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ORIGINAL ARTICLE

# Genetic basis of wavy grain in sycamore maple (*Acer pseudoplatanus* L.): Indications for a locus with dominant effect

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## Abstract

Wavy grain is a rare and highly valued wood characteristic that significantly increases the market price of sycamore maple (*Acer pseudoplatanus* L.) timber. However, the genetic basis of this striking trait has remained unclear. Here, the inheritance of this trait was investigated using a unique two-generation pedigree including progeny of 21 parental sycamore maple clones, several of which exhibit wavy grain. Parentage analysis based on 12 microsatellite markers enabled the reliable assignment of most of the 599 offspring to defined parental combinations in this tetraploid species. Wood structure was assessed macroscopically in 113 felled trees from a 35-year-old field trial and classified as either wavy or straight grain. The observed segregation patterns were consistent with a dominant mode of inheritance: 71% of offspring with at least one wavy-grained parent developed wavy grain, whereas none of the offspring from two straight-grained parents exhibited the trait. The occurrence of wavy grain among offspring of wavy-grained fathers and straight-grained mothers suggests genetic inheritance through the nuclear genome. Taken together, the results provide first indications for a nuclear genetic contribution to the inheritance of wavy grain in sycamore maple. Due to the limited sample size and the tetraploid genome structure, more complex inheritance patterns cannot be completely excluded. Nevertheless, these findings offer a basis for future studies aimed at elucidating the underlying mechanisms of this rare wood characteristic and may support breeding and conservation strategies.

## Key Message

Wavy grain in sycamore maple wood appears heritable and may be associated with a nuclear locus showing a dominant mode of inheritance.


**Keywords** Acer pseudoplatanus · Fiddleback maple · figured wood · inheritance · two-generation pedigree · tetraploidy

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## Introduction

Timber from sycamore maple (*Acer pseudoplatanus* L.) is one of the more valuable hardwoods on the market. It is very light-coloured, ranging from creamy white to almost white, rarely tending toward reddish (Richter 1988; Jeske and Grosser 2009). Its fine and uniform texture makes it especially suitable as a veneer for high-quality furniture and interiors. Due to its vulnerability to wood-destroying organisms, it is rarely used for construction purposes (Richter 1988; Rusanen and Myking 2003; Jeske and Grosser 2009). In contrast, because of its good physical-acoustic properties and aesthetic reasons, this wood is highly appreciated for the manufacturing of musical instruments (Richter 1988; Jeske and Grosser 2009). The occurrence of wavy grain wood is known from several tree species, but is best documented from sycamore maple (Eisold et al. 2023). Traditionally, the backs of stringed and plucked instruments such as violins are made primarily of maple. In particular, highly figured maple is often preferred for this purpose (Jeske and Grosser 2009). Therefore, the term "fiddleback maple" is often used to describe this distinctive grain formation. It refers to a wavy grain pattern that runs radially across the axis of the tree trunk and is not visible on the surface of the tree. As a result of the vascular cambial activity, straight, spiral, interlocked, or even wavy wood grains are produced. The fusiform and ray cambial cells concertedly produce vertically and horizontally orientated elements of the vascular system (Krishnamurthy et al. 2015, 2019). The formation of wavy grain is characterised by a periodical change of fibre orientation, creating a wave structure within the annual rings (Scholz 1960; Richter 2015) (Fig. 1A, B). However, the wavy grain structure only appears from an indeterminate age of the tree and is never visible from an early developmental stage of the maple. The underlying biological mechanism that initiates this transition is still unclear (Hejnowicz and Romberger 1979; Sopushynskyy and Teichinger 2013). A possible explanation has been proposed by Haag et al. (2019, 2020), based on a series of studies addressing wood development and recent observations (Haag et al. 2023; Haag and Lehne, unpublished data). They suggest that the formation of wavy grain may be related to changes in cell morphology during the transition from juvenile to adult wood.

The wavy structure can be both seen and felt when a piece of wavy grain wood is split in the radial direction because it separates along the rays and the undulating grain (Hein et al. 2009) (Fig. 1C). Conversely, the tangential surface of the stem remains smooth, and while the wavy grain is visible, it is not tactile (Hein et al. 2009). When the radial surface of wavy grain wood is planed, the undulating tissue gets

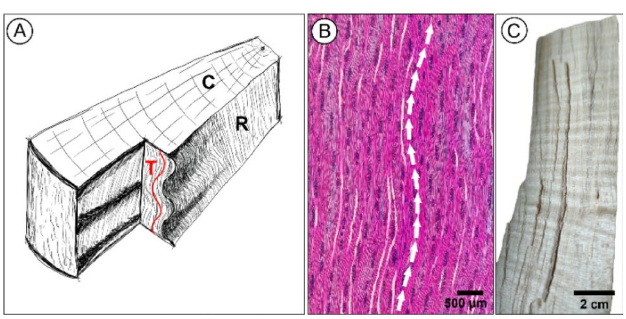



**Fig. 1** Wavy grain in sycamore maple timber. **A**) Schematic representation of wavy grain structure in wood, in style of Richter 2019; C = Cross section, R = Radial section, T = Tangential section; **B**) stained microscopic tangential section of sycamore maple, white arrows highlight the wavy grain orientation; **C**) "Washboard Effect" on a piece of sycamore maple split in radial direction

cut, and depending on its cellular orientation, light will be reflected differently across the surface. This results in a distinct pattern of alternating light and dark stripes, as well as the unique aesthetic of this feature (Beals and Davis 1977; Conrad 1988; Richter 1988, 2019). At the microscopic level, wavy grain is most easily identified in the tangential plane. Here, the feature is defined by a sinuous alignment of all cell types, which can be best observed by following the course of the vessel elements (Lewandrowski et al. 2024) (Fig. 1B). Wavelengths and amplitudes can vary individually within a trunk and are rarely uniform. The wavelength can range from 0.7 to 2 cm, while the amplitude can reach up to 0.3 cm (Wedel 1964).

