

Recent genetic research in 4 European maple species

Acer campestre, A.opalus, A. platanoides, A. pseudoplatanus

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Cover photo. A flowering *Acer platanoides* tree in the Ecopark, Uppsala. Photograph Gösta Eriksson

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Preface

Acer is a genus of about 200 species in the north temperate zone and tropical mountains, a few in S.E Asia. It was formerly placed in the family *Aceraceae*, but DNA sequencing has led to reclassification, along with *Aesculus*, in the family *Sapindaceae* (Harrington et al. 2005). Here we shall summarize published reports from year 2000 and onwards on recent genetic research mainly on 4 European *Acer species – A. campestre, A. opalus, A. platanoides,* and *A. pseudoplatanus,* .

The names *platanoides* and *pseudoplatanus* arose because their leaves resemble those of the plane tree, *Platanus*. The natural distribution of *A. platanoides* – called 'Norway maple' in English, and 'skogslönn' in Swedish – includes most of Europe, except Britain and Holland, and into Armenia and the Caucasus (e.g., Vedel and Lange 1965). The natural range of *A. pseudoplatanus* – 'sycamore' in English, 'tysklönn' in Swedish – is unclear, as it has been planted for hundreds of years outside its presumed indigenous area in central Europe, and has spread as a weed; it grows on all but the most acid soils and is tolerant of strong winds and salt spray. *A. campestre* – 'field maple' in English, 'naverlönn' in Swedish – has a natural range from Spain and Britain, through Europe south of Sweden to south-west Russia, Algeria and Asia Minor. *A. opalus* is an extremely variable species, a native of the Mediterranean hills, extending northwards to the Jura, the southern Alps and mountains of Illyria.

These 4 *Acer* species are of limited importance economically. *A. platanoides* is planted in cities and along avenues, and the wood is used in joinery, furniture and turnery; the wood of *A. pseudoplatanus* has similar uses (Vedel and Lange 1965; Wikipedia). *A. campestre* is sometimes planted ornamentally as a tree in parks and gardens or used in hedges. *A. opalus* is an attractive ornamental tree that is surprisingly infrequently planted. These species, however, are of considerable taxonomic, ecological and evolutionary genetic interest. *A. platanoides, A.campestre* and *A. opalus* all have the diploid chromosome number 2n = 26, whereas *'A. pseudoplatanus,* an autotetraploid, has 2n = 52(TreeGenes Database). All four species are insect-pollinated and the genetic variation in sub-populations has been studied, partly for comparison with appropriate wind-pollinated tree species. A feature of special interest in *Acer* species is the occurrence of multiple forms of flowers – morphs – on the same tree. Trees of e.g. *A. platanoides* can have male and hermaphrodite flowers on the same tree, while being functionally male, or functionally dioecious. Some female flowers have rudimentary stamens, some male flowers have rudimentary stigmas (e.g., Vedel and Lange 1965).

As usual, graphic illustrations are in focus in our review. It should be noted that none of the illustrations were taken from the original papers. As with our previous reviews, papers written in languages that are not widely understood by the scientific community are not treated. We apologize for missing reports in our search for recent genetic studies on the 4 European maples reviewed here.

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1. Genetic variation among and within populations

Caudulio and Rigo (2016) published a brief summary of the distribution and ecology of *A. platanoides* with reference to its practical use and environmental threats. This species does not form its own stands but grows in mixed stands with other broadleaf tree species. It was stated that *A. platanoides* under normal conditions does not experience any serious threats from diseases or pests but under urban conditions it may suffer from diseases and other stresses such as soil compaction.

1.1 Metric traits

Two populations from each of the species *A. platanoides* and *Betula pendula* were selected for exposure to restricted access to nitrogen in an investigation of the impact of life history traits on genetic variation among and within populations (Black-Samuelsson and Eriksson 2002). One Norwegian and one Swedish population originating from latitudes 61.16°N (Lillehammer) and 56.72°N (Öland) were included in this investigation. Each population was represented by 10 open-pollinated families with 20 seedlings each. The cultivation of the seedlings took place in a growth chamber under controlled conditions with respect to day/night length, temperature, and nitrogen availability. The night length was gradually increased in order to determine the critical night length for budset. Two nitrogen treatments were applied: free access to nitrogen and restricted access to nitrogen. The latter nitrogen solution was pipetted in amounts corresponding to a growth rate of 3% per week. In all, 13 different traits were measured or recorded, mainly growth traits.

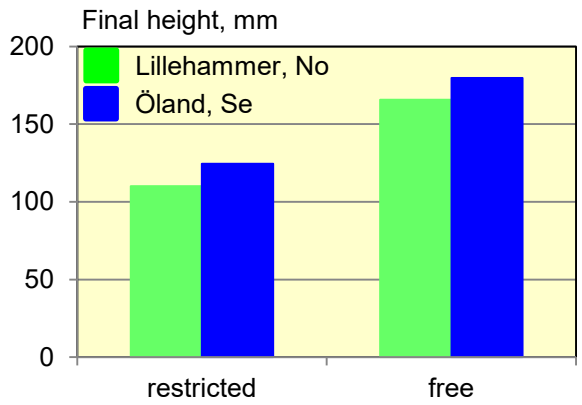


Figure 1. Final height after cultivation for one growth season under free access to nitrogen or restricted access to nitrogen in 2 A. platanoides *populations. One population originated from southern Norway (green, lat. 61.16°N) and the other from Sweden (blue, lat. 56.72°N). Each population was represented by 10 open-pollinated seedlings. Black-Samuelsson and Eriksson 2002.*

For the majority of traits there was a significant difference between the 2 treatments. The plants in the restricted nitrogen treatment showed *typical nitrogen deficiency symptoms*. The final plant height in the restricted nitrogen treatment was approximately 67% of that in the free access treatment (Fig. 1). The Norwegian population grew less in both treatments. This was probably due to faster response to the prolongation of the night length. The number of traits showing significant population effect was lower in the restricted nitrogen treatment than in the free access treatment.

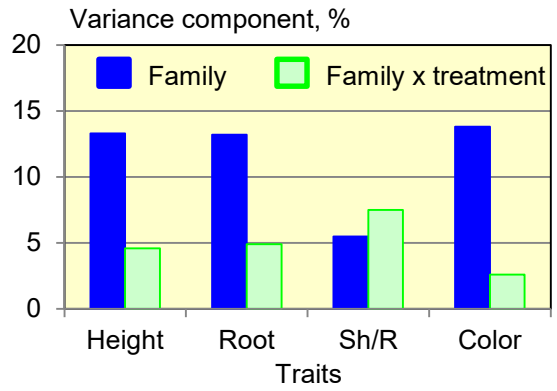


Figure 2. Variance components for families and family x treatment for 10 open-pollinated families from 2 A. platanoides *populations cultivated under free access to nitrogen or restricted access to nitrogen. One population originated from southern Norway (lat. 61.16°N) and the other from southern Sweden (lat. 56.72°N). Each family was represented by 20 seedlings. Sh/R = shoot/root dry weight ratio. Black-Samuelsson and Eriksson 2002.*

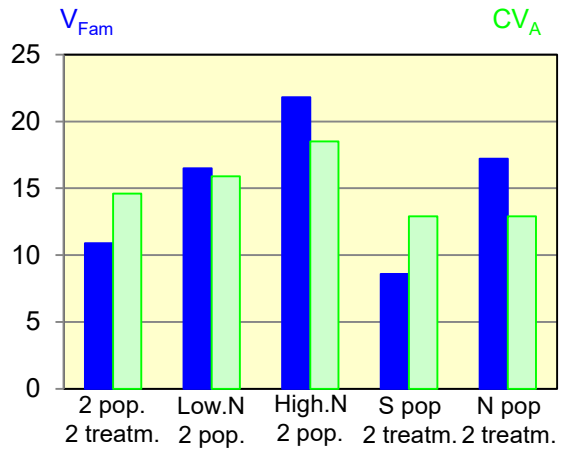


Figure 3. Mean family variance component (blue) and coefficient of additive variance (green) across 4 growth traits in an investigation with 2 treatments, free access to nitrogen or restricted access to nitrogen, in 2 A. platanoides *populations. One population originated from Norway (lat. 61.16°N) and the other from Sweden (lat. 56.72°N). Five different types of ANOVA were run. Eriksson et al. 2003.*

Family variance and family x treatment interaction variance components for some traits are shown in Fig. 2. As seen from this figure the family variance components were much larger than the interaction variance components for 3 of the 4 traits, the shoot/root dry weight ratio being the deviating trait. As seen from Fig. 2 in the paper there were many family rank changes for root weight and 5 of the 20 families had their largest root weights in the restricted nitrogen treatment. These results explain the larger interaction variance component than the family variance component for shoot/root ratio. A joint analysis across 4 growth traits was run for the 2 populations in both treatments and separately for the 2 treatments as well as separately for each population in the 2 treatments (Eriksson et al. 2003). This analysis showed the highest family variance and CV_A for the joint analysis of the 2 populations in the free access treatment (Fig. 3).

The separate analysis of the Norwegian and the Swedish populations showed much higher variance components for the Norwegian population than for the Swedish population. Even estimates larger than the maximum allowed, 25%, were exceeded for 3 traits. The mean value for the Norwegian population was 20.3 while the corresponding figure for the Swedish population was 12.5. It was stated that there was no support for the hypothesis that stressful conditions would lead to less genetic variation than non-stressful conditions. This is also reflected in Fig. 4. The homogeneous ambient conditions in the growth chambers could be a strong contribution to this observation, leading to low environmental variance and thereby a high heritability.

The coefficient of variation (CV) was used as an estimate of phenotypic plasticity. The CV for root dry weight was low (Fig. 5), which must be attributed to the investment in root growth in the restricted nitrogen treatment. Two of the Swedish families had larger root dry weights in the restricted nitrogen treatment than in the free access treatment. This pattern was observed for 3 Norwegian families too, but the differences were much smaller. The CVs of the other traits were fairly large, suggesting considerable phenotypic plasticity. This means that the populations have good possibilities to adapt to different nitrogen conditions if this pattern remains into adulthood.

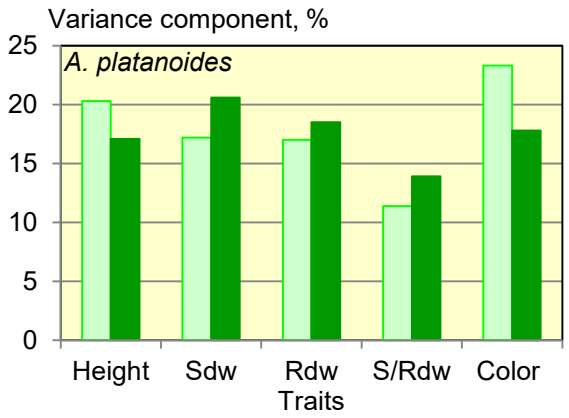


Figure 4. Variance components for families for 10 open-pollinated families from one Norwegian A. platanoides *population cultivated under free access to nitrogen (dark green) or restricted access to nitrogen (light green). Each family was represented by 20 seedlings. S = shoot, R = root, dw = dry weight, color = autumn color. Black-Samuelsson and Eriksson 2002.*

Summary. Strong treatment effect was observed for all traits except root weight in an experiment with 2 nitrogen treatments, restricted access and free access to nitrogen. In spite of the strong treatment effects, the family variance component for most traits was much larger than the family x treatment component. The largest genetic differentiation was noted for the free access treatments. Large phenotypic plasticity estimated by the coefficient of variation was found for all traits except root dry weight, owing to the investment in root growth in the restricted N-treatment.

