



# Flowering behavior of clones in a Norway maple (*Acer platanoides*) seed orchard and mating system analysis using nuclear SSR markers

Heike Liesebach<sup>1</sup> · Dagmar Schneck<sup>2</sup>

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## Abstract

Norway maple (*Acer platanoides* L.) is a tree species native to Central Europe and occurs in scattered or in small populations mixed with other tree species. Since Norway maple is considered to be adaptable to climate change, it has increasingly become a focus of forestry as one of the so-called alternative tree species to diversify species composition in forests. However, little knowledge exists on the phenotypic variation in the natural range, and no studies on the reproductive behavior of this monoecious and insect-pollinated tree species. The sexual system of Norway maple is known as heterodichogamous, with male-first and female-first flowering individuals mixed in a population. In a first step, we conducted a mating system analysis in a seed orchard. We used a recently developed set of species-specific SSR markers to genotype the parental clones and respective seed samples. The total seed had proportions of 68% outcrossed offspring between clones of the seed orchard, 11% selfing and 20% external pollination. Four flower types were observed, with protogynous and hermaphrodite types contributing more female gametes, while the protandrous type is highly variable in its female or male contributions. The number of ramets per clone in the seed set has a significant impact on the proportion of genetic contribution per clone to total seed yield. Conclusions are drawn for the establishment of new seed orchards and for further research.

**Keywords** Heterodichogamy · Protogynous · Protandrous · Parentage analysis · Forest reproductive material (FRM)

## Introduction

The Norway maple (*Acer platanoides* L.) is a tree species native to Central Europe and Germany. It occurs in scattered or in small populations and is predominantly mixed with other tree species. The species prefers to grow on deep, nutrient-rich soils with sufficient water supply. However, Norway maple is also adaptable to other conditions, such as moderately moist to very dry sites (reviewed in Caudullo and de Rigo 2016). To date, Norway maple has played only a minor role in forests, although the wood is similar to that of sycamore (Roloff and Pietzarka 1998). Better knowledge of

the adaptability and reproductive behavior of Norway maple populations may help to increase future consideration of this tree species, which is suitable as a mixed tree species, to diversify species composition in forests.

Norway maple is known as a monoecious, insect-pollinated tree species. It flowers at 10–15 years in the open, but after about 25–30 years in closed forests. The species exhibits heterodichogamy with different temporal and individual sex expressions as a feature of its sexual system. As described by Scholz (1960) for the floral biology of maple species, both protogynous and protandrous individuals occur, i.e., bisexual trees that flower first female or first male. Very detailed studies on flowering of maple species were conducted, e. g., by de Jong (1976) and by Tal (2006).

Norway maple is a diploid species with a chromosome number of  $2n = 26$  (Arohonka 1982). Compared to the tetraploid sycamore maple (*Acer pseudoplatanus* L.), it should therefore be methodically better accessible to genetic characterization. Nevertheless, very few population genetic studies have been carried out for this tree species. Initial studies were conducted in Finland to characterize intraspecific variation using isozyme markers (Rusanen et al. 2000,

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✉ Heike Liesebach  
heike.liesebach@thuenen.de

<sup>1</sup> Thünen Institute of Forest Genetics, Sieker Landstrasse 2, 22927 Grosshansdorf, Germany

<sup>2</sup> Forest State Office of Brandenburg, Authority for Forest Reproductive Material, Eberswalder Chaussee 3, 15377 Waldsiedersdorf, Germany

2003; Eriksson et al. 2003). Recently, a first analysis was performed in Latvian populations where SSR markers were transferred from other maple species (Ruņģis and Krivmane 2021).

Since Norway maple is considered to be adaptable to climate change, it has increasingly become a focus of forestry as one of the so-called alternative tree species. Several research projects have begun to fill the knowledge gap that exists compared to many dominant forest tree species. These include the establishment of provenance and progeny tests, as well as marker-based population genetic studies. Seed orchards play an important role in providing forest reproductive material for the rarer forest species such as Norway maple. For these rarer species, approved seed stands are often not available in sufficient numbers. Knowledge of sexual reproduction associated with flowering behavior is essential for seed orchard establishment. Here, we present first results on the flowering behavior of seed orchard clones and a mating system analysis using species-specific nuclear SSR (Simple Sequence Repeats) markers.