To ensure clarity in terminology throughout this study, we adopt the following definitions: Figured wood is used as an umbrella term encompassing various distinctive fibre patterns such as wavy grain, bird's eye, flame, and burl. In the following, we refer to the phenomenon of undulating fibres in the tangential plane as wavy grain, whereas wood with regularly aligned fibres is referred to as straight grain.

Although studies have shown promising results in investigating wood defects as well as curly birch using ultrasound (Bucur 2005; Salmi et al. 2007, 2009), these methods rely on local density variations caused by ingrown bark (e.g., curly birch) or decayed areas caused by fungi. However, these phenomena are fundamentally different from the subtle fibre undulations that create the wavy grain (fiddleback) figure investigated in this study (Fig. 1). On a standing tree, the wavy grain structure can currently only be identified invasively by removing parts of the bark. These bark windows can give a hint of the wood's appearance in the trunk. If wavy grain is present, it can be recognised by the wavy pattern of the pore grooves (Wedel 1964). However, this method does not allow a reliable statement about the appearance of the wood trait throughout the entire trunk (Lewandrowski et al. 2024). Furthermore, this method is not very suitable, since such an injury creates an entry point for microorganisms that can severely degrade the quality of the wood over time. In most cases, this feature can only be reliably evaluated after the tree has been felled.

Trunks of sycamore maple and other tree species with this special wood structure regularly achieve top prices at timber auctions. Rieder (1998) reports a 1.5- to 2-fold increase in value when the wood anomaly occurs. However, more recent studies indicate that wavy-grained sycamore maple can fetch significantly higher prices, exceeding the value of straight-grained sycamore maple by a factor of 20–40 or even 50 (Eisold et al. 2024).

According to current knowledge, the occurrence of the natural anomaly of wavy structure is relatively rare. Conrad (1957, Conrad 1977a, b) reported that the trait was found in 3% of standing trees in the late 1950s during the search for suitable breeding material in northern Hesse, Germany. From a felling in 1960/61, 6% of 185 trunks showed wavy grain structures. Since only a small area of the wood surface could be observed during the tests, this likely represents the lower threshold (Wedel 1964). The occurrence and intensity of wavy grain can vary along the trunk. Some stems show the phenomenon only on one side, while in others the whole stem and even branches exhibit wavy grain (Conrad 1957; Wedel 1964). It can also be easily confused with static fibre compression or wrinkling at the root flares and branch axils (Conrad 1977b).

The fundamental causes of the wavy grain structure have not yet been clarified. Initially, specific site and environmental conditions were considered as possible causes for this rare wood feature. However, Krajnc et al. (2015) found no large-scale geographic variation in the frequency of wavy grain occurrence. Their results indicate that environmental conditions or provenance alone are unlikely to explain its formation. This is consistent with earlier studies reporting no correlation with soil type, climate, altitude, or wind exposure (Conrad 1957). Nevertheless, reports of local clusters in some regions, such as in the Göttingen area in Germany (Conrad 1977b), suggest that local genetic effects or small-scale environmental influences might play a role. Based on many years of observation, forest practitioners have assumed that certain wood structures, such as wavy grain or bird's eyes, may be influenced by both genetic and environmental factors, which have not yet been conclusively separated. However, a purely genetic determination of wavy grain has not yet been confirmed in practice or in science regarding the appearance of wavy grain (Conrad 1977a, 1988). In the 1980s, there were indications of the stability of trait expression through grafting (Conrad 1988; Naujoks et al. 2013), suggesting the involvement of genetic factors and a possible inheritance.

It is hypothesised that the orientation of cambial cells is the most important factor in the formation of wavy grain patterns and thus contributes to the formation of the wavy grain appearance (Harris 1989; Kramer 2006; Kúdela and Kunštár 2011). However, the reasons for the reorientation of cambial cells and how this process is influenced are still unclear. In addition to the expression of certain genes, which could play a role, phytohormones or even anatomical factors could also contribute to the formation of figured wood. Moreover, epigenetic changes have also been taken into consideration as potential contributors to wavy grain formation (Naujoks et al. 2013). Since wavy grain also occurs in other hardwoods, such as walnut (Michler et al. 2007; Wagenführ and Wagenführ 2022), ash (Sopushynskyy and Teischinger 2013; Wagenführ and Wagenführ 2022), oak (Riesco Muñoz 2021; Wagenführ and Wagenführ 2022), aspen (Fan et al. 2013), as well as in various tropical woods (Richter 2019) it is a growth anomaly occurring in different taxonomic groups that may be related to general wood formation processes.