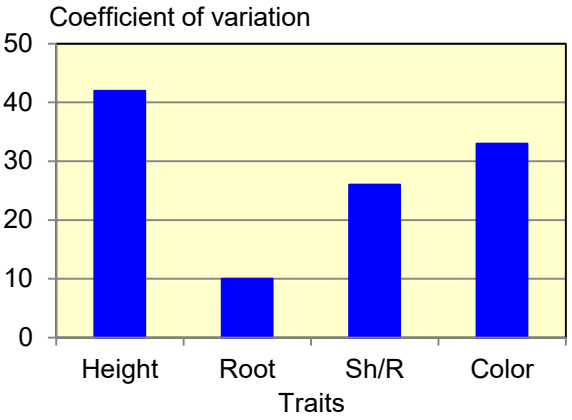


Figure 5. Coefficient of variation for 4 traits in an investigation with 2 treatments, free access to nitrogen or restricted access to nitrogen, in 2 A. platanoides *populations. One population originated from Norway (lat. 61.16°N) and the other from Sweden (lat. 56.72°N). Each population was represented by 10 open-pollinated seedlings. Sh/R = shoot/root ratio for dry weight. Black-Samuelsson and Eriksson 2002.*

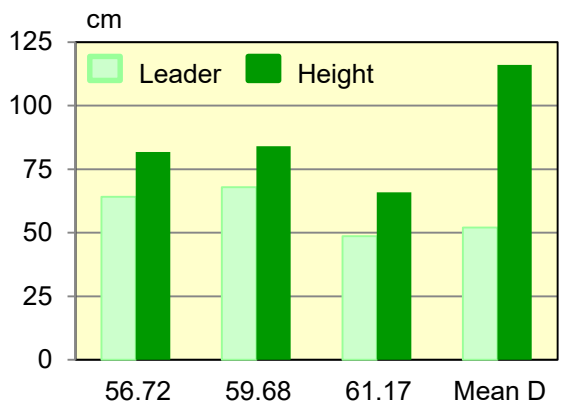


Figure 6. Leader length and plant height at age 3 in 3 A. platanoides *populations in a Norwegian field trial and the mean leader length and plant height in a Danish field trial. The population original latitudes are indicated. Eriksson et al., 2003.*

Another paper, Eriksson et al. 2003, reported on growth and phenology in the same populations in one Danish (lat. 55.30°N) and one Norwegian field trial (lat. 59.67°N). In addition to the 2 populations in the previous study, another Norwegian population (lat. 59.67°N) was included. These trials contained 24–28 open-pollinated families, each with 28–40 seedlings. Six classes of bud flushing and leaf coloring were recorded. Final height was measured at harvest of the trials. The result of isozyme analysis of these populations was briefly reported in this paper (see also Rusanen et al. 2000).

Based on the isozyme analysis, the F_{ST} for the 3 populations was estimated at 0.097, which must be regarded as considerable for populations from such a limited geographic area. It should be noted that this estimate refers to evolution that occurred in the past.

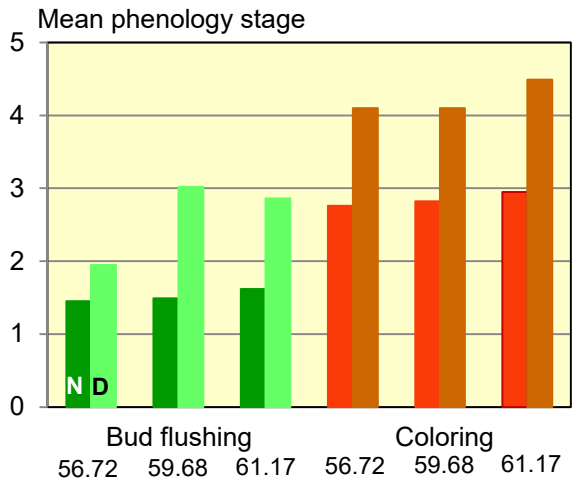


Figure 7. Population mean phenology stage of 3 A. platanoides *populations recorded in one Norwegian (left column in each pair) and one Danish field trial (right column in each pair). The latitudinal origins of the 3 populations are indicated. Eriksson et al., 2003.*

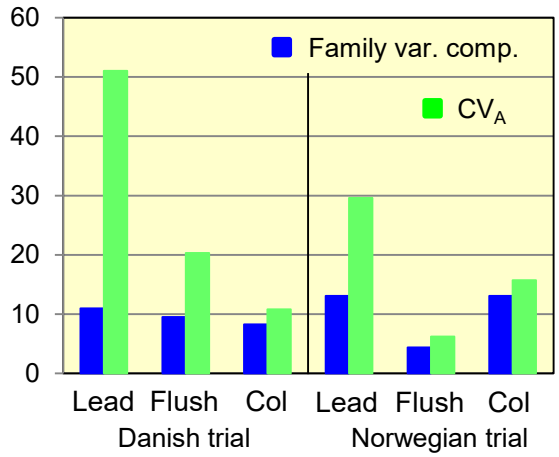


Figure 8 Percentage family variance components and coefficients for additive variance, CV_A in one Danish and one Norwegian field trial with 3 A. platanoides *populations, each with 12–16 populations. Lead = leader length 2nd growth period, Flush = bud flushing 3rd growth period, Col= coloration 2nd growth period. Eriksson et al., 2003.*

The population effect on growth and phenology traits was significant for all traits in the Norwegian trial while only coloring showed significance for population effect in the Danish trial.

Fig. 6 reveals that the northern population had the lowest plant height at age 3 and that most of the height growth took place during the 3rd growth period. The latter might be attributed to establishment problems. No individual population growth results were presented for the Danish trial, but the mean data indicate that plants in this trial, on average, showed better growth performance than in the Norwegian trial. It is possible that maternal effects have influenced the growth traits in young plants, which might have exaggerated the genetic effect estimates.

As regards bud flushing, the development was faster in the Danish trial than in the Norwegian trial and the southern population was significantly later in the Danish trial (Fig. 7). The among-population growth did not vary much in the Norwegian trial, nor were there any large differences in coloring in any of the trials.

The family variance component and CV_A for bud flushing were both low in the Norwegian trial, while all other variance components were around 10% (Fig. 8). The CV_As for leader length were large in both trials.

It should be added that the family effect was significant for all traits studied, which suggests that the populations have good opportunities to respond to any future environmental change.

The family means for height, leader length and leaf coloration were significantly correlated between the 2 trials. Unfortunately, the individual correlation coefficients were not given, and the lowest r was = 0.49, which means that the degree of explanation for this relationship was rather low.

Finally, it was discussed that related matings might occur in *A. platanoides* as a consequence of its scattered distribution, which might be most pronounced in the northernmost population growing close to the limit of distribution of *A. platanoides*. If occurrence of related mating exists, exaggeration of the family variance estimates would occur. Therefore, the estimates obtained should be regarded as upper limits of these variance components.

Summary. The height growth of 3 *A. platanoides* populations in one Danish field trial grew taller than in one Norwegian trial. The family

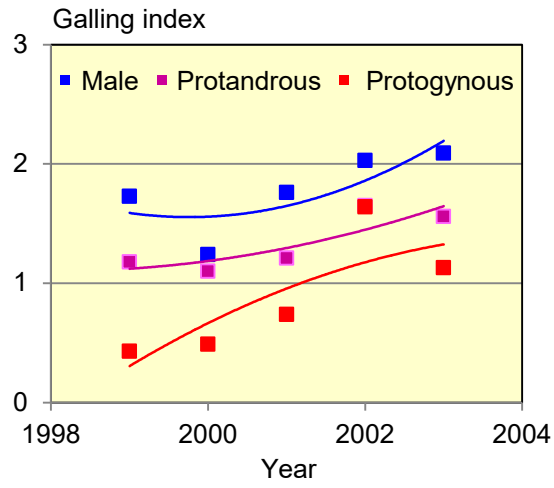


Fig. 9. The development of galling index during the period 1999–2003 for 3 different sexual morphs of A. opalus *in La Font Roja Natural Park in eastern Spain. Galling was caused by* Aceria macrorhynchus. *In 2002 the protandrous and protogynous trees had the same index.* Verdú *et al., 2004.*

variance for all traits in both trials was close to 10% except for the low estimate for bud flushing in the Norwegian trial. The CV_As were much larger for leader length in both trials than for other traits. Bud flushing and leaf coloring occurred earlier in the Danish trial than in the Norwegian trial.

Verdú et al. (2004) carried out an investigation on the effect of *Aceria macrorhynchus* galls on 3 sexual morphs of *A. opalus* over 5 years. The 44 trees included in this study were selected along a 2,000 m linear transect in La Font Roja Natural Park in eastern Spain. The sexual morph of the same trees was recorded during a 5-year period. The weighted proportion of staminate to the total number of flowers was used as an index for maleness. A gall index in 4 classes was determined: 0 = no galled leaves, 1 = 0–1% galled leaves, 2 = 1–10% galled leaves, 3 = > 10% galled leaves. According to the authors *This index reflected the real percentage of galled leaves in the tree*. Leaf area, photosynthesis, and carbon isotope discrimination were recorded.

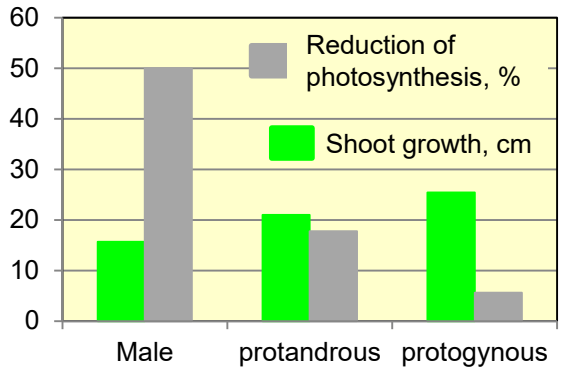


Fig. 10. Shoot growth in cm and percentage reduction of photosynthesis in leaves with galls compared to control leaves in 3 sexual morphs of A. opalus *in La Fonta Roja National Park in eastern Spain. The galling was caused by the mite* Aceria macrorhynchus. Verdú *et al., 2004.*

The male and protogynous trees kept their sexual morph during the 5-year period of observation while 7 of the 10 protandrous trees produced male structure only some years. The galling indices for the years 1999–2004 (Fig. 9) revealed that males are most affected and that the protogynous morph was the least affected. The shoot growth increased significantly in the order male – protandrous – protogynous (Fig. 10, Table 1)). Similarly, the photosynthetic rate was affected according to the same sequence of morphs. As seen from Table 1, there was no significant effect on leaf size among the morphs while a small, but significant, difference in carbon isotope discrimination was noted. This

Table 1 The significances of galling, sexual morph and their interaction on 3 metric traits caused by the mite Aceria macrorhynchus *in a population of* A. opalus *in La Font Roja Natural Park in eastern Spain. Verdú et al. 2004.*

Source	*shoot length*	*leaf size*	*Carbon discrimination*
morph	**	ns	ns
galling	ns	ns	*
source x galling	ns	ns	ns

might be a sign of stress in galled leaves. It was cautioned against too far-reaching conclusions owing to the small difference. The photosynthetic rate was severely affected in male galled leaves, 50% reduction in the photosynthetic rate in control leaves.