## Material and methods

### Seed orchard clones

The Norway maple clones for the seed orchard in Waldsiedersdorf (State Brandenburg) were selected between 1995 and 2006 in northern and eastern regions of Brandenburg. Most were found in natural forest stands or as spontaneous immigration of Norway maple into patchy, artificially established stands. The quality of the trunks and the health condition were primarily considerations for the selection. Since not enough suitable trees were found, slight deficiencies in the characteristics of trunk shape and twig formation had to be accepted. In addition to the evaluation of the single characteristics, each tree was given a score for overall impression. Flowering could not yet be addressed at this time, because the trees were evaluated in winter. After the grafting of clones, the planting of the seed orchard began in 2006 and was gradually completed. Thirty clones with one to eight ramets per clone were randomly distributed in a 5 × 5-m grid so that the area can be used both as an archive and as a seed orchard. The trees had reached heights of up to 10 m when they were first pruned in the fall of 2020. The plants are in good health, although the location is not optimal for this tree species.

### Assessment of flowering and fruit set

Single flowers of the first flush of an inflorescence were evaluated in four types:

- Hermaphrodites: Single flowers with fully developed pistil and stigma and simultaneously distinct anthers. Since a partially continuous trait manifestation was observed, the evaluation of whether the flower was to be classified as protogynous or hermaphrodite was often difficult.
- Protogynous: Pistil and stigma fully developed. The anthers are set, but shortened and delayed in development (Fig. 2, left side). If this type was found, the whole plant was considered protogynous.
- Protandrous: The anthers were fully formed, pistil was set on, but not (yet) fully developed. In contrast to the plants classified as purely male, the presence of pistils in some individual flowers of an inflorescence was sufficient to classify the tree at least as protandrous. Flowers with fully developed pistils and stigmas were found primarily in the last stage of an inflorescence at the end of the flowering season (Fig. 1).
- Males: The flowers showed exclusively anthers. The formation of a pistil was macroscopically not recognizable. This flower type did not change even at the end of the flowering period (Fig. 2, right side).

Flowering was recorded on one day in 2017 (April 21) and two days in 2018 (April 17 and 23). All trees were scored to determine if stamens or stigmas were fully developed in their individual flowers. Individual assessments of ramets at the different dates were summarized to an assessment of the clone to one of the four flower types. Sporadic receptive flowers were noted even at the late date on April 30, 2018, when fruit set was scored at five levels. These five levels are “No,” “Little,” “Medium,” “Abundant” and “Numerous” seed set, related to the observed variation range.

### Sampling and genotyping

Leaf samples from all ramets of the seed orchard were collected to verify clone identity. The available seed was harvested in 2020, despite the assumed suboptimal mating and low seed yield that year after a warm, sunny and very dry flowering period. Seed came from 21 clones in the seed orchard, with the number of seeds per clone ranging from 2 to 33. During embryo preparation, special care was taken to completely remove the brown seed coat to avoid contamination with the maternal genotype, and also to recognize possible twins. DNA extraction from leaf and embryo tissues was performed according to the procedure described by Dumolin et al. (1995).

A set of 15 species-specific nuclear microsatellite markers was recently developed by Lazic et al. (2022). It was optimized with partially redesigned primers for effective runs with two multiplex polymerase chain reactions (PCRs, Table 1). For locus Ap\_361727, the redesigned

**Fig. 1** Trunk shape of Norway maple trees (left: straight, right: crooked). Photographs kindly provided by Frank Becker, Eberswalde



**Fig. 2** Different flower types in Norway maple (left protogynous, right male)

forward and reverse primers are 5-CAACTCCAAATC CGGACAGG-3 and 5-ATCGAACCATGATGTTGATGT TTTT-3, making the amplicons 75 bp longer. For the locus Ap\_411647, the redesigned primers are 5-TGAGTC CCTTCATTTCCATTGT-3 and 5-TTTGGGTAACCA ATCGGTCC-3, respectively, resulting in 37 bp longer amplicons. For locus Ap\_658195, only the reverse primer was newly designed with 5-TCAATTATGCAGACAAAC ACACAT-3 to shorten the amplicons by 61 bp. Standard protocols for PCRs were applied using the Qiagen multiplex kit (Qiagen, Hilden, Germany) according to the manufacturer's instructions. Amplicons were separated on a Beckman Coulter capillary sequencer (Beckman Coulter, Framingham, MA, USA).