Some efforts have already been made to investigate the inheritance of particular wood characteristics in different tree species. In some cases, such as curly birch (*Betula pendula* var. *carelica*) (Kärkkäinen et al. 2017) and hybrid aspen (*Populus* × *canescens* hybrid) (Fan et al. 2013), there is evidence of a genetic component. In contrast, for black walnut (*Juglans nigra* L.) (McKenna et al. 2015), environmental factors appear to play a more dominant role. First indications of the genetic inheritance and stability of wavy grain structure in sycamore maple were provided by Quambusch et al. (2021), which have been incorporated into the inheritance analysis of this study. By examining 21 trees from progeny trials at Romrod and four parental samples from plus tree grafts at the Reinhardshagen seed orchard, Quambusch et al. (2021) concluded that wavy grain is most likely genetically determined. These findings provided an important basis for further analysis in this study, particularly with regard to the hypothesis of genetically dominant inheritance of the trait.

For sycamore maple, we took advantage of globally unique experimental material to test hypotheses on possible modes of inheritance of this distinct wood trait. This material included clones from an old seed orchard, comprising several wavy-grained parental clones and their open-pollinated progeny grown in a field trial. This type of material allowed us to reconstruct a two-generation pedigree by using genetic markers. Both the exact pedigree reconstruction and the disentanglement of the inheritance mode of neutral alleles at microsatellite markers in this tetraploid tree species were part of another comprehensive study (Bäucker and Liesebach, unpublished data). Here, we focus on the results of the wood structure analysis, which suggest that the wavy grain trait in sycamore maple is influenced by genetic factors and may follow a Mendelian mode of inheritance. The inheritance analysis of sycamore maple is challenging because the species is tetraploid, with a chromosome number of $2n=4x=52$ (Foster 1933; Siljak-Yakovlev et al. 2010; Contreras and Shearer 2018). This differs from the diploid level found in several other *Acer* species ($2n=26$; Petrova et al. 2007). Sycamore maple is often referred to as an autotetraploid species, which means that it arose through an intraspecies duplication, but an allotetraploid origin, which arose through hybridisation, cannot be ruled out. However, the species shows bivalent chromosome arrangements in meiosis (Foster 1933) and a diploid-like segregation of microsatellite markers (Bäucker and Liesebach, unpublished data).

Obviously, tetraploidisation was followed by diploidisation, so that today a quasi-diploid mode of inheritance is present. This scenario is taken into account in the genetic modeling presented in this study.

## Materials and methods

### Experimental plots

#### Parental material

From 1959 to 1964, a seed orchard was established by the former Hessian Forest Research Institute in the Reinhardshagen forestry district, Hesse (Germany), consisting of sycamore maple clones from Bovenden (Bov), Göttingen (Goe), Meißner (Me), and Sooden-Allendorf (Sal), Germany. Twenty-one clones were propagated by grafting, and 28–29 ramets per clone were planted in the field. This material was mentioned by Conrad (1957) as part of the systematic search for breeding material. The primary intention of this seed orchard was to obtain high-quality sycamore maple seed. Therefore, selection criteria focused on stem straightness and mass but also included special wood properties, such as wavy grain and bird's eyes (Quambusch et al. 2021). Further details on the selection, establishment, and management of the seed orchard are provided in Quambusch et al. (2021).

#### Progeny material

To evaluate the performance of progeny from this seed orchard, open-pollinated seeds were harvested from 13 of the 21 clones. With the plants raised from this material, a field trial was established in 1986 at two experimental sites in the forestry districts of Romrod and Schotten, Hesse (Germany). The soil composition, trial design, and genetic background of the tested progeny have been described in detail by Quambusch et al. (2021).

### Genotyping and parentage analysis

For the genotyping of the 21 parental clones and 599 offspring individuals, 12 microsatellite markers from different *Acer* species were combined into three different multiplex PCR sets as described by Bäucker and Liesebach (2018). All markers were known from the literature and have been shown to function well for sycamore maple in other studies (e.g. Neophytou et al. 2017; 2019). After PCR, the DNA fragments were electrophoretically separated on a capillary sequencer CEQ-8000 (Beckman-Coulter). For allele scoring, the software GeneMarker Version 3.1 was used. The parentage analysis was performed using the software COLONY (Jones and Wang 2010; Wang 2013) and adapted to the tetraploid state of the species by coding all alleles of the 12 markers as presence/absence (Wang and Scribner 2014).

The parentage analysis also included a stepwise partial genotype reconstruction for the most frequently unsampled parents. In the majority, these reconstructed genotypes belonged to the meanwhile removed rootstocks of grafted clones, which were frequent contributors to the progenies.

Microsatellite genotypes were used to assign the offspring individuals to different groups of full- and half-sib families. These groups represent different parental combinations of wood structure, such as (i) wavy grain mother and a straight grain father, (ii) straight grain mother and a wavy grain father, (iii) both parents with wavy grain structure, and (iv) both parents without this trait. Out of these different parental combination groups, a total of 113 offspring individuals were felled and analysed both micro- and macroscopically for indications of wavy grain.

In order to estimate the reliability of the parentage analysis, the exclusion probabilities were calculated using the CERVUS software version 3.0.7 (Kalinowski et al. 2007). The probabilities for the identification of an incorrect first parent are $4*10^{-3}$, for the identification of an incorrect second parent $7*10^{-7}$ and for the identification of an incorrect parent pair $9*10^{-6}$. Although deviations from the Hardy–Weinberg population model may exist in the seed orchard, these values provide a good orientation.