It was suggested that the differences with respect to mite attacks among morphs might be attributed to the quality of plant tissues for herbivore consumption. The allocation of resources to seed development in protogynous and protandrous trees may also contribute to the differences. Still another interpretation of the preference of males by the mites is that they prefer slow-growing trees.

Summary. A clear demonstration that the mite *Aceria macrorhynchus* most affects the male morph of *A. opalus* leading to the highest galling index in this morph. The shoot growth increased in the sequence male – protandrous – protogynous morph.

Vitasse et al. (2009b) studied the canopy duration in 8 *A. pseudoplatanus* populations from different elevations (≈450–1,600 masl) at 2 north-facing slopes in the French Pyrenees. The 2 slopes are located at 30 km from each other. This paper also deals with 3 other broadleaf tree species. Canopy duration was defined as the period between leaf unfolding and senescence, which mostly is referred to as growth period. The focus was especially on the temperature impact on phenology. Leaf unfolding was classified in five stages at intervals of 10 days during March–June over 2 years. The authors considered leaf unfolding as reached when at least one of the leaves in a bud was fully unfolded.

Senescence. Senescence was monitored every 10 days during September to December. Percentages of missing leaves, as well as percentages of colored leaves of the total remaining leaves in the canopy, were assessed visually. It was considered that senescence date was reached in a tree when 50% of its leaves were either colored or had fallen.

The following formula was used to calculate the

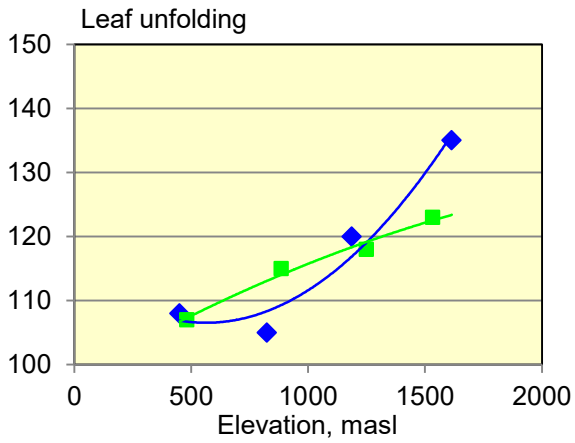


Figure 11. The relationship between elevation and leaf unfolding day from January 1 in 8 A. pseudoplatanus *populations in 2 valleys in the Pyrenees, France. Recordings were from year 2006. Blue = Ossau and green = Gave valley. Vitasse et al. 2009b.*

relative gain in canopy duration, G_d:

$$G_d = \frac{(X_l - Xs)/X_s}{\Delta T}$$

in which X_l and Xs are the longest and shortest canopy duration recorded along the slope and ΔT is the corresponding temperature change rate. A corresponding estimate for gain in solar radiation was calculated.

As expected, there was a positive relationship between population elevation and number of days to leaf unfolding (Fig 11), which took place a little earlier in 2006 than in 2005. Based on all the data from the 2 valleys and the 2 years of recording, the estimated change was 4.5±0.6 days per 100 meters in elevation, while the corresponding estimate for temperature impact was 5.4±0.6 days per degree centigrade. The difference in leaf unfolding between the 2 years was attributed to the weather conditions during these years. Since the trees on each slope grow under more or less the same photoperiodic conditions, flushing was mostly regulated by temperature and not by photoperiod.

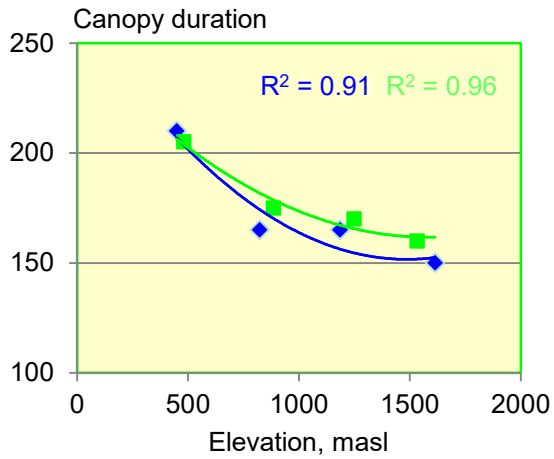


Figure 12. The relationship between elevation and canopy duration in 8 A. pseudoplatanus *populations in 2 valleys in the Pyrenees, France. Recordings were from year 2006. Blue = Ossau and green = Gave valley. Vitasse et al. 2009b.*

Senescence occurred much later at the 2 low elevations than in the populations from the 3 other elevations. The absence of differences among the high elevation populations (800–1,600 masl) suggested that photoperiodic conditions regulated growth cessation.

In spite of the absence of a clear difference among the populations from the 3 higher elevations (800–1,600 masl) as regards senescence, there were strong relationships between population elevation and canopy duration for both years. As seen from Fig. 12 there were strong fits to the 2nd degree polynomials for both valleys. It was stated that leaf unfolding had a greater impact on canopy duration than growth cessation. The estimated change was 9.7±1.5 days per degree centigrade.

It is remarkable that the strong relationships between leaf unfolding and canopy duration on the one hand, and elevation or solar radiation on the other hand, were so strong in spite of the large number of days between recordings of the phenology traits.

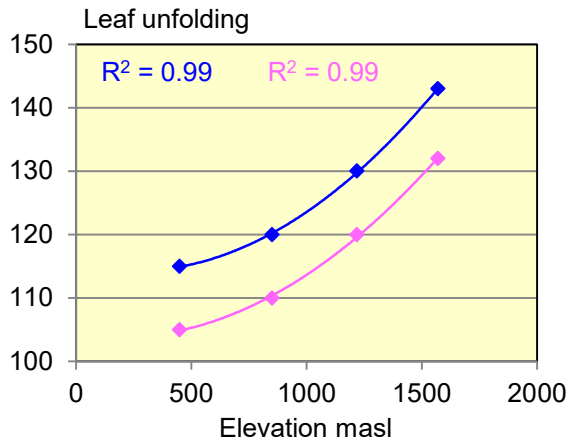


Figure 13. The relationship between mean elevation and flushing of A. pseudoplatanus *populations in 2 valleys in the Pyrenees, France. Recordings were from year 2005 (blue) and 2006 (purple). Vitasse et al. 2009a.*

The same material was presented once more in Vitasse et al. (2009a). As in the other paper there was a focus on differences among 4 deciduous tree species.

We have used the data in Fig. 2 of the paper and calculated the relationship between mean elevation of the populations from the 2 valleys and day of leaf unfolding. As seen from Fig. 13 there is an extremely good fit to the polynomials for the 2 years. Year 2006 was warmer than 2005, which resulted in an earlier leaf unfolding in 2006. This indicates that spring temperatures are decisive for bud leaf unfolding. Based on a linear relationship between temperature and leaf unfolding, the change in leaf unfolding per degree centigrade was estimated at –5.6 days.

Summary of the 2 Vitasse et al. papers. Clear trends between leaf unfolding and population elevation, with later leaf unfolding the higher the origin: 4.5 days per 100 m and –5.6 days per degree C. A similar pattern was noted for canopy duration, while growth cessation did not influence canopy duration.

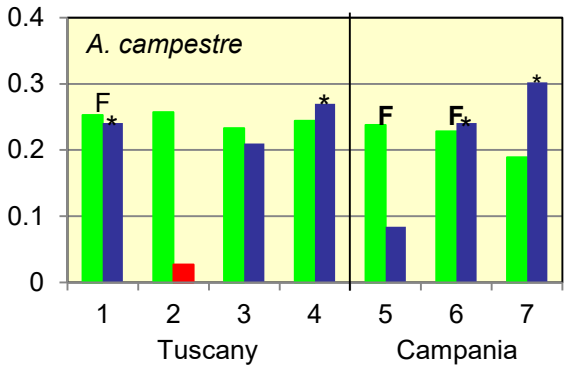


Figure 14. Mean expected heterozygosity (blue) and inbreeding coefficient (green) within 4 Tuscany populations and 3 Campania populations. Red column denotes negative inbreeding coefficient. Asterisks indicate inbreeeding coefficients significantly different from 0. F indicates forest populations. Ducci et al. 2009.

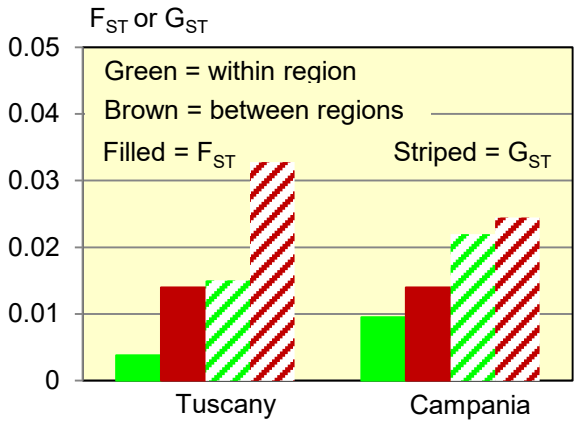


Figure 15. Mean F_{ST}s (green) within 4 Tuscany A. campestre *populations and 3 Campania populations and corresponding mean G_{ST}s for interpopulation comparisons (brown). Eleven isozyme loci were analyzed. Ducci et al. 2009.*

1.2 Markers

1.2.1 Genetic diversity and differentiation

This section is organized in the following way:

1.2.1 Genetic diversity and differentiation
1.2.1.1 Autochthonous populations
1.2.1.2 Artificial populations
1.2.2 Sexual morphs

In each part the species are presented in letter order and then in order of publication year.

