1007/s00122-002-0957-6.
- Németh C, Papp N, Nosková J & Höhn M (2020) Speciation by triparental hybridization in genus *Sorbus* (Rosaceae). *Biologia Futura* 71: 209–222. doi:10.1007/s42977-020-00003-x.
- Nicolescu VN, Hochbichler E, Coello Gomez J, Ravagni S & Giulietti V (2009) Ecology and silviculture of wild service tree (*Sorbus torminalis* (L.) Crantz): A literature review. *Die Bodenkultur – Journal for Land Management, Food and Environment* 60: 35–44.
- Oddou-Muratorio S, Aligon C, Decroocq S, Plomion C, Lamant T & Mush-Demesure B (2001a) Microsatellite primers for *Sorbus torminalis* and related species. *Molecular Ecology Notes* 1: 297–299. doi:10.1046/j.1471-8278.2001.00116.x.
- Oddou-Muratorio S, Guesnet D, Ozdemir E, Petit RJ & Demesure B (2001b) Patterns of seed dispersal in a scattered forest tree species (*Sorbus torminalis*) based on multi-scale investigations of populations genetic structure for chloroplast DNA: Genetic response of forest systems to changing environmental conditions, (ed. by G Muller-Starck & R Schubert) Kluwer Academic Publisher: Dodrecht, The Netherlands, pp. 271–280. doi:10.1007/978-94-015-9839-2_22.
- Oddou-Muratorio S, Houot ML, Demesure-Musch B & Austerlitz F (2003) Pollen flow in the wildservice tree, *Sorbus torminalis* (L.) Crantz. I. Evaluating the paternity analysis procedure in continuous populations. *Molecular Ecology* 12: 3427–3439. doi:10.1046/j.1365-294X.2003.01989.x.
- Oddou-Muratorio S, Demesure-Musch B, Pélissier R & Gouyon PH (2004) Impacts of gene flow and logging history on the local genetic structure of a scattered tree species, *Sorbus torminalis* L. Crantz. *Molecular Ecology* 13: 3689–3702. doi:10.1111/j.1365-294X.2004.02373.x.
- Oddou-Muratorio S, Klein EK & Austerlitz F (2005) Pollen flow in the wild service tree, *Sorbus torminalis* (L.) Crantz. II. Pollen dispersal and heterogeneity in mating success inferred from parent–offspring analysis. *Molecular Ecology* 14: 4441–4452. doi:10.1111/j.1365-294X.2005.02720.x.
- Oddou-Muratorio S, Klein EK, Demesure-Musch B & Austerlitz F (2006) Real-time patterns of pollen flow in the wild-service tree, *Sorbus torminalis* (Rosaceae). III. Mating patterns and the ecological maternal neighbourhood. *American Journal of Botany* 93: 1650–1659. doi:10.3732/ajb.93.11.1650.
- Paganová V (2007) Ecology and distribution of *Sorbus torminalis* (L.) Crantz. in Slovakia. *Horticultural Science* 34: 138–151. doi:10.17221/1896-HORTSCI.
- Pellicer J, Clermont S, Houston L, Rich TCG & Fay MF (2012) Cytotype diversity in the *Sorbus* complex (Rosaceae) in Britain: sorting out the puzzle. *Annals of Botany* 110: 1185–1193. doi:10.1093/aob/mcs185.
- Piagnani MC, Costa C, Minotta G & Bassi D (2018) Context Sensitive Links 1 of 1 Preliminary phenotypic characterization of *Sorbus domestica* and *S. torminalis* under selection for timber production. *Agroforestry systems* 92: 589–597. doi:10.1007/s10457-016-9995-y.
- Proctor MCF, Proctor ME & Groenhof AC (1989) Evidence from peroxidase polymorphism on the taxonomy and reproduction of some *Sorbus* populations in south west England. *New Phytologist* 112: 569–575. doi:10.1111/j.1469-8137.1989.tb00352.x.
- Prudič Z (2000) Pěstování jeřábu břeku a oskeruše. *Lesnická Práce* 79: 301–303.
- Qiu J, Chen L, Yi X, Li M, Chen X & Tang G (2019) The complete chloroplast genome of *Sorbus folgneri* (C.K.Schneid.) Rehder (Rosaceae). *Mitochondrial DNA Part B* 4: 728–729. doi:10.1080/23802359.2018.1558127.