### Wood analysis

A total number of 113 sycamore maple trees from the two progeny trial sites were selected for felling for wood analysis in 2017 (Quambusch et al. 2021), 2022 and 2023. At the time of felling, the trees had reached heights of up to 30 m, and had a maximum diameter at breast height (dbh) of 40 centimetres. The trees chosen for felling were selected based on their family affiliation, as determined by the parentage analysis, and their minimum diameter for technical reasons.

As described in Lewandrowski et al. (2024), the surfaces of the harvested trees were macroscopically analysed to detect any irregularities indicating an underlying wavy grain structure. In a second step, the bottom 1-metre stem segments of the trees were ripped into quarter-sawn boards using a horizontal bandsaw. The resulting radial surfaces were planed and evaluated. To reduce the number of categories for hypothesis development on inheritance, the presence or absence of wavy grain had to be determined visually for each tree (Fig. 2), initially without considering the qualitative or quantitative characteristics of the detailed wood analyses.


**Fig. 2** Planed radial surfaces of 36-year-old sycamore maple, **A** = wavy grain, **B** = straight grain, b = bark, o = outer surface, i = inner surface

## Results

### Pedigree reconstruction

The genotypic multilocus information from 599 progeny samples and 28 parents (both 21 parental clones and 7 reconstructed genotype rootstocks of grafted clones) was used to reconstruct the pedigree. Moreover, the experimental design of the two field trials was considered to decide whether one of the two parents was the female or the male. For 436 of 599 progeny samples, the mother was identified as one of the seed orchard clones. The other 163 progenies descended from at least seven rootstocks of grafted clones with unknown wood structure. For 530 offspring individuals, the father was identified as one of the seed orchard clones. The remaining 69 individuals were pollinated by unknown fathers or partly by rootstocks of clones.

Based on the results of the parentage analysis, the offspring individuals were grouped according to the known wood characteristics of the seed orchard clones (Table 1). A total of 16 trees were found to descend from two wavy-grained parents. Furthermore, 239 trees had one parent with wavy-grained wood. Of these trees, 211 were derived from the combination of a wavy-grained mother and a father with a straight or unknown grain structure. The remaining 28 offspring had a wavy-grained father in combination with a straight-grained or unknown mother.

In the case of unknown parents, they were assumed to be more likely to have a straight wood structure, since the occurrence of wavy grain has been reported at 1–6% in natural populations of sycamore maple (Conrad 1957; Wedel 1964; Rohr and Hanus 1987; Maurer 1997; Rieder 1998).

### Wood traits in offspring samples

The inner surface areas of all samples, roughly the first 10–15 years of growth, consistently appeared as straight grain (Fig. 2A). If the characteristic light and dark stripes, serving as the typical indicator for wavy grain, occur, the wavy pattern is initially inconspicuous and becomes more and more distinct with increasing age of the tree.

The wood analysis of the 113 selected sycamore maple trees resulted in a classification of 66 wavy-grained and 47 straight-grained individuals. Variations in the expression of the wavy grain feature were observed.

### Wavy grain traits of selected offspring individuals

In principle, the wood traits of all progenies with at least one wavy-grained parent (grey fields in Table 2) are informative for the development of hypotheses about the type of inheritance. In practice, however, the focused was placed on members of larger full-sib and half-sib families and on trees with sufficient diameter, as the capacity for wood analysis was limited. Following this, of the 113 analysed trees, 93

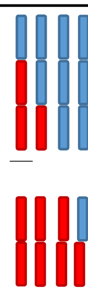
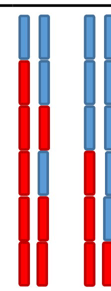
**Table 1** Assignment of 599 offspring individuals from the seed orchard to parent pairs grouped by parental wood trait. "Unknown" refers to rootstocks of grafted clones (mother and father) or to external pollination (father). Fields highlighted in dark grey represent offspring with two wavy grain parents, while fields highlighted in light grey indicate offspring with one wavy grain parent ($N$=239). Numbers in brackets represent the number of felled trees used for the wood analysis

| Mother \ Father | Wavy grain | Straight grain | Unknown |
|---|---|---|---|
| Wavy grain | 16 (9) | 183 (69) | 28 (8) |
| Straight grain | 16 (5) | 181 (5) | 12 (0) |
| Unknown | 12 (2) | 122 (14) | 29 (1) |

**Table 2** Counts of wavy- and straight-grained offspring individuals per family, assigned to their parental clones, given in the format "Wavy : Straight". Parent clones in bold are wavy-grained. Fields highlighted in light grey indicate offspring that originated from one wavy grain parent. Fields highlighted in dark grey indicate offspring that originated from two wavy grain parents. The table includes 113 felled offspring individuals that were used for wood analysis