1.2.1.1 Autochthonous populations

An initial survey of *A. campestre* resources in Italy was presented by Ducci et al. (2009). They studied 4 populations from Tuscany and 3 populations from Campania in Italy. Some of the populations were sampled in abandoned vineyards. Therefore, all populations cannot be regarded as natural or autochthonous. Each population was represented by 9–21 trees. Eleven isozyme loci were analyzed, 7 of them being polymorphic. Traditional population diversity estimates were calculated. The number of migrants (N_m) was estimated by 2 methods:

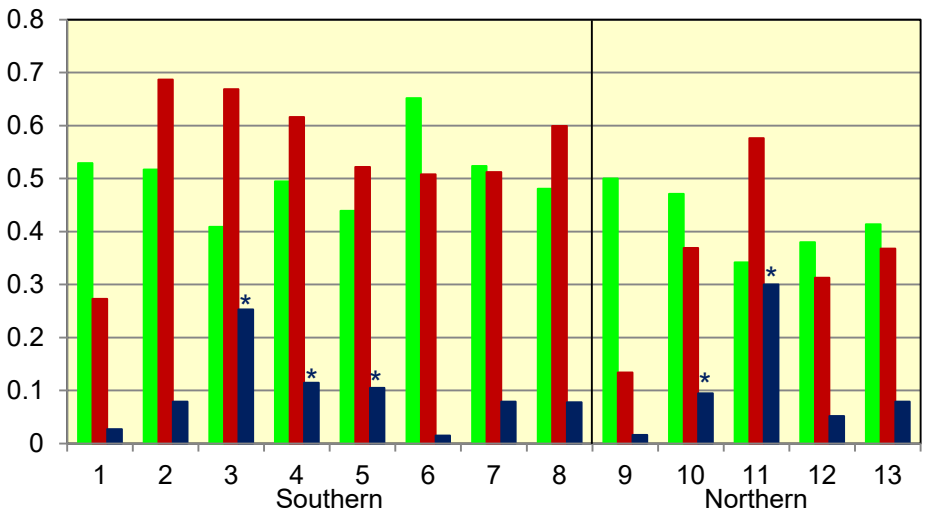
$N_m = (1–F_{ST})/4F_{ST}$

Private alleles method (unique alleles found in one population) according to GENEPOP version 4.0.7.

The number of effective alleles did not differ much between the 2 regions. The expected heterozygosity varied in the range 0.189–0.257 with a grand mean of 0.235 (Fig. 14) and with a slightly higher mean in the Tuscany population than in the Campania population, 0.247 versus 0.218. Except for population 2 in Tuscany the observed heterozygosity was lower than the expected heterozygosity. Population 2 was the only one with a negative inbreeding coefficient (Fig. 14). The high and in some cases significant inbreeding coefficients were attributed to the type of the sampled trees as seedlings from one or a few trees. The diversity observed in this investigation did not differ much from the German populations studied in the dissertation by Bendixen (2001).

The global mean F_{ST} was estimated at 0.059. We found it worthwhile to separate F_{ST}s within the 2 regions from F_{ST}s for inter-region comparisons. The among-population differentiation within regions was larger in Campania than in Tuscany, 0.010 versus 0.004 (Fig. 15). The inter-region F_{ST}s were much larger than within-region F_{ST}s. The G_{ST}s showed a similar pattern (Fig. 15).The 2 methods for estimation of number of migrants per generation resulted in fairly similar estimates, 4.02 and 4.19. It was concluded that there was a strong gene flow among the studied populations. Such a high gene flow over a distance

Figure 16. The observed heterozygosity (green), admixture level (brown), and fixation index (dark blue) in 8 "southern" and 5 "northern" Polish A. campestre *populations studied with 6 microsatellite loci. Asterisks indicate inbreeding coefficients significantly different from zero. Chybicki et al. 2014.*



of more than 300 km of an insect pollinated species with heavy seeds is surprising. It was suggested that the "manipulation" of the species during the past 10 centuries had stimulated gene flow among the populations.

Summary. Seven *A. campestre* populations, 4 from Tuscany and 3 from Campania, were genotyped with 7 polymorphic isozyme loci. There was a slight difference in expected heterozygosities between the 2 regions, means 0.247 for Tuscany versus 0.218 for Campania. The estimation of the difference between populations from the 2 regions was surprisingly low considering the geographic distance between these 2 regions, both F_{ST}s means = 0.014. There might be a human impact on the species in the past, since the gene flow over such a distance for an insect-pollinated species is unlikely.

The objectives of a study of 13 *A. campestre* populations in Poland by Chybicky et al. (2014) were:

To study the genetic variation and structure of this species in Poland

To study the impact of fragmentation on genetic structure and variation

All populations originated from natural reserves and were grouped into 8 southern and 5 northern populations. However, the difference in latitude was limited. The most northern population in the southern group originated from latitude 52.79°N while the most southern in the northern group originated from lat. 53.00°N (see Fig. 19). The range of mean annual temperature did not differ much, 7.6–8.4°C, and the corresponding range for total annual precipitation was 515–547 mm. Six polymorphic microsatellites were analyzed.

Traditional population genetics parameters were estimated. In addition, the admixture level for each population, D_j, was estimated. D_j equals the probability that two random individuals in the jth population are assigned to different genetic clusters.

The mean observed heterozygosity was somewhat higher in the southern populations than in the northern populations, (Fig. 16), 0.51 versus 0.42.. The larger distances among the northern populations might have caused a larger effect on genetic drift in the north than in the south. The slightly higher mean inbreeding coefficients in the northern populations lends some support to this explanation, 0.108 versus 0.094. All inbreeding coefficients were positive and in 5 of the populations the inbreeding coefficients were significantly different from 0. The absence of negative inbreeding coefficients was attributed to the presence of null alleles. Generally, the admixture level was much higher in the southern than in the northern populations, which also supports the assumption that the impacts of genetic drift in the 5 northern populations were greater.

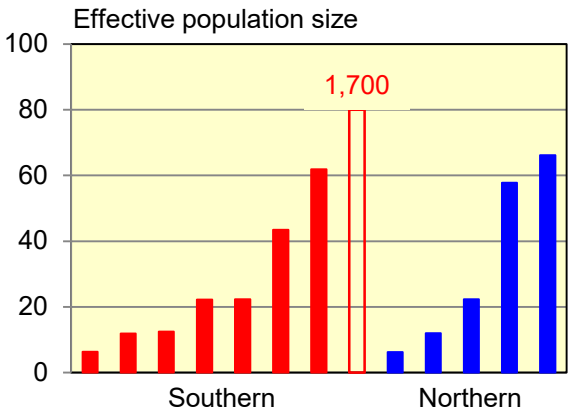


Figure 17. Effective population size in 5 (northern) and 8 (southern) A. campestre *populations in 2 regions in Poland. One outlier population had an estimated effective population size of 1,700. Six microsatellite loci were anayzed. Chybicki et al. 2014.*

With the exception of the southern outlier population with an estimated value of 1,700, there was no pronounced difference in effective population size between the 2 regions (Fig. 17). The AMOVA revealed that most of the variation occurred within populations (85.1%) while there was limited variation between the 2 regions (Fig. 18). The rest of the variation, 11.8%, was found among populations within regions. As a corollary of this, high F_{ST} estimates were noted especially for the northern populations (Fig. 19). The cluster analysis resulted in 4 clusters

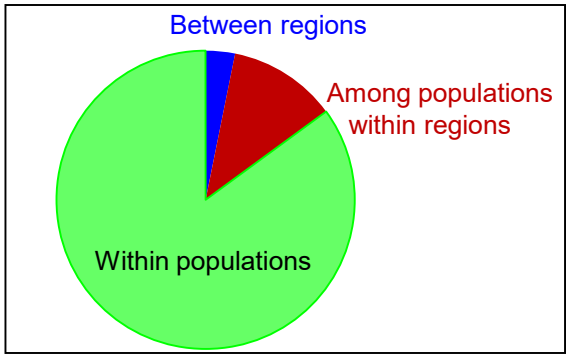


Figure 19. The partioning of the variance between regions, among populations within regions, and within populations in an investigation of 5 and 8 A. campestre *populations in 2 regions (northern and southern) in Poland. Six microsatellite loci were anayzed. Chybicki et al. 2014.*

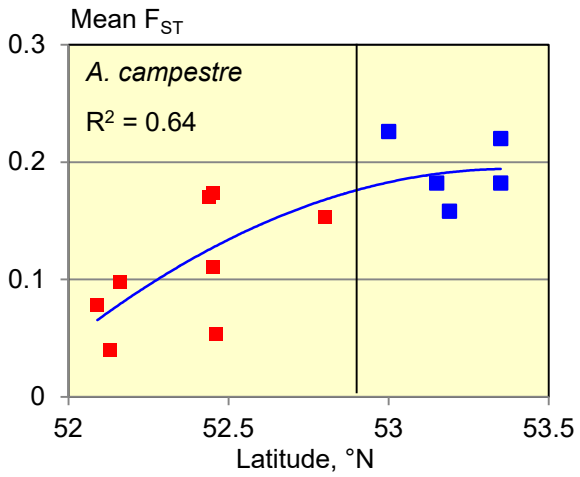


Figure 19. The relationship between latitude at population origin, °N, and population mean F_{ST}s of 5 and 8 A. campestre *populations in 2 regions in Poland, northern = blue and southern = red. Six microsatellite loci were anayzed. Chybicki et al. 2014.*

as the optimal number. The 5 northern populations were separated into 2 geographically distinguished clusters. Such a clear separation of the southern populations was not found, which resulted in higher admixture levels in the south than in the north (Fig. 20). It would have been interesting to separate the F_{ST}s for comparisons within regions from the corresponding F_{ST}s for between regions. However, Fig. 5 in the paper weakly suggests that long distance between po-

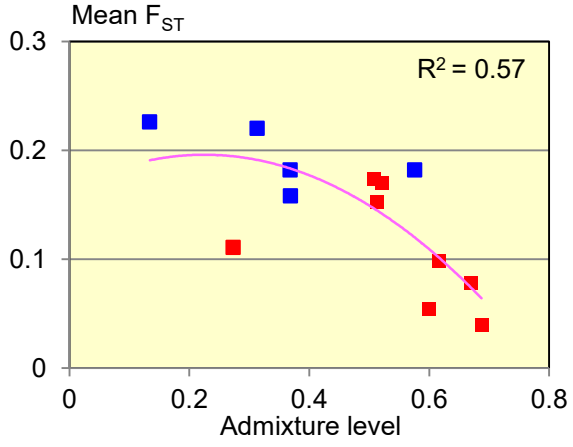


Figure 20. The relationship between admixture level and F_{ST}s of 13 Polish A. campestre *populations in 2 regions in Poland, southern = red squares and northern = blue squares. Six microsatellite loci were anayzed. Chybicki et al. 2014.*

pulations resulted in larger F_{ST} estimates.
The genetic parameters were related to density, latitude, and longitude at population origin. Only the latitude showed significant relationship with rarefacted allelic richness (regression slope = –0.090) and expected heterozygosity (regression slope = –0.34). All other relationships were non-significant for these two parameters as well as for admixture and inbreeding coefficients. The moderate relationship between admixture level and F_{ST} supports the assumption that genetic drift is more prevalent among the northern populations growing at larger distance from each other than is the situation among the southern populations.
Summary. To our knowledge this is the first genetic investigation of autochthonous populations of *A. campestre.* There was slightly higher heterozygosity in the southern than in the northern populations and the inbreeding coefficients were slightly higher in the northern than in the southern populations. The optimal number of clusters was 4 with a geographic separation in the north but not in the south. Population latitudinal origin showed significant relationships with rarefacted allelic richness and expected heterozygosity.