## Data analysis

Allele calling with some manual additions in the case of out-of-ladder alleles was performed using Genome Lab software version 10.2.3 (Sciex, Framingham, MA, USA). The software CERVUS 3.0.7 (Marshall et al. 1998; Kalinowski et al. 2007) was used to estimate combined exclusion probabilities assuming Hardy–Weinberg equilibrium. Parentage analysis was performed with COLONY software version 2.0.6.6 (Jones and Wang 2010; Wang 2013). This package can handle null alleles and typing errors and furthermore reconstruct unsampled parents. All 236 available seeds were included in this parentage analysis along with their known mothers. Genotypes from all 30 seed orchard clones and 28 additional previously genotyped ornamental Norway maple cultivars served as potential pollen donors. The full likelihood model was applied, and parameter settings chosen were polygamy with inbreeding, not updating allele frequencies and no sibship size prior. Replicated runs were done with different random seed numbers. Pearson correlation and corresponding p values were calculated using SAS 9.4 (SAS Institute Inc. (2016). In addition, the effective number of seed orchard clones and the effective clonal contribution to the analyzed seed were calculated according to Kang et al. 2001.



**Table 1** Set of 15 species-specific SSR markers in according to Lazic et al. (2022), optimized for a two-multiplex run (\*markers with redesigned primers using GenBank Accessions MT895404-MT895418)

Marker abbreviation	Original designation	PCR multiplex	Dye	Fragment length range (bp)	Number of alleles, total	Number of alleles (30 clones)
A64	Ap_64069	Set 1	Cy5.5	74–107	11	8
A65	Ap_658195 *	Set 1	Cy5.5	127–151	7	4
A27	Ap_274758	Set 1	Cy5	161–191	15	9
A63	Ap_638034	Set 1	Cy5.5	173–205	15	9
A67	Ap_671221	Set 1	DY751	188–216	10	8
A33	Ap_33364	Set 1	Cy5	224–240	10	8
A18	Ap_188503	Set 1	DY751	239–259	5	5
A36	Ap_361727 *	Set 1	Cy5	261–285	10	7
A48	Ap_488207	Set 2	Cy5	87–107	5	3
A44	Ap_44827	Set 2	Cy5.5	86–110	13	9
A54	Ap_541809	Set 2	DY751	107–140	6	3
A20	Ap_20237	Set 2	Cy5	176–212	13	9
A50	Ap_501482	Set 2	DY751	232–244	7	5
A37	Ap_374910	Set 2	Cy5.5	214–260	14	8
A41	Ap_411647 *	Set 2	Cy5	261–287	13	9

## Results

### Flowering behavior

Flowering behavior was studied in a year with medium flowering intensity in 2018 and low to medium intensity in 2017. Despite a good flowering onset in 2019 and 2020, many flowers did not open due to harsh weather conditions. In general, good synchrony was observed among clones, with no visible outliers of extremely early or late flowering, despite occasional single late flowers observed. Of the 30 clones analyzed here, flower type could be scored on more than one date in 2017 and 2018 in 27 cases. Thirteen cases led to the same result, and in 14 cases no or only a weakly developed male flower was visible in 2017. Of the clones classified as pure male in 2018, two showed a fruit set in 2020, albeit low. These were assigned to the protandrous clone group, leaving only four pure male clones. Overall, a uniform flowering behavior was observed for the ramets within a clone. Some individual cases with non-uniform flower types were suspected to be mislabeled clones, which was then confirmed by genetic analysis and corrected in the assignment.

The summarized classification of fruit set depending on flower type per clone is shown in Table 2. As expected, fruit set is higher in clones with protogynous and hermaphrodite flowers (Table 3). Fruits of these flowers are numerous and densely arranged, and were observed in the first level with short fruit stalks. Surprisingly, three of the protandrous clones also still showed an abundant fruit set. In protandrous flowers, often only a few fruits are formed at the end of a long, multiply-bent fruit stalk.

### Mating system analysis

The high resolution of the applied marker set allowed a reliable clone identification and parentage analysis. This was demonstrated by preliminary exclusion probabilities, which could be estimated from a natural population located in Brandenburg (Germany). The identity per chance of unrelated individuals at all genotyped markers can be expected with a probability of  $4.6 \times 10^{-16}$ , and for sibling individuals with a probability of  $1.3 \times 10^{-6}$ . The average probability of excluding an unrelated candidate from parentage, when considering the genotypes of offspring and the other parent, was estimated to be  $6.4 \times 10^{-6}$ .