| Parental clones acting as mothers | Parental clones acting as fathers: Goe2 | Goe4 | Goe5 | Goe10 | Goe12 | Goe15 | Goe16 | Me1 | Me3 | **Me4** | **Me6** | **Me10** | Sal3 | Unknown | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Goe4 | — | — | — | — | — | — | — | 0 : 1 | — | 1 : 1 | — | — | — | — | 1 : 2 |
| Goe5 | — | — | — | — | — | — | — | — | — | — | 1 : 0 | — | — | — | 1 : 0 |
| Goe16 | — | — | — | — | 0 : 1 | — | — | 0 : 1 | — | — | 1 : 0 | 1 : 0 | — | — | 2 : 2 |
| **Me4** | — | — | — | — | 1 : 0 | — | — | — | — | — | — | — | 5 : 1 | 0 : 1 | 6 : 2 |
| **Me6** | — | — | 9 : 0 | 2 : 0 | — | 1 : 4 | — | — | 0 : 1 | 2 : 0 | — | — | — | 1 : 0 | 15 : 5 |
| **Me7** | 0 : 1 | — | 3 : 1 | — | — | — | 1 : 0 | — | | 3 : 0 | — | — | — | 0 : 1 | 7 : 3 |
| **Me10** | 0 : 1 | 0 : 1 | 13 : 5 | — | — | — | 0 : 1 | 1 : 0 | 10 : 7 | 1 : 2 | 1 : 0 | — | — | 4 : 1 | 30 : 18 |
| Sal3 | — | — | 0 : 1 | — | — | 0 : 1 | — | — | — | — | — | — | — | — | 0 : 2 |
| Unknown | — | 0 : 3 | 1 : 2 | 1 : 1 | 0 : 1 | 0 : 2 | — | — | — | — | 1 : 1 | — | 1 : 2 | 0 : 1 | 4 : 13 |
| Total | 0 : 2 | 0 : 4 | 26 : 9 | 3 : 1 | 1 : 2 | 1 : 7 | 1 : 1 | 1 : 2 | 10 : 8 | 7 : 3 | 4 : 1 | 1 : 0 | 6 : 3 | 5 : 4 | 66 : 47 |

**Table 3** Possible genotypic configurations at a hypothetical tetraploid locus responsible for the wavy grain wood structure in sycamore maple. Phenotypes are shown under the assumption of dominant inheritance, with the wavy allele (W, red) being dominant over the straight allele (s, blue).

| Allele counts | | Autotetraploid genotypes | | Quasi-diploid genotypes | | Phenotype |
|---|---|---|---|---|---|---|
| Wavy | Straight | | ABCD  | | AB-CD  | |
| 0 | 4 | ssss | | ss-ss | | Straight |
| 1 | 3 | Wsss | | Ws-ss | | Wavy |
| 2 | 2 | WWss | | WW-ss | | Wavy |
| 2 | 2 | — | — | Ws-Ws | | Wavy |
| 3 | 1 | WWWs | | WW-Ws | | Wavy |
| 4 | 0 | WWWW | | WW-WW | | Wavy |

were suitable for hypothesis testing, since they had at least one wavy-grained parent. Of these 93 trees, the wavy grain structure was found in 66 individuals, which corresponds to a proportion of 71% of the progeny. Furthermore, we analysed five individuals that originated from two known straight-grained parents. Here, we found no indications of wavy grain (Table 2).

## Segregation analysis and inheritance modelling of wavy grain in sycamore maple

Overall, a wavy grain wood structure was observed in three different groups of progenies: (i) trees with a wavy-grained mother and a straight-grained father, (ii) individuals with a straight-grained mother and a wavy-grained father, and (iii) trees with two wavy-grained parents. For 84 individuals that had one wavy-grained parent (groups (i) and (ii)), 56 exhibited a wavy grain structure. Furthermore, among nine trees with two wavy-grained parents (group (iii)), seven individuals showed wavy grain (Table 2). Across all families, these observations were consistent with a dominant inheritance pattern of the wavy grain trait.

As a simple working model, inheritance was explored assuming a single locus with a dominant allele "Wavy" and a recessive allele "Straight". Due to the tetraploid nature of sycamore maple, four alleles are present, each of which can be either "Wavy" or "Straight". In the following, two alternative inheritance scenarios are considered (Table 3): (i) an autotetraploid model, in which all four homologous chromosomes can pair randomly during meiosis (tetravalent formation); and (ii) a quasi-diploid model, in which chromosomes consistently pair as bivalents, leading to a diploid-like inheritance pattern.

The quasi-diploid model is emphasised because results from microsatellite-based parentage assignments were consistent with disomic segregation patterns (Bäucker and Liesebach, unpublished data). This interpretation is further supported by earlier cytogenetic studies, which observed exclusively bivalent formation during meiosis in sycamore maple (Foster 1933), a typical feature of disomic inheritance. Under the quasi-diploid model, which considers two corresponding loci with diploid inheritance, six distinct genotypes can be expected, whereas in the case of strict autotetraploidy, five possible genotypes are expected at this locus (Table 3). To explore possible inheritance mechanisms, four hypothetical alleles (A, B, C and D) were considered at a locus controlling the wood phenotype, representing alternative variants wavy (W) or straight (s). Depending on the dosage of the dominant wavy (W) allele versus the recessive straight (s) allele, trees may carry between zero and four W alleles (Table 3).

In the case of strict autotetraploidy, the random pairing of any two of the four homologous chromosomes during meiosis results in six possible diploid gametes: AB, AC, AD, BC, BD and CD. The rare event of double reduction was neglected here. For quasi-diploid inheritance, two corresponding loci with alleles AB and CD were assumed. In this model, pairing occurs only between alleles of different loci (i.e. one from AB and one from CD), resulting in four possible combinations of gametes: A–C, A–D, B–C and B–D. Unlike in the autotetraploid model, combinations such as A–B or C–D are impossible. Considering the dosage of the wavy allele as an individual variable ranging from zero to four, gametes can be grouped into those with no wavy alleles, one wavy allele or two wavy alleles, with different expected frequencies depending on the parental genotype (Table 4).