Kvesić et al. (2020) sampled 21–25 *A. campestre* trees from 25 populations in Bosnia-Herzegovina and used 8 polymorphic microsatellite markers for an analysis of different population genetics variables. The populations covered the distribution area in this country and they are growing close to the range of distribution of this species. The elevational range of the populations was wide, 50–1,015 masl. The relationships between genetic variables and geographic or environmental (mean annual temperature) variables were calculated.
We have summarized the major results from this investigation in Table 2. Allelic richness did not vary much, with a mean of 5.06. The genetic diversities estimated as H_e and H_o did not differ much, 0.581 and 0.561, which are in the range of other *Acer* species. The inbreeding coefficients were in 24 of the populations non-significant. The inland Kreševo population with the highest estimate, +0.119, was the only deviating population. Seventeen of the populations had positive estimates of F_{IS}. The non-significances from 0 in most populations suggest that genetic drift had not played a great role in the studied populations.
The AMOVA indicated that the overwhelming variation occurs within populations, 96.4%, and only 3.6% of the variation was attributed to among-population differentiation. In agreement with this, the mean pairwise estimate of F_{ST} was low, 0.036, but significant, probably owing to

Table 2. Compilation of main results in the investigation of 25 A. campestre *populations from Bosnia-Herzegovina.* Kvesić *et al. 2020*

Source	*Mean (range)*	*Notes*
Allelelic richness	5.06 (4.58–5.66)	
Private alleles	0.56 9 populations	6 pops:1 private allele, 1:2, 2:3
Expected heterozygosity	0.58 (0.53–0.64)	
Observed heterozygosity	0.56 (0.47–0.63)	
Inbreeding coefficient	–0.050–0.119	
AMOVA	96.4% within, 3.6% among	
Cluster analysis	2 (4)	
F_{ST}	0.036 (0.00–0.15)	
Isolation by distance	$R^2 = 0.057$	
Isolation by environment	$R^2 = 0.194$	
Geographic - environmental	$R^2 = 0.03$	

the large number of pairwise F_{ST} estimates, 300. Considering the large variation in the elevation of populations, the mean F_{ST} estimate is surprisingly low. It is expected that there would be a large variation in the time of both receptivity and pollen dispersal among the populations, reducing the gene flow among populatons. Two main clusters were identified; one of them consisted of populations along the Adriatic Sea. In addition, subgrouping of the rest of the populations was also presented. The results suggest that long-distance gene flow is more common than expected for an insect-pollinated species.

Significant relationships between genetic and geographic as well as between genetic and annual temperature variables were obtained (Table 2). However, the degree of explanation was in both cases lower than 20%.

Summary. Twenty-five *A. campestre* populations from a broad range of elevations, 50–1,050 masl, in Bosnia-Herzegovina were genotyped with 8 polymorphic microsatellites. Fairly high estimates of observed and expected heterozygosities were noted, around 0.57. Only one population had a significant and positive estimate of the inbreeding coefficient, 0.119. The among-population differentiation was surprisingly low (estimated at 3.6% in the AMOVA) considering the broad elevational range of the populations. This is another investigation indicating that gene flow is more important than believed for a scattered and insect-pollinated species.

With the ultimate purpose of formulating the post-glacial colonization of *Acer campestre,* Wahlsteen et al. (2023) studied 61 populations covering a wide range of the distribution of the species in Europe as well as a few populations from neighboring countries in Africa and Asia. To reach this goal the genetic structure was investigated by sampling 10 trees per population and genotyping by 12 microsatellites. For 6 alleles exhibiting clines, Mantel Tests were conducted to reveal the strength of the relationships between geographic and genetic variables. Several methods were used to identify any possible genetic structures. Delta K statistics and other K statistical methods were applied to identify optimal numbers of clusters. Principle component analysis was also applied. Bottleneck 1.2.02 was used to identify any bottleneck events in the past.

Eleven of the 12 loci showed strongly significant deviations from Hardy-Weinberg equilibrium expectations. The mean expected and obtained heterozygosities were moderately large, 0.50 and 0.67, respectively. Wide ranges among loci were noted for the 2 heterozygosities, 0.28–0.74 and 0.32–0.92. The range of observed heterozygosities varied in the range 0.37–0.63 (Fig. 21). The corresponding range for expected heterozygosity was somewhat higher, 0.46–0.71. The inbreeding coefficients were positive in 58 of the 61 populations and significantly different from 0 in as many as 46 populations (Fig. 22). None of the populations had significant negative estimates of F_{IS}. This suggests that genetic drift occurred frequently in *A. campestre* populations. In addition, significance for occurrence of bottlenecks was noted for 9 populations, 4 of them from Serbia and 3 of them from Hungary. Private alleles occurred in 15 populations.

Three groups of populations were identified, eastern, western, and central but without sharp

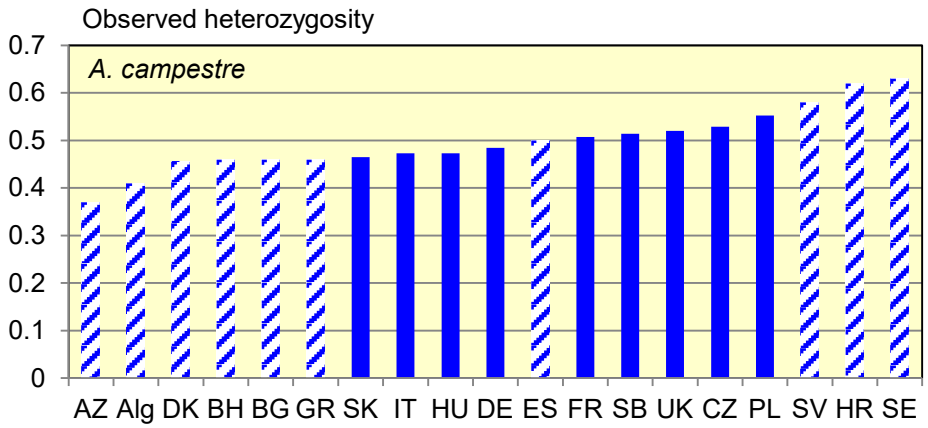


Figure 21. Observed heterozygosity in A. campestre *populations from various countries. Striped columns refer to countries with one or 2 populations analyzed. Country identification letters according to European standard are used: Alg = Algeria, AZ = Azerbaijan. Wahlsteen et al. 2023.*

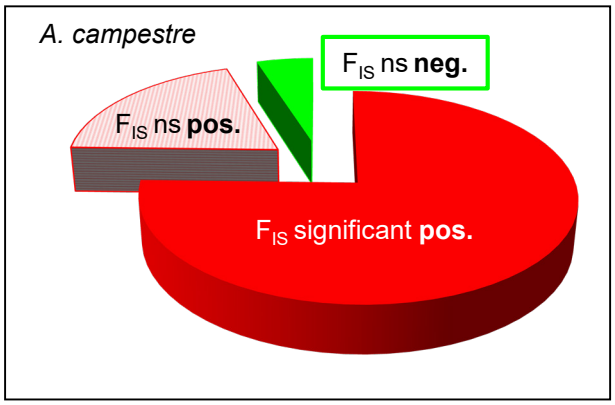


Figure 22. The fraction of F_{IS} estimates being positive and significant and non-significantly different from zero as well as negative and non-significant. Wahlsteen et al. 2023.

boundaries among the 3 groups.

For the pooled material the relationship between geographic and genetic distances was significant, p = 0.015 and R = 0.37. When separate relationships for certain regions were estimated the degree of explanation was higher. (How this separation was done was not clearly expressed in the paper.) Four alleles showed a clinal variation.

The correlations between genetic distance and the four climatic variables tested were:

Temperature seasonality, p = 0.01 R = 0.19

Mean temperature of the wettest quarter, p = 0.03 R = 0.12

Mean temperature of the driest quarter, ns

Precipitation of driest month, ns

As seen from this compilation, no strong relationships were noted for any of the climatic variables. Two reasons might be responsible for the absence of strong genetic–geographic and genetic–climatic correlations:

1. The ambient conditions over the sampling area are complex without clear east–west or north–south trends.
2. The alleles in the loci studied do not correlate with alleles regulating adaptive traits.

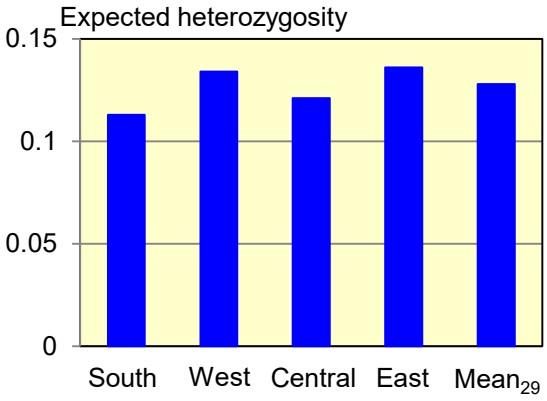


Figure 23. Mean expected heterozygosity in natural populations of A. platanoides *in 4 regions in southern Finland as well as mean estimate for 29 natural and non-natural populations. Rusanen et al. 2003.*

Summary. An impressive number of populations was studied with respect to 12 microsatellite loci. As many as 11 of the 12 loci deviated significantly from Hardy-Weinberg equilibrium, which renders interpretation of the obtained data somewhat uncertain. Significant correlations for the relationships between genetic and geographic or climatic variables were noted but the degrees of explanation for them were all low. Three clusters without sharp boundaries were identified. The results suggested that spreading of the species after the latest glaciation took place from 3 gene pools.

Rusanen et al. (2000) studied the genetic diversity and differentiation of 26 marginal and scattered *A. platanoides* populations from southern Finland. Twenty of the populations were regarded as natural populations and 15 of them were grouped into 4 regions. Two of the populations were split into 2 or 3 subpopulations, resulting in a total of 29 populations. Nine isozyme loci were analyzed.

The mean expected heterozygosity for all 29 populations amounted to 0.128 (Fig. 23) and the corresponding estimate for observed heterozygosity was 0.131. These levels were regarded as moderate and so was the allelic richness, 1.9.

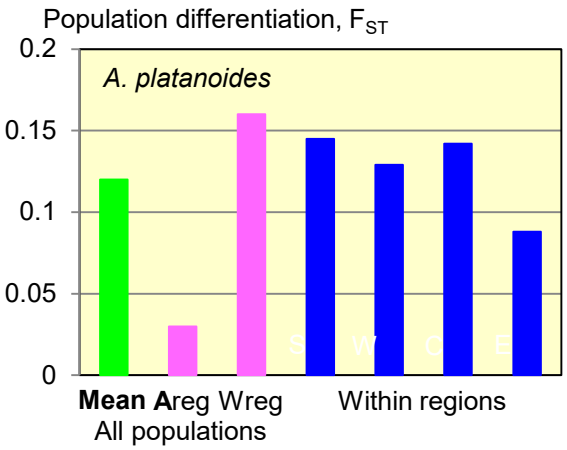


Figure 24. F_{ST}s for all populations (green), for differentiation among 4 regions (Areg), within regions (Wreg), and within individual regions (South, West, Central, East) after exclusion of non-natural populations. Rusanen et al. 2000.