Replicated COLONY runs showed that all individual seeds could be matched to their known mothers and identical pollinators among the seed orchard clones, while all horticultural cultivars previously recorded were completely excluded as pollinators. The number of assumed, unsampled parents was nearly identical among the runs. Specifically, 27 seeds originated from self-pollination (11.4%), 161 seeds were from cross-pollination within the seed orchard (68.2%), and 48 seeds resulted from pollination of unidentified trees outside the orchard (20.3%). In addition to the 21 clones that served as maternal parents, 24 clones from the seed orchard were involved as pollinators. In total, 27 clones participated in seed production, plus approximately 20 unknown pollinators, each involved between one and four times (Table 2). Thus, the crossing scheme of all 236 seeds could be fully resolved (Table S1, Supplementary information).

The effective number of clones in the seed orchards is 22.1 according to Kang et al. 2001. The relative effective clone number of 0.74 is based on the census number of 30

**Table 2** Flowering behavior of seed orchard clones, seed set and number of contributed gametes per clone derived from parentage analysis

Clone designation	Number of ramets	Summarized flowering behavior 2017, 2018	Seed set 2018	Number of seeds/ female gametes 2020	Number of pollen contributions	Number of selfings
0501	5	Hermaphroditic	Numerous	33	9	4
0512	3	Hermaphroditic	Medium	3	1	
0702	1	Hermaphroditic	Medium	2		
0710	3	Hermaphroditic	Medium	20		
0712	3	Hermaphroditic	Numerous	14	6	2
0716	1	Hermaphroditic	Numerous	10	6	3
0502	3	Protogynous	Abundant			
0503	2	Protogynous	Medium	2	3	
0507	6	Protogynous	Abundant	11	6	
0704	2	Protogynous	Abundant	13	10	2
0711	6	Protogynous	Abundant	15	7	4
0504	4	Protandrous	Little		9	
0506	1	Protandrous	Little		5	
0508	4	Protandrous	Medium	3	13	
0509	3	Protandrous	Little	15	8	
0510	2	Protandrous	Little	8	5	2
0513	6	Protandrous	Little	26	10	3
0706	2	Protandrous	Little	3	9	
0708	2	Protandrous	Abundant	5	3	1
0714	8	Protandrous	No	9	23	1
0715	1	Protandrous	Little			
1502	6	Protandrous	Abundant	23	3	1
1503	4	Protandrous	Medium	11	16	2
1504	5	Protandrous	Abundant		9	
1505	3	Protandrous	Medium	5	7	2
1508	1	Protandrous	No	5		
0701	3	Male	No		12	
0703	1	Male	No		1	
1506	2	Male	No			
1507	1	Male	No		7	
Unknown					48 (20.3%)	
Sum	94			236	236	27 (11.4%)

**Table 3** Characteristics of Norway maple clones in a seed orchard assigned to four flower types along with their fruit set classification and amount of genetic contributions to seed

Flower type	Number of clones	Fruit set 2018					Number and percentage of gamete contributions 2020		
		No	Little	Medium	Abundant	Numerous	Female	Male	Selfings
Hermaphroditic	6			3		3	82 79%	22 21%	9
Protogynous	5			1	4		41 61%	26 39%	6
Protandrous	15	2	7	3	3		113 48%	120 52%	12
Male	4	4						20 100%	

Percentages of female and male contributions refer to each flower type

clones and corresponds to the unbalanced number of ramets. In the seed sample, this value reduces to 18.7 and 0.62, respectively, indicating additional effects.

The dependence of the gametic contributions of the clones to the total seed on the number of ramets per clone proved to be highly significant (coefficient of determination  $R^2=0.479$ ,  $p<0.0001$ , Fig. 3). For female contributions, the coefficient of determination is  $R^2=0.247$ ,  $p=0.0083$ , and for male contributions, it is  $R^2=0.320$ ,  $p=0.0021$ .

Some additional observations could be made. From a total of 43 analyzed cases of seeds from paired wings, 22 pairs were pollinated by the same father (full-sibs), whereas 17 pairs were pollinated by two different fathers (half-sibs). In addition, embryo preparation from two mother trees revealed three cases of twins. Each pair of twins consists of two separate embryos with distinct seed coats within one seed. In all cases, their multilocus genotypes indicate that two different maternal haplotypes were pollinated to form a twin seed. Two twin pairs were pollinated by the same father, and the third twin pair has two different fathers. All observed twins are clearly dizygotic.