The expected frequencies of allele combinations in the offspring of all possible mating events involving at least one wavy parent are presented under the hypothesis of quasi-diploid inheritance (Supplementary Table S1). Since all progenies of the four wavy-grained parental clones Me4, Me6, Me7 and Me10 also have straight-grained individuals (Table 2), these clones are expected to carry the wavy allele in a heterozygous state at one (Ws–ss) or at both corresponding loci (Ws–Ws). Therefore, frequency distributions of 0.5 : 0.5 or 0.75 : 0.25 are expected for the wavy : straight wood traits in progenies descending from one wavy and one straight parent, regardless of the female or male parent. Because of the limited number of individuals per parental combination, none of the individual tests showed a significant deviation from the expected ratios. However, when pooling the data across all four clones, a significant deviation from the expected 0.5 : 0.5 ratio was detected ($p = 0.0030$; Table 5). This suggests that at least one of the four clones carries two wavy alleles in a heterozygous configuration (Ws–Ws), resulting in a higher proportion of wavy-grained offspring. The clones Me6 and Me10 with p-values close to the conventional significance threshold of 0.05 for rejecting the ratio 0.5 : 0.5 are candidates for this. The alternative assumption of a recessive wavy allele is inconsistent with the observed phenotype frequencies in the data, although additional genetic or regulatory factors may also contribute to the observed variation.

To estimate the frequency of the wavy allele in natural sycamore maple populations, criteria of the Hardy–Weinberg equilibrium and selective neutrality of the hypothesised locus were assumed. Based on reported frequencies of up to 6% wavy-grained trees in natural populations, graded allele frequencies between 0 and 1 were generated

**Table 4** Possible combinations of wavy and straight alleles in gametes under autotetraploid (without double reduction) and quasi-diploid inheritance. In the quasi-diploid model, we assume two corresponding loci: Locus 1 (A and B) and Locus 2 (C and D). Gametes are formed with one allele from each locus (e.g. A–C or B–D). Grey fields indicate gametes carrying at least one wavy allele. Allele combinations are shown as Ws (autotetraploid) and W–s (quasi-diploid, by locus); wavy allele (W, dominant), straight allele (s, recessive)

| Allele combination in a parent tree | | Gametes in autotetraploidy | | | | | | Gametes in quasi-diploidy | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Wavy | Straight | AB | AC | AD | BC | BD | CD | A–C | A–D | B–C | B–D |
| — | A, B, C, D | ss | ss | ss | ss | ss | ss | s–s | s–s | s–s | s–s |
| A | B, C, D | Ws | Ws | Ws | ss | ss | ss | W–s | W–s | s–s | s–s |
| A, B | C, D | WW | Ws | Ws | Ws | Ws | ss | W–s | W–s | W–s | W–s |
| A, C | B, D | — | — | — | — | — | — | W–W | W–s | W–s | s–s |
| A, B, C | D | WW | WW | Ws | WW | Ws | Ws | W–W | W–s | W–W | W–s |
| A, B, C, D | — | WW | WW | WW | WW | WW | WW | W–W | W–W | W–W | W–W |

**Table 5** Observed frequencies and expected ratios of wavy- and straight-grained phenotypes in progenies derived from wavy-grained parental clones (Me4, Me6, Me7, Me10). The null hypothesis (no significant deviation between observed and expected frequency distributions) was tested using Fisher's exact test under different assumptions of tetraploid inheritance. One wavy × one straight parent: Offspring groups from crosses between one wavy-grained (Me4, Me6, Me7, or Me10) and one straight-grained parent. One wavy × one wavy parent: Offspring groups from crosses between two wavy-grained parents (Me4, Me6, Me7, or Me10).

| Cross type / Offspring group | Observed frequency (Wavy : Straight) | Expected ratio (genotype assumption) | p-value (Fisher test) |
|---|---|---|---|
| One wavy × one straight parent | | | |
| Offspring of clone Me4 | 7 : 3 | 0.5 : 0.5 (Ws–ss) | 0.3438 |
| | | 0.75 : 0.25 (Ws–Ws) | 1 |
| Offspring of clone Me6 | 16 : 6 | 0.5 : 0.5 (Ws–ss) | 0.0525 |
| | | 0.75 : 0.25 (Ws–Ws) | 1 |
| Offspring of clone Me7 | 4 : 3 | 0.5 : 0.5 (Ws–ss) | 1 |
| | | 0.75 : 0.25 (Ws–Ws) | 0.3771 |
| Offspring of clone Me10 | 29 : 16 | 0.5 : 0.5 (Ws–ss) | 0.0725 |
| | | 0.75 : 0.25 (Ws–Ws) | 0.1199 |
| Sum (pooled data) | 56 : 28 | 0.5 : 0.5 (Ws–ss) | 0.0030 ** |
| | | 0.75 : 0.25 (Ws–Ws) | 0.1002 |
| One wavy × one wavy parent | | | |
| Sum (pooled data) | 7 : 2 | 0.75 : 0.25 (Ws–ss × Ws–ss) | 1 |
| | | 0.875 : 0.125 (Ws–Ws × Ws–ss) | 0.6134 |
| | | 0.9375 : 0.0625 (Ws–Ws × Ws–Ws) | 0.1049 |

(see Supplements Table S2) and expected frequencies of the wavy-grained phenotype were calculated under the working assumption of a dominant wavy allele. In this estimation, a phenotype frequency of up to 6% corresponds to an underlying wavy-allele frequency of up to approximately 2%. These calculations are purely theoretical and not based on empirical population data, but are intended to illustrate the possible magnitude of the underlying allele frequency.