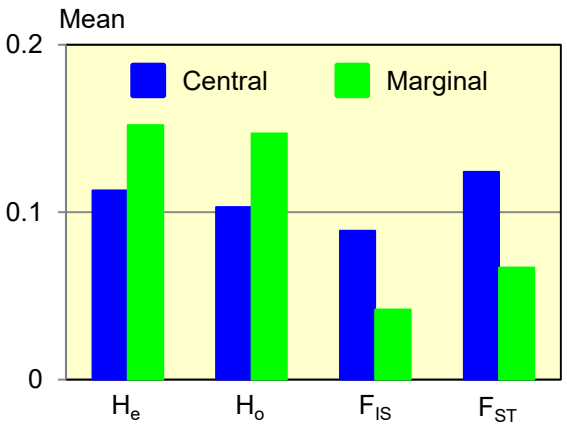


Figure 25. Mean values for expected heterozygosity, observed heterozygosity, inbreeding coefficient, and genetic differentiation in 6 central and 6 marginal populations of A. platanoides. *Eleven isozyme loci were analyzed. Rusanen et al. 2003.*

The mean F_{ST} for all 29 populations was estimated at 0.12, which is fairly high considering the limited distribution in southern Finland (Fig. 24). This figure reveals that the differentiation among regions was more than 5 times lower than within regions. It is expected that the scattered distribution accompanied with limited population size and insect pollination would favor genetic drift. However, the estimates of the fixation indices did not differ significantly from zero in any of the populations. Thus the fixation indices do not support the expectation of considerable genetic drift in the investigated populations. Moreover, equal numbers of negative and positive estimates were found. The climatic conditions at the growth localities in southern Finland do not differ to such an extent that adaptation to varying climatic conditions has occurred.

Summary. A Finnish study of 29 scattered populations of *A. platanoides* with 9 isozyme loci resulted in an F_{ST} estimate of 0.12, which must be regarded as high for populations from a geographically limited area. This estimate might originate from genetic drift but the low F_{IS} estimates did not give any support for such an interpretation.

The hypothesis that marginal populations have less genetic diversity, higher inbreeding coefficient, and larger diversity among populations was tested by Rusanen et al. (2003) in 6 marginal and 6 central populations of *A. platanoides* in Europe. Eleven isozyme loci were studied. This paper also deals with a comparison of *A. platanoides* and *B. pendula*, 2 species with different life history traits, insect pollinated versus wind pollinated. The latter species is partly dominating in stands while *A. platanoides* mainly grows in mixed stands. Traditional estimates of genetic parameters were calculated.

The essence of the results as regards *A. platanoides* is illustrated in Fig. 25. None of the parameters illustrated in this figure supports the hypothesis outlined above. The differences were not significant but the results rather contravened the hypothesis. Nor was there any support from the number of alleles per locus, which was 2.0 for both categories of populations. It was suggested that the scattered occurrence of *A. platanoides* was not a result of migration from a more central distribution but was a result of reduction of the species from an earlier continuous distribution. Therefore, a possible effect of genetic drift will appear in later generations.

Generally, the genetic diversity was fairly limited in *A. platanoides*.

Summary. The hypothesis that marginal populations have less genetic diversity, higher inbreeding coefficients, and larger diversity among populations than central populations was tested in 6 marginal and 6 central populations of *A. platanoides* in Europe. Eleven isozyme loci were studied. There was no support for this hypothesis; rather the opposite result was obtained.

Inter-simple sequence repeats (ISSR) were used by Akhmetov et al. (2021) in a study of genetic diversity differentiation in 10 *A. platanoides* populations from its eastern marginal distribution in Russia. The latitudinal range of the populations was 52.78–56.55°N, and the corresponding range for longitude was 53.59–56.89°E. The 5 primers used generated 117 bands, of which 95 were polymorphic. Expected heterozygosity, effective numbers of alleles, private alleles, and population differentiation (G_{ST}) were estimated.

Fig. 26 reveals that the genetic diversity was low in 9 of the 10 populations. The Arc population grows in an area in which *A. platanoides* is a dominant species. This in combination with its high number of private alleles explained its high genetic diversity. The lowland populations were geographically isolated and had mostly low genetic diversity. It was suggested that the Arc, Slv, and Kmr populations were of greater historical age and were refugia during the latest glaciation.

The grouping of the populations according to the principle component analysis resulted in 5 groups as indicated in Fig. 26. Two groups consisted of just one population each, Kud and Arc. The mean differentiation, G_{ST}, was high and estimated at 0.59. The genetic distance (D) according to Nei and Li (1979) was estimated at 0.25. The Arc population contributed most to the differentiation among the populations. It would have been valuable to have mean values of these parameters for each population. The fragmented distribution might be a contributing factor for these results. It was stated that genetic drift had not taken place to any great extent.

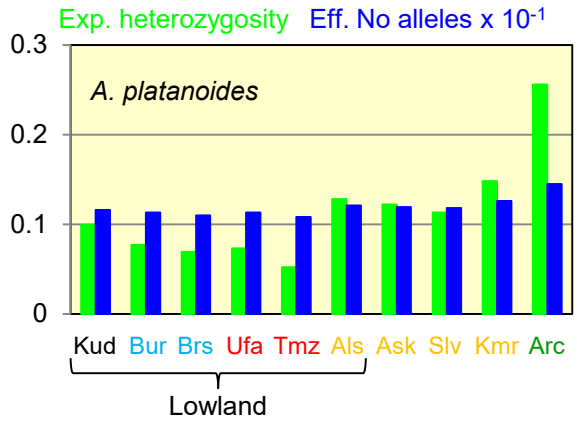


Figure 26. Expected heterozygosity and effective number of alleles x 10^{-1} in 10 Russian populations of A. platanoides. *Populations classified as lowland are indicated. Populations belonging to the 5 groups identified in the cluster analysis are shown with different colors. Akhmetov et al. 2021.*

Since no inbreeding coefficients were presented it is unclear what this statement was based on. The existing fragmentation was recent in connection with transformation of forests to agricultural land.

Summary. Genetic diversity differentiation in 10 *A. platanoides* populations from its eastern marginal distribution in Russia was studied. Generally, low genetic diversity was observed, particularly in fragmented lowland populations. Pronounced differentiation among the populations was found. The PCA analysis revealed 5 clusters.

Lazic et al. (2022) analyzed 11 microsatellites for a study of the genetic diversity and differentiation in 30 Austrian *A. platanoides* populations. In addition, 2 populations from each of Bosnia Herzegovina, Germany, Hungary and northern Europe (Estonia and Finland) were included in the study. Four of the Austrian populations were either non-natural or planted.

Traditional population genetics estimates were obtained from GenAlEx 6.503 and ADZE v.1.0 for allelic richness. Population clusters were estimated using STRUCTURE v.2.3.4. FSTAT was applied to estimate population differentiation. BOTTLENECK v1.2.02 was used to test changes in population size. Isolation by distance was analyzed for the Austrian natural popu-

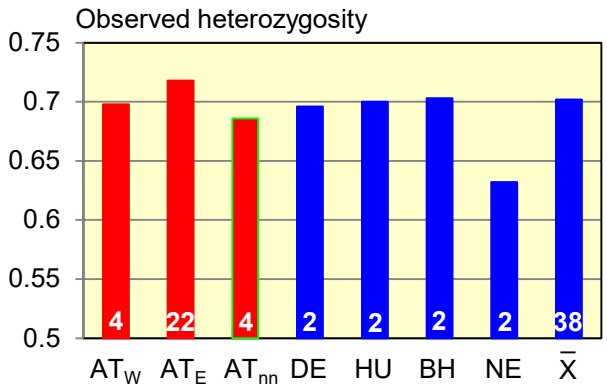


Figure 27. Mean observed heterozygosity in groups of Acer platanoides *populations estimated by 11 microsatellites. AT_W = Western Austria, AT_E = Eastern Austria, AT_{nn} = non-natural populations, DE = German, HU = Hungarian, BH = Bosnia Herzegovina, NE = northern Europe, Estonia and Finland. The number of populations in each group is given. Lazic et al. 2022.*

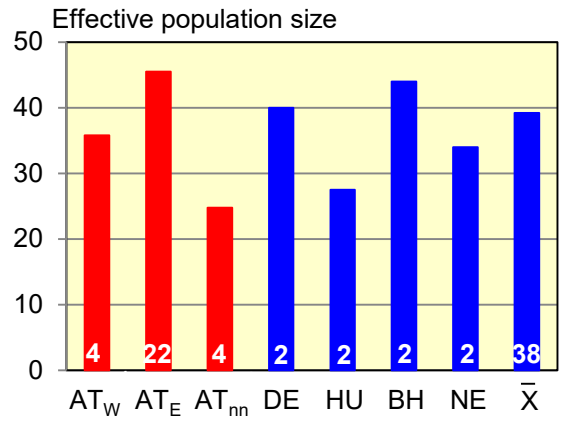


Figure 29. Mean effective population size in groups of Acer platanoides *populations estimated by 11 microsatellites.AT_W = Western Austria, AT_E = Eastern Austria, AT_{nn} = non-natural populations, DE = German, HU = Hungarian, BH = Bosnia Herzegovina, NE = northern Europe, Estonia and Finland. The number of populations in each group is given. Lazic et al. 2022.*

lations by the Mantel Test and spatial genetic structure analysis by GENEALEX.

Significant deviations from Hardy-Weinberg equilibrium were detected in several of the populations. Except for an Austrian seed tree stand there was an excess of homozygotes. The 3 parameters for genetic diversity illustrated in Figs. 27-29 all show the same pattern. The northern populations and the non-natural Austrian populations show lower estimates. The mean observed and expected heterozygosities were high and did not vary much, 0.70 and 0.72, respectively. The lowest observed heterozygosity was noted for the Finnish population, 0.59, which contributed to the lowest mean for the North European populations in Fig.27. It also had a low allelic richness, 3.76. The low estimates for the Finnish population were attributed to its character as marginal population growing close to the northern edge of *A. platanoides* distribution as well as to the low number of trees in this population, 9 (In Table 1 of the paper the number is 31 but 9 agrees with the presentation of this population in Rusanen et al. 2000). The mean heterozygosities for the Western Austrian populations was somewhat lower than for the Eastern Austrian populations. Both Hungarian populations had low estimates of effective population size, 14 and 27. The absolute lowest estimate for this trait, 7, was noted for an Austrian seed tree stand.