- Rasmussen KK & Kollmann J (2004) Poor sexual reproduction on the distribution limit of the rare tree *Sorbus torminalis*. *Acta Oecologica* 25: 211–218. doi:10.1016/j.actao.2004.02.001.
- Rasmussen KK & Kollmann J (2007) Genetic diversity, spatial patterns, and growth of root sprouts in a temperate tree at the northern distribution limit. *Ecoscience* 14: 250–258. doi:10.2980/1195-6860(2007)14[250:GDSPAG]2.0.CO;2.

- Rasmussen KK & Kollmann J (2008) Low genetic diversity in small peripheral populations of a rare European tree (*Sorbus torminalis*) dominated by clonal reproduction. *Conservation Genetics* 9: 1533–1539. doi:10.1007/s10592-007-9492-y.
- Raspé O & Kohn JR (2007) Population structure at the S-locus of *Sorbus aucuparia* L. (Rosaceae: Maloideae). *Molecular Ecology* 16: 1315–1325. doi:10.1111/j.1365-294X.2007.03233.x.
- Rich TC, King C, Brown AP & Fay MF (2022) 1050. *SORBUS TORMINALIS*: Rosaceae. *Curtis s Botanical Magazine* 39: 753–762. doi:10.1111/curt.12484.
- Robertson A, Rich TCG, Allen AM, Houston L, Roberts C, Bridle JR, Harris SA & Hiscock SJ (2010) Hybridization and polyploidy as drivers of continuing evolution and speciation in *Sorbus*. *Molecular Ecology* 19: 1675–1690. doi:10.1111/j.1365-294X.2010.04585.x.
- Roper P (1993) The distribution of the Wild Service Tree, *Sorbus torminalis* (L.) Crantz, in the British Isles. *Watsonia* 19: 209–229.
- Rotach P (2000) Endangerment of rare tree species in Switzerland: Basic considerations, current situation and two examples. *Forest Snow and Landscape Research* 75: 267–284.
- Saravi AT, Tabari M, Espahbodi K, Nodoushan HM & Enayati B (2008) Phenotypic correlation between selected characters of parent trees and progenies in wild service tree (*Sorbus torminalis* L. Crantz.). *Asian Journal of Plant Sciences* 7: 579–583. doi:10.3923/ajps.2008.579.583.
- Šedivá J, Velebil J & Zahradník D (2023) Micropropagation as a tool for the conservation of autochthonous *Sorbus* species of Czechia. *Plants* 12: 488. doi:10.3390/plants12030488.
- Šeho M, Kavaliauskas D, Kleinschmit JRG, Karopka M & Fussli B (2018) Wild Service Tree – Importance and installation of provenance tests in the face of climate change. *Allgemeine Forst und Jagdzeitung* 189: 41–57. doi:10.23765/afz0002020.
- Sennikov AN & Kurtto A (2017) A phylogenetic checklist of *Sorbus* s.l. (Rosaceae) in Europe. *Memoranda Societatis pro Fauna et Flora Fennica* 93: 1–78.
- Silfverberg-Dilworth E, Matasci CL, Van de Weg WE, Van Kaauwen MPW, Walser M, Kodde LP, Soglio V, Gianfranceschi L, Durel CE, Costa F, Yamamoto T, Koller B, Gessler G & Patocchi A (2006) Microsatellite markers spanning the apple (*Malus x domestica* Borkh.) genome. *Tree Genetics & Genomes* 2: 202–224. doi:10.1007/s11295-006-0045-1.
- Siljak-Yakovlev S, Pustahija F, Šolić EM, Bogunić F, Muratović E, Bašić N, Catrice O & Brown SC (2010) Towards a genome size and chromosome number database of Balkan flora: C-values in 343 taxa with novel values for 242. *Advances Science Letters* 3: 190–213. doi:10.1166/asl.2010.1115.
- Slach T, Volařík D & Maděra P (2021) Dwindling coppice woods in Central Europe – natural and cultural heritage disappearing. *Forest Ecology and Management* 501: 119687. doi:10.1016/j.foreco.2021.119687.
- Sonneveld T, Tobutt KR & Robbins TP (2003) Allele-specific PCR detection of sweet cherry self-incompatibility (S) alleles S1 to S16 using consensus and allele-specific primers. *Theoretical and Applied Genetics* 107: 1059–1070. doi:10.1007/s00122-003-1274-4.