## Discussion

In the sycamore maple trees felled and examined for wood structure, 71% of the offspring with at least one wavy parent showed the wavy grain pattern. This proportion is significantly higher than the average frequency of up to 6% reported in natural populations, suggesting that genetic factors contribute substantially to the expression of this trait. The marked deviation from random occurrence in nature strongly supports the hypothesis of genetic inheritance. The occurrence of wavy grain in offspring with either a wavy-grained mother or a wavy-grained father indicates a nuclear, rather than cytoplasmic or maternal, localisation of the underlying genetic factor.

For the purpose of statistical evaluation, the observed variation in grain expression was simplified into two discrete categories: "Wavy" and "Straight". This simplification allowed statistical testing of the hypothesis while avoiding an excess of categories. Within this framework, the data were compatible with a simple inheritance scenario that can be described by a major locus with a dominant allelic variant "Wavy" and a recessive variant "Straight", acknowledging that this represents a simplified working model of the underlying genetic architecture according to the parsimony principle.

This hypothesis is consistent with the high frequency of wavy-grained offspring from wavy-grained parents and the absence of the trait among offspring from two straight-grained parents. Although sycamore maple is a tetraploid species, the patterns observed in this are compatible with disomic segregation and a quasi-diploid mode of inheritance involving two corresponding loci. Support for this interpretation comes from both cytological and molecular sources. Foster (1933) observed exclusively bivalent chromosome pairing during meiosis in sycamore maple, a hallmark of disomic inheritance. In addition, the material from the parentage analysis enabled the microsatellite markers to be resolved into loci with diploid segregation patterns (Bäucker and Liesebach, unpublished data). Taken together, these observations lend support to our working hypothesis of a quasi-diploid, nuclear inheritance of the wavy grain trait with a dominant effect.

Despite the strength of the observed patterns, several limitations should be taken into account when interpreting the results. A key factor was the deliberately small sample size, chosen to preserve the globally unique genetic material for future research. In addition, the availability of trees with a sufficiently large diameter at breast height was limited, as the wavy grain pattern is known to typically manifest only in older, larger-diameter trees. Thus, only pooled date could give statistical significance.

Nevertheless, among the trees that could be analysed, a broad spectrum of phenotypic variation in wavy grain was observed, for example in intensity, wavelength or amplitude. Wood analysis also revealed differences in spatial distribution, ranging from localised patches to the entire stem (Lewandrowski et al. 2024). Dosage effects may contribute to this variation (e.g. WWWs, WWss, Wsss), but additional genetic or regulatory factors may also modulate the appearance of the trait. Although epigenetic mechanisms have been discussed, the results of this study suggest that wavy grain is influenced by genetic factors, while environmental influences on the fine-scale manifestation of the pattern cannot be fully excluded.

The dominant inheritance of curly grain in *Betula pendula* var. *carelica* (curly birch), a diploid species, was demonstrated by Kärkkäinen et al. (2017). Their comprehensive crossing experiments led to the hypothesis that the trait could be controlled by a single dominant allele, with homozygosity for this allele being lethal. The diploid nature of *B. pendula* simplifies its genetic architecture, allowing the trait to follow Mendelian inheritance patterns. Similarly, the present study supports the view that simple inheritance models with a dominant effect of a "Wavy" allele may contribute to the occurrence of figured wood traits. However, the tetraploid genetic structure of sycamore maple introduces additional complexity. This difference in ploidy levels highlights the additional challenges of understanding inheritance in polyploid species such as sycamore maple. Therefore, multi-generation pedigrees are required for disentangling the underlying inheritance patterns as Kärkkäinen et al. (2017) used in their study. In line with this, the two-generation pedigree analysed in this study revealed the identification of transmission patterns of the wavy grain trait across different parental combinations. Together, both studies highlight the value of long-term field trials and pedigree resources for elucidating the genetic control of economically important wood traits.

Besides the genetic trait, also the influences of environmental factors on the expression of wavy-grained wood was discussed in previous studies. Fan et al. (2013) investigated the inheritance of figured grain in *Populus* × *canescens* (grey poplar) through grafting experiments and progeny trials. In their study, the authors introduced the term Scattered Moiré for a species-specific figure type that differs from wavy grain by its irregular, moiré-like light reflections. The trait was shown to be under genetic control, but its inheritance appeared complex and deviated from a simple Mendelian model. The authors suggested that partial dominance, environmental factors, and hybrid-specific influences such as sex linkage and segregation bias might have played a role in the expression of the trait. These findings contrast with the relatively straightforward inheritance patterns observed in sycamore maple in the present study, where the data support genetic control of the wavy trait by a single dominant nuclear allele. However, the work of Fan et al. (2013) highlights the potential for environmental modulation and genetic complexity that may also influence the expression of wavy grain to some extent in sycamore maple. Their results emphasise the need to consider hybrid effects and potential epigenetic influences when studying wavy grain traits in different species.