## Discussion

The four observed flower types with various sexual organs in Norway maple seed orchard clones (protogynous, hermaphrodite, protandrous and male) show good agreement within clones when comparing individual ramets and also between observation years. Thus, our observation confirms once more many other studies, which documented that the flower type of an individual or clone remains largely constant over years in Norway maple trees, despite occasional deviations, which are described repeatedly (e. g., Wright 1953; de Jong 1976; Tal 2006). In our study, deviations occurred

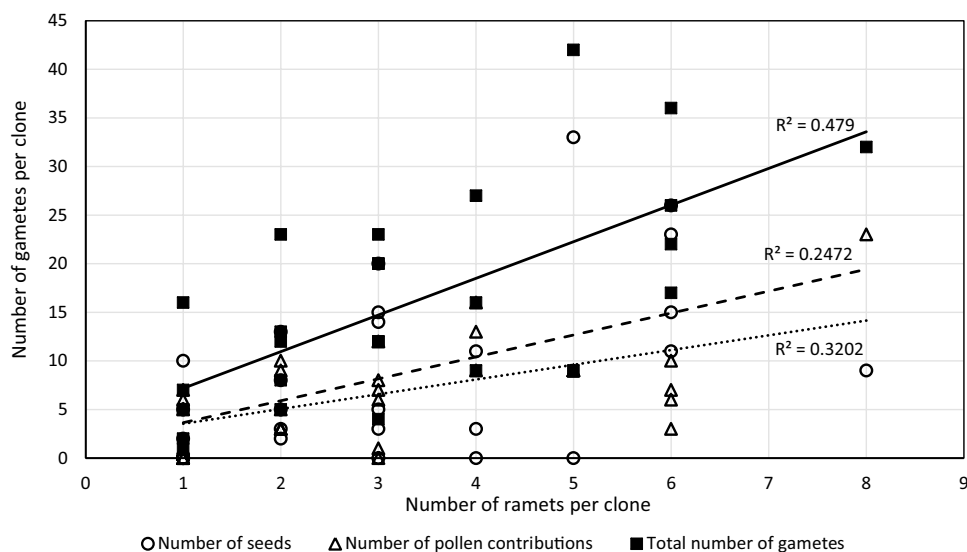
in particular for clones originally evaluated as purely male, which then developed a few functional female flowers. Since the plants examined are young, a dependence on the age of the ramets cannot be ruled out.

In the clonal material studied here, the protandrous flower type is most common, while the other three flower types, hermaphrodite, protogynous and male, are less common and in relative balance. For comparison, we made a roughly estimate of the frequency of flower types of Norway maple in natural populations using data from more than 400 individuals from various studies and sites (compiled by de Jong 1976). Protogynous and protandrous types appear to be the most frequent at about 40% each, followed by duodichogamous types (flowering order male–female–male) and pure males at about 10% each. Other types appear to be relatively rare. However, the large variability between studies was striking. When our two types, hermaphrodites and protogynous, are combined, the frequency distribution does not vary as much from other reports. The combination into one type seems to be justified, especially since the hermaphrodites are probably functional females.

Extremely unbalanced female and male contributions per clone to the total seed sample were revealed by the reliable parentage analysis applying highly variable, species-specific genetic markers. First, this appears to be influenced by the clone specific flower type. As expected, clones with hermaphrodite or protogynous flowers contribute exclusively or at least predominantly as female parents. Protandrous types, however, show a broad variability in their relative male and female contributions. Second, the number of parental contributions to the total seed is significantly affected by the number of ramets per clone. Thus, nearly half of the total variance in seed yield is explained by the ramet numbers.

Further factors may have influenced the mating pattern, particularly the heterodichogamous breeding system

**Fig. 3** Number of contributed female and male gametes per clone to the total seed sample in dependency from the number of ramets per clone in a Norway maple seed orchard (Linear correlations: Continuous line for total number of gametes  $p<0.0001$ , dashed line for number of seeds  $p=0.0083$ , dotted line for number of pollen contributions  $p=0.0021$ )



of Norway maple, which is thought to influence to the frequency of certain parental pairs. This breeding system, which mainly combines two reciprocal forms in populations, the male first- and the female first-flowering individuals, acts as a biological mechanism to prevent or reduce self-fertilization.