- Sułkowska M & Mohytych V (2024) *Sorbus torminalis* (L.) Crantz survival rate of two common garden trials during the first ten years after planting. *Folia Forestalia Polonica, Series A* 66: 249–260. doi:10.2478/ffp-2024-0018.
- Svoboda P (1942) Břek (*Sorbus torminalis* Crantz) neprávem opomíjená dřevina. Krása našeho domova, Břeclav, Czech Republic.
- Szymura TH (2012) How does recent vegetation reflects previous systems of forest management? *Polish Journal of Ecology* 60: 859–862.
- Szymura TH, Szymura M & Pietrzak M (2014) Influence of land relief and soil properties on stand structure of overgrown oak forests of coppice origin with *Sorbus torminalis*. *Dendrobiology* 71: 49–58. doi:10.12657/denbio.071.005.
- Tabandeh A, Tabari M, Nadoushan HM & Espahbodi K (2007) Heritability of some characteristics of *Sorbus torminalis* seedling. *Pakistan Journal of Biological Sciences* 10: 2760–2763. doi:10.3923/pjbs.2007.2760.2763.
- Tang CQ, Chen X, Deng YF, Geng L, Ma JH & Wei XY (2022) Complete chloroplast genomes of *Sorbus sensu stricto* (Rosaceae): comparative analyses and phylogenetic relationships. *BMC Plant Biology* 22: 495. doi:10.1186/s12870-022-03858-5.
- Thomas PA (2017) Biological flora of the British Isles: *Sorbus torminalis*. *Journal of Ecology* 105: 1806–1831. doi:10.1111/1365-2745.12857.
- The Ministry of Agriculture of the Czech Republic (2024) Národní program ochrany a reprodukce genofondu lesních dřevin. Egri.cz. <https://mze.gov.cz/public/app/erma2/web/Genofond/UjIndex>.
- Turok J, Collin E, Demesure B, Eriksson G, Kleinschmit J, Rusanen M & Stephan R (1998) Noble hardwoods network. Report of the second meeting, 22–25 March 1997, Lourizán, Spain. International Plant Genetic Resources Institute, Rome, Italy.
- Tylkowski T (2016) Przedsięwzięcie traktowanie nasion drzew, krzewów, pnączy i krzewinek. Warszawa, General Directorate of State Forests.

- Ulaszewski B, Sandurska E, Sztupecka E & Burczyk J (2017) The complete chloroplast genome sequence of wild service tree *Sorbus torminalis* (L.) Crantz. Conservation Genetics Resources 9: 419–422. doi:10.1007/s12686-017-0701-9.
- Ulaszewski B, Jankowska-Wróblewska S, Świło K & Burczyk J (2021) Phylogeny of Maleae (Rosaceae) Based on Complete Chloroplast Genomes Supports the Distinction of *Aria*, *Chamaemespilus* and *Torminalis* as Separate Genera, Different from *Sorbus* sp. Plants 10: 2534. doi:10.3390/plants10112534.
- Velebil J (2012) *Sorbus omissa*, a new endemic hybridogenous species from the lower Vltava river valley. Preslia 84: 375–390.
- Vít P, Lepší M & Lepší P (2012) There is no diploid apomict among Czech *Sorbus* species: a biosystematic revision of *S. eximia* and discovery of *S. barrandienica*. Preslia 84: 71–96.
- Walentowski H, Falk W, Mette T, Kunz J, Bräuning A, Meinardus C, Zang C, Sutcliffe L & Leuschner C (2017) Assessing future suitability of tree species under climate change by multiple methods: a case study in southern Germany. Annals of Forest Research 60: 101–126. doi:10.15287/afr.2016.789.
- Werres J & Blanke M (2019) Wild service tree (*Sorbus torminalis*) - queen of wild indigenous fruit. Erwerbs-Obstbau 61: 165–177. doi:10.1007/s10341-018-00413-1.
- Wilhelm GJ & Ducos Y (1996) Suggestions pour le traitement de l'alisier torminal en melange dans les futaies feuillues sur substrats argileux du Nord-Est de la France. Revue Forestiere Francaise 48: 137–143. doi:10.4267/2042/26817.
- Wojciechowski A & Bednorz L (2000) Estimation of mating-compatibility of the wild service tree (*Sorbus torminalis* (L.) Crantz) by observing pollen tube germination. Journal of Applied Genetic 41: 253–258.
- Zeitlinger HJ (1990) Die Elsbeere. Österreichische Forstzeitung 12: 35–37.