One challenge in researching the formation of wavy grain wood is the fact that this characteristic only occurs in the wood of mature trees. Anatomical investigations in sycamore maple have been conducted with stems of trees that are 36 years old with a maximum dbh of 40 cm (this study, Lewandrowski et al. 2024). As the wave amplitude of the grains increases with the age of the trees, a correlation between dbh and the probability of the detectability of wavy grain can be hypothesised.

McKenna et al. (2015) investigated figured wood in *Juglans nigra* L. (black walnut), focusing on wavy grain, by analysing grafted trees propagated in the 1970s and seedlings grown from open-pollinated seeds of a figured clone. Only one of the grafted trees showed a small amount of figure, but the authors did not specify the exact pattern. None of the ten-year-old seedlings showed the wavy grain trait. The authors speculated that the juvenile stage of the trees and environmental factors may have contributed to the lack of figured grain. However, since the grafted trees were approximately 25–33 years old at the time of evaluation, the absence of figured grain cannot be solely attributed to their age. Instead, the authors suggested that physiological disruptions caused by grafting, such as alterations in the auxin : cytokinin ratio between scion and rootstock, might suppress the expression of figured grain, despite a possible genetic predisposition. Research on *Fraxinus excelsior* (ash) has also investigated the development of wavy grain. Sopushynskyy and Teischinger (2013) reported that the characteristic typically begins to develop between 11 and 20 years of age, which aligns with the developmental timing observed in sycamore maple in the present study. Hejnowicz and Romberger (1973) found that in wavy-grained ash, the innermost section of the stem, approximately the first 10–20 annual rings, is consistently straight-grained. At this stage of development, wavy-grained ash showed differences in diameter growth and crown formation compared to straight-grained trees. Notably, wavy-grained ash often had denser or more asymmetrical crowns, suggesting underlying physiological or growth-related differences.

The wavy structure appears to develop gradually and, once established, remains stable in the wood formed in subsequent years. These findings provide a useful comparative basis for interpreting the age-related expression of wavy grain in sycamore maple. This highlights the importance of tree maturity, as younger individuals often lack the anatomical distinctiveness required for reliable assessment. Based on these insights, selecting trees beyond the juvenile stage is crucial for consistent identification and for studying the inheritance of the trait. These findings could provide a basis for future studies to investigate similar patterns in sycamore maple. However, Quambusch et al. (2021) found no negative effects of the wavy grain trait on growth parameters such as stem diameter or tree height in sycamore maple. It suggests that selecting trees with wavy grain for breeding programmes does not result in a reduction of important growth characteristics. The identification of wavy grain can be challenging, particularly when distinguishing it from other tissue deviations near knots, branch junctions or the stem base. Accurate detection requires anatomical expertise, a factor also noted by Ewald and Naujoks (2014), who first reported signs of wavy grain in a ten-year-old sycamore maple derived from a rooted cutting taken from a known wavy-grained donor tree.

The results of this study provide valuable insights into the genetic basis of wavy grain in sycamore maple for tree breeding, forestry and timber production. The understanding of the inheritance of this trait may support the selection of trees with this valuable wood characteristic and could contribute to improving the efficiency of propagation programmes aimed at producing high-quality seed for commercial forestry.

Nevertheless, the study offers a solid basis for further research. Future research should explore the development of non-invasive methods to identify trees with wavy grain in natural and managed populations. Current efforts in differential gene expression analysis in cambium tissues aim to identify candidate genes that could potentially contribute to the development of rapid testing systems (Wallbraun and Fuchs, unpublished data). Such systems would allow early selection without damaging valuable trees, although further research is needed to determine their feasibility and effectiveness. A non-invasive test would be of great benefit for forest owners, since it would allow an early identification of trees with wavy grain patterns followed by a more targeted forest management and resource allocation. In addition, such tests would help to conserve valuable trees by avoiding the need for felling or damage during the selection process. This would ensure that high quality trees remain in the forest stand, maximising their long-term economic and environmental value. Building on the vision of Conrad (1977b), who highlighted the rarity and economic value of wavy grain in sycamore maple and other hardwood species, future efforts should focus on advancing genetic tools to better understand patterns of inheritance and to support the development of practical applications, such as non-invasive identification methods.

To evaluate trait stability and developmental dynamics, long-term field trials were established using in vitro propagated clones derived from sycamore maples with confirmed wavy grain. These clones are currently being monitored under field conditions (Bäucker et al. 2020), with a follow-up evaluation planned for 2032, fifteen years after establishment. As a prerequisite for optimal growth and wood development, thinning and further measures to prevent competition for growth should also be taken into consideration.

## Conclusion

This study provides the first systematic indications of a genetic contribution to the inheritance of wavy grain in sycamore maple and suggests a dominant effect consistent with a quasi-diploid inheritance model. By combining genetic and phenotypic information from a unique two-generation pedigree, the inheritance of this economically valuable wood trait could be evaluated. Limited sample size and tetraploidy prevent definitive conclusions on genetic architecture, but the results are consistent with simple inheritance models and provide a basis for future work. These findings contribute to a better understanding of wavy grain and may underlie breeding and conservation approaches, such as the establishment of selected clonal collections or seed orchards. Future studies should prioritise larger datasets, the underlying mechanisms and develop non-invasive tools for early detection. Improved knowledge of the genetic background of wavy grain may support the sustainable use of sycamore maple and facilitate the integration of this rare and highly valued wood trait into forestry and breeding programmes.

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## Declarations

**Competing Interests** The authors declare that they have no competing interests.



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