An almost complete temporal separation of sexes within individuals was observed by Haas (1933). He described a mostly very sudden change between the sexes within an individual according to his daily observations during the flowering period of 15 Norway maple trees over three years. Simultaneous functional male and female flowers were observed in only 1–5% of cases depending on the year of observation. A slightly overlap of sexes within trees under average humidity and temperature conditions was observed by Gabriel (1967) for *Acer saccharum*. A detailed study of four large Norway maple trees (more than 30 m in height, one tree protandrous and duodichogamous and three trees protogynous) was conducted by Tal (2006). He observed a proceeded flowering process from lower to upper crown. Despite a clear temporal gender separation within inflorescences, some overlap of sexes occurs within crowns of large trees.

The fact that 11.4% of the seeds were from self-fertilization, as found in the parentage analysis in our study, clearly indicates that there is at least a partial overlap between the male and female flowering periods even in smaller trees. This overlap could exist between individual flowers within an inflorescence, but more probably between different inflorescences of a single tree, or between ramets of a clone in the seed orchard. Self-fertilization occurs in all three of the four flower types studied here, with the exception of the pure males. Our results agree well with those of Kikuchi et al. (2009), who determined the self-fertilization rate in a natural *Acer mono* population with more than 1000 seeds collected from four trees. This analysis was also performed with microsatellite markers, and the self-fertilization rate averaged 9.8%. In addition to genetic evidence of self-fertilization in heterodichogamous *Acer* species, a crossing experiment with controlled self-pollinations was conducted by Gabriel (1967). He self-pollinated more than 700 flowers from seven *Acer saccharum* trees, resulting in an average seed set of 15.2%.

Despite a certain amount of selfing, the heterodichogamous breeding system obviously promotes crossbreeding, as 70.2% of cross-pollinated offspring was derived from matings between different flower types in our study, even when summarizing hermaphroditic and protogynous clones into one group (see also Table S1). A very similar result was reported by Kikuchi et al. (2009) with 72% of seeds with identified male parent in an *Acer mono* population, which were pollinated by trees of the reciprocal morph.

The results of our study are from a relatively small and young seed orchard in a non-mast year and should therefore

be considered preliminary. The effective number of seed orchard clones is significantly lower than in many seed orchards of conifer species (e.g., reported by Kang et al. 2001), but the relative effective clone number, reflecting imbalances in ramet numbers, is of a comparable order of magnitude.

## Conclusions

Currently, only about 10 ha of approved seed stands (category “Selected”) and two seed orchards (category “Qualified”) are available for the supply of forest reproductive material for the German lowlands and midlands (national statistics, BLE 2019). There is a need for more seed orchards for this tree species, not only because of its predominantly scattered distribution pattern, but also for more efficient seed harvesting (Paul et al. 2020). For future seed orchards, priority will be given to clones of at least medium quality and at least medium seed set, which is typically present in hermaphrodite and protogynous trees. Protandrous and male flowering clones will be involved if they scored above average in the quality criteria. In addition, a well-adjusted number of ramets per clone in future seed orchards should be achieved for a balanced genetic diversity (Liesebach et al. 2021).

The established multiplex system using nuclear microsatellite markers is very reliable and efficient to analyze mating systems in Norway maple populations. This is important for seed orchards, where the female contribution of clones to seed yield can be easily assessed, while the contribution of pollen can only be quantified by marker-based parentage analyses. Moreover, the marker system will allow detailed analysis of the mating system in natural populations of this heterodichogamous and insect-pollinated tree species to provide information on the transfer of genetic diversity from adult plants to the progeny generation. Knowledge of spatial structures and pollination distances will support approval procedures for seed stands as well as develop recommendations for representative seed harvest. In addition to questions about gene flow within populations, research should be conducted to determine whether there is evidence of outcrossing from ornamental or horticultural varieties into natural populations or approved seed stands of Norway maple.

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**Availability of data and material** Upon acceptance for publication of the manuscript, all data on SSR genotypes will be made available on request.

## Declarations

**Conflict of interest** The authors have no conflicts of interest to declare that are relevant to the content of this article.

**Consent to participate** The authors agreed to participate in the described study.

**Consent for publication** The authors agreed to publish the results described in this manuscript.

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