A low F_{ST} estimate for the Austrian populations was noted, 0.04. Nor was the F_{ST} for all po-

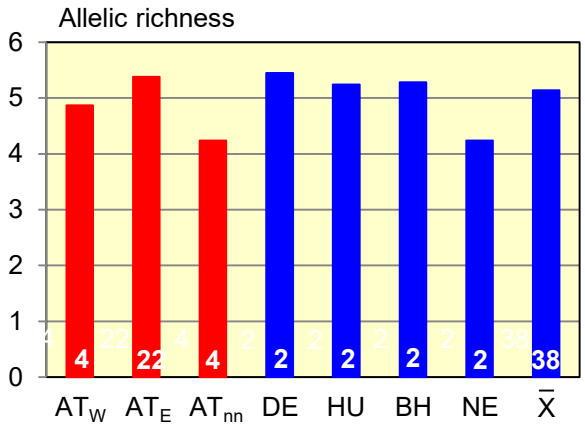


Figure 28. Mean allelic richness in groups of Acer platanoides *populations estimated by 11 microsatellites. AT_W = Western Austria, AT_E = Eastern Austria, AT_{nn} = non-natural populations, DE = German, HU = Hungarian, BH = Bosnia Herzegovina, NE = northern Europe, Estonia and Finland. The number of populations in each group is given. Lazic et al. 2022.*

pulations high, 0.06. It is evident that there is substantial gene flow among these insect-pollinated populations. The STRUCTURE analysis resulted in 8 groups, with the western Austrian populations and the man-influenced populations differentiated from the rest of the Austrian populations. The Finnish population and the Bosnia-Herzegovina populations constituted 2 separate groups, while the Estonian population grouped together with Central European populations. One of the Hungarian populations formed a rather well-defined cluster. The isolation by distance was tested by plotting genetic distance against geographic distance of the natural Austrian populations. A weak relationship was obtained, with $R^2 = 0.20$. As judged from the plotting in Fig. 4 in the paper, the R^2 seems rather high for such a wide dispersal along the regression line.

Some sibship was noted for the majority of populations. The seed tree stand population and its progeny showed pronounced sibship. In contrast, limited sibship was found in another planted Austrian population. Evidently the genetic structure of a population is dependent on the genetic quality of the regeneration material.

Summary. A fairly high genetic diversity was found in most of the 30 populations. Man-influenced populations and one marginal population had lower genetic diversity. Sibship was more common in man-influenced populations than in the rest of the populations. There was a weak relationship between genetic and geographic distances among the Austrian populations, $R^2 = 0.06$. The genetic differentiation was limited among the Austrian populations, $F_{ST} = 0.04$. Even after inclusion of 8 populations from other countries, F_{ST} remained fairly low, 0.06. Pronounced sibship was found in non-natural populations.

The objective of a study by Belletti et al. (2007) was to get information on genetic variation among *A. pseudoplatanus* plantations to guide genetic conservation, as well as to identify seed sources of this species. Between 10 and 30 trees were sampled from 12 northwestern Italian populations. In all, 16 polymorphic isozyme loci

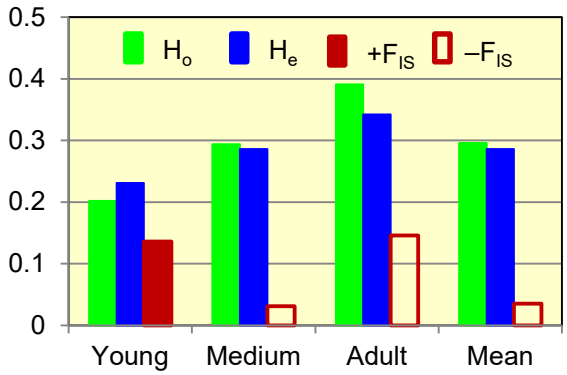


Figure 30. Mean observed heterozygosity, mean expected heterozygosity, and inbreeding coefficients in 3 age classes of A. pseudoplatanus *from 12 populations in north western Italy. Belletti et al. 2007.*

were included. Traditional population genetics parameters were estimated. A separation of the material into 3 age classes was used with stem diameters as a proxy for age. U statistics was used to estimate significances for age classes.

Limited variability among populations was noted for mean number of alleles per locus and effective number of alleles: 2.78 and 1.47, respectively. The means for observed and expected heterozygosities were 0.293±0.009 and 0.280±0.005. Four of the populations had positive estimates of the inbreeding coefficient, in one population significantly different from 0. There was a high gene flow among the populations, 4.4, which prevents a large differentiation among the 12 populations. All data suggest that there is substantial gene flow among the 12 populations and that genetic drift was of limited importance for the population genetics results. It was suggested that this part of Italy had been a refuge for *A. pseudoplatanus* during the latest glaciation, which could explain the fairly high genetic variability observed in this investigation. The large population sizes and efficient pollen and seed dispersal also contribute to the large variability within populations and limited differentiation among populations.

Both heterozygosities showed significantly increased estimates with increasing age of the material (Fig. 30). The inbreeding coefficient showed an opposite pattern, with significantly decreasing estimates with increasing age. This

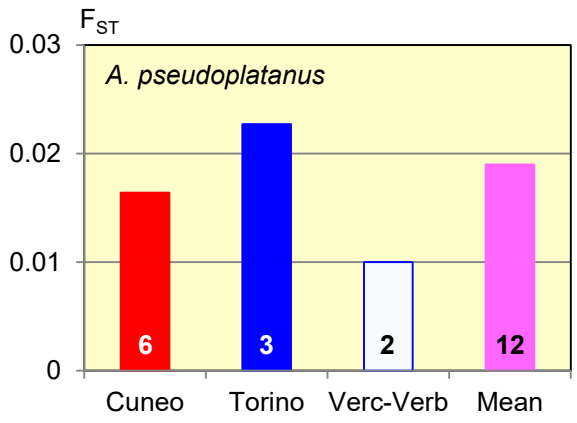


Figure 31. Mean F_{ST} for 3 geographic regions and for all 12 populations of A. pseudoplatanus *in northwestern Italy. The number of populations is indicated. Verc = Vercelli, Verb = Verbania. Belletti et al. 2007.*

result suggests that there was a selection against homozygotes with increasing age.

The mean F_{ST} for all 12 populations was low, 0.019 (Fig. 31). The range of estimates was 0.014–0.027. The highest estimate was noted for a high-elevation Torino population. This population contributed to the high F_{ST} of the Torino region in Fig. 31. In spite of the result of the separation of the F_{ST}s in this figure, isolation by distance was non-significant according to the Mantel Test.

Summary. Low among-population differentiation among 12 northwestern Italian populations of *A. pseudoplatanus*, F_{ST} = 0.019. The inbreeding coefficient decreased with age of the plant material while the heterozygosity increased with age. Selection against homozygotes was suggested as an explanation for this observation.

The spatial genetic structure (SGS) has bearing on seed collection of material for applied forestry as well as for sampling for genetic conservation. SGS in 2 contrasting populations of *A. pseudoplatanus* close to Leipzig in Germany was studied by Pandey et al. (2012). The stands were denoted as compact and elongated. The latter stretches over 2 km along a creek in Central Germany and has a density of reproductive trees of 1.26 trees/ha. The compact stand is a stand of almost square form on flat ground with a density of reproductive trees = 45 trees/ha.

SGS is influenced by:

The mating pattern in the previous generation which in turn is dependent on:

The fecundity, the variation of female and male flowering, flowering phenology and pollinator occurrence

The dispersal of seeds, wind or animal.

Studying the mating pattern in the present populations will give information on likely processes in past generations. Six microsatellite markers were used by Pandey et al. (2012) in this study. A progeny population in the compact stand was also analyzed.

Since *A. pseudoplatanus* is an autotetraploid it is impossible to determine the number of copies of an allele in a heterozygotic tree. Therefore, scoring was 1 for presence of an allele and 0 for absence of the allele. The pairwise kinship model according to Loiselle et al. (1995) was used to estimate the pairwise kinship coefficient, Fij, for the 3 populations. Wright's neighborhood size (Nb) = $4\pi De\sigma^2_g$ was estimated, in which De is the effective population density and σ^2_g is axial variance of gene dispersal.

The mean numbers of alleles per locus in the 3 population were:

Compact adults	13.3
Compact progeny	11.5
Elongated adults	14.2

The lower mean value for the compact progeny population emanated from the difference in one locus with 12 alleles in the progeny population

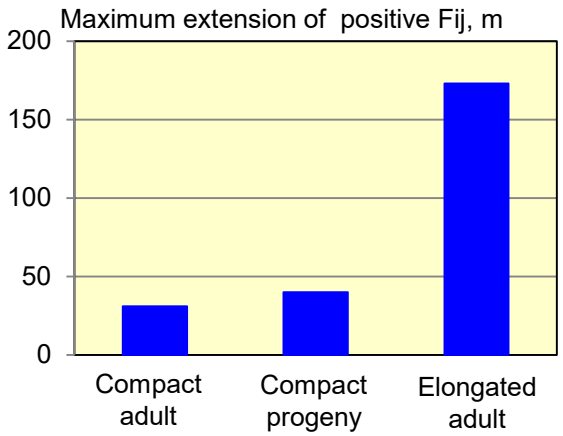


Figure 32. The maximum extension in meters of significant positive estimates of the kinship coefficient, Fij, in 2 Central German A. pseudoplatanus *stands with different densities of reproductive trees per hectare, 1.26 and 45. Pandey et al. 2012.*

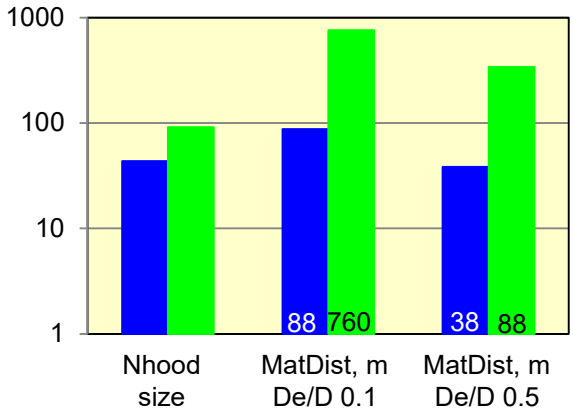


Figure.33. The neighbourhood size (Nhood) and mating distance (MatDist) in meters in 2 Central German A. pseudoplatanus *stands with different densities of reproductive trees per hectare, 1.26 (green) and 45 (blue). De = effective population density, D = census density. The estimated distances are given. Pandey et al. 2012.*

versus 20 and 22 alleles in the 2 adult populations.

The maximum extension of the kinship coefficients differed significantly between the compact populations and the elongated population (Fig. 32). The mating distance (called gene flow in the paper) in the elongated population was almost 9 times longer than in the compact population.There was limited difference between the adult and the progeny generations in the compact stand as regards significant positive kinship coefficients (Fig. 32). Most other studies of similar character have shown differences between the adult and progeny generations. The obtained result suggests that natural selection had not affected the 2 populations or alternatively that the effect of natural selection was more or less the same in the adult and progeny generation. Fig. 33 reveals that neighborhood size was twice as large in the elongated population as in the compact population, 92 versus 44. The ratio De/D (effective population density/census density) did not differ between the 2 types of population. The results were attributed to the difference in the density of reproductive trees per hectare in the 2 populations. It was assumed that the higher density facilitated random mating in the compact population. The shape of the 2 populations as well as the difference in the reproductive density of these 2 populations might have caused different mating patterns in them. In the compact population the spreading of the fruits might be more prevented than in a population with low density of trees. At large mating distance between the trees, significant negative estimates of the kinship coefficients were noted in the 2 adult populations.

Summary. There was a substantial difference in the extension of the significant sibship coefficients in the compact and the elongated population. The neighborhood size and mating distance were larger in the elongated population than in the compact population. Both shape of the 2 populations and the difference in density of reproductive trees in the 2 populations might at least partly explain the results observed.

Even if all factors regulating the spatial genetic structure were not revealed or addressed, important steps for understanding the spatial structure were reached.

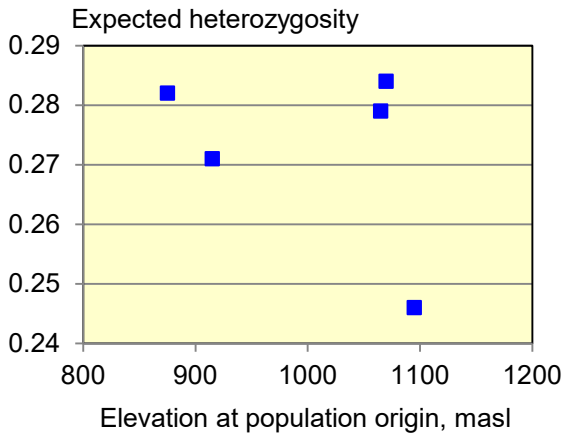


Figure 34. The relationship between population elevation and expected heterozygosity of 5 A. pseudoplatanus *populations from Romania. Eight sequence-related amplified polymorphism markers were used. Rebrean et al. 2019.*

Fifteen *A. pseudoplatanus* trees from each of 5 regions in the Carpathian Mountains in Romania were sampled for an analysis of genetic diversity by Rebrean et al. (2019). Wide ranges of elevations of the populations were given. We have used mean values in our presentation. Eight sequence-related amplified polymorphism dominant markers were used in this study. Traditional population genetics estimates were calculated.

The mean expected heterozygosity was fairly low and estimated at 0.27. The mean Shannon index was 0.416 and with a good agreement with the expected heterozygosity, $R^2 = 0.86$. It is expected that populations close to the margin of distribution of the species would have less genetic diversity than populations in central parts of the distribution. Therefore, we have illustrated the relationship between mean elevation at population origin and expected heterozygosity in Fig. 34. As seen from this figure such a relationship did not exist in the present material. The G_{ST} was fairly high for populations from a geographically limited area and was estimated at 0.114. The AMOVA showed that 8% of the variation was attributed to among-population differentiation. The UPGMA revealed that the 1,070 masl population differed most from the other 4 populations. It should be noted that this population had the largest elevation range of all

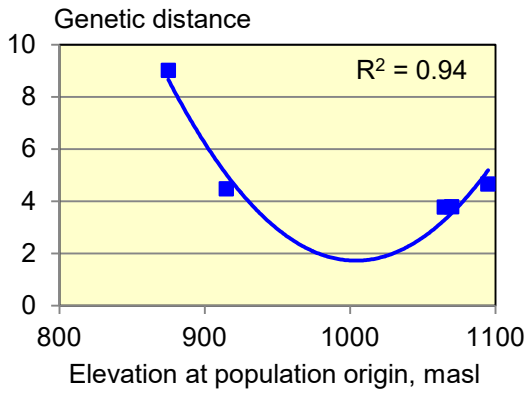


Figure 35. The relationship between population elevation and mean genetic distance of 5 A. pseudoplatanus *populations from the Carpathian Mountains in Romania. Eight sequence-related amplified polymorphism markers were used. Rebrean et al. 2019.*

populations, from 790 to 1,350 masl. The principle coordinate analysis suggested that there were 2 groups, in agreement with the UPGMA analysis. A Mantel Test was performed to enable a test of the relationship between genetic and geographic distances. Such a relationship did not exist. We tested the relationship between population mean elevation and genetic distance (Fig. 35). We used the figures for genetic distances in Table 6 in the paper. There was a strong relationship to the second-degree polynomial, $R^2 = 0.94$. However, the biological meaning of such a relationship is unclear. Since the sampling of the materials at each elevation had ranges varying between 230 and 560 m it is likely that a large variation within each of the populations exists. Our use of mean elevations might not be appropriate but we have used them as a proxy to possible relationships between geographic and genetic data.

Summary. Five marginal *A. pseudoplatanus* populations from the Carpathian Mountains in Romania were studied. Eight sequence-related amplified polymorphism dominant markers were used in this study. Fairly low expected heterozygosities were noted, 0.27. A relatively high G_{ST} was estimated, 0.11, which might be attributed to the elevational range of the populations, 875–1,100 masl.

1.2.1.2 Artificial populations

The thesis by Kathrin Bendixen from 2001 is probably the first comprehensive genetic study of flowering and mating patterns in *A. campestre*. The ultimate objective of this investigation was to give guidance for sampling of *A. campestre* seeds for commercial nurseries. She studied 31 planted trees from the Forest Botanical Garden in Göttingen, Germany, and 87 trees planted along a bike path, Gartetal, in the neighborhood of Göttingen. We shall concentrate on the genetic part of this investigation, in which 10 polymorphic isozyme loci were analyzed. Seeds were genotyped one or 2 years.

Phenological observations of the flowers in the 31 trees in the Botanical Garden were followed daily during the entire flowering period in years 1999 and 2000. As far as we can understand, a mean estimate of open flowers for each tree was recorded.

The occurrence of wind pollination was studied following isolation of flowers with insect screens, which allows pollen to pass the screen. The seeds formed might originate from:

Wind pollination
Selfing
Asexual processes

Selfing was assessed by isozyme analysis of seeds from flowers isolated with paper bags. Three trees with suitable genotypes for determination of wind pollination and selfing were selected for this purpose.

Occurrence of asexual propagation was tested following isolation by paper bags of emasculated flowers.

Seed set was estimated as filled seeds per tested flowers.

Although the flowers are bisexual, usually one sex is dominating. Generally, male flowering occurred earlier than female flowering. The flowering period was more extended in 1999 than in 2000, 40 days versus 24 days. There was a substantial variation in the extension of the flowering periods and overlapping in male and female flowering periods among the trees. Examples for 5 trees are given in Fig. 36.

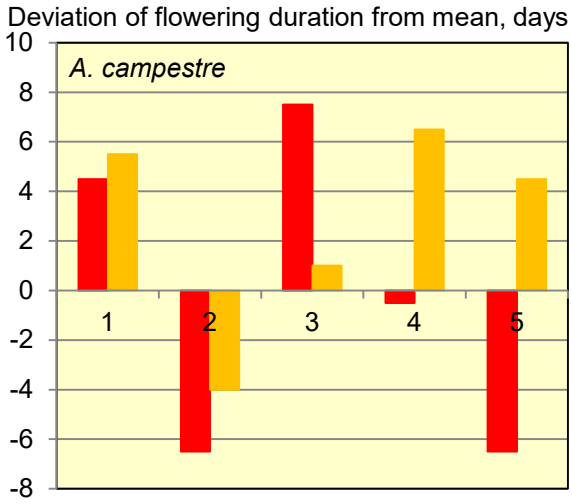


Figure 36. The deviation in 5 A. campestre *trees of the duration of female (red) and male (orange) flowering in days from the mean duration in all 31 trees. Observations were made in 1999. Positive values = longer duration, negative values = shorter duration than the mean duration. Bendixen 2001.*

Three types of flowering performance were distinguished:

1. One sex only during the entire flowering period
2. The onset with either female or male flowering followed by the opposite sex later during the flowering period
3. Three phases according to the succession:
   Male – female – male, tree No 19 in Fig.37
   Female –Male – male, tree No 3 in Fig.37

Type 1 was represented by one male flowering tree only.

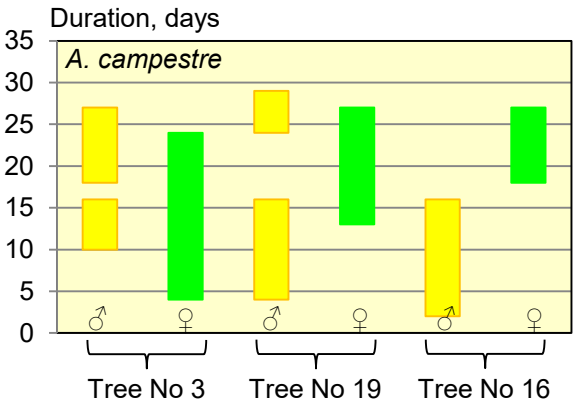


Figure 37. The duration in days of pollen dispersal and female receptivity in 3 trees from the Forest Botanical Garden, Göttingen, Germany, in 1999. Day 0 was the starting day of observation. Bendixen 2001.

A large variation in duration of female and male flowering was noted. We have illustrated some extreme examples of the deviation in duration from the mean for all 24 trees from the Forest Botanical Garden in 1999 (Fig. 37).

In the study of wind pollination, only 31 filled seeds were obtained from the 658 flowers in the 3 trees (Fig. 38). The multiple-locus genotype analysis revealed with certainty that 13 of them were the result of fertilization with unrelated

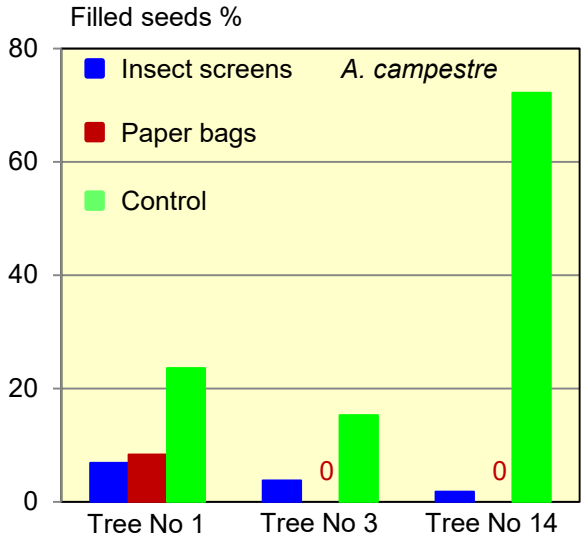


Figure 38. Percetage of seed set following isolation by insect screens, paperbags, and unisolated control in 3 trees of A. campestre *growing in the Forest Botanical Garden, Göttingen, Germany. Ten isozyme loci were used. Bendixen 2001.*

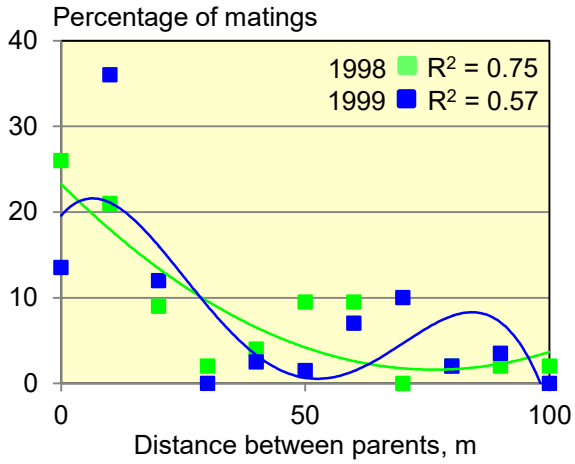


Figure 39. The relationship between distance of A. campestre *parents in successful matings in the Forest Botanical Garden in years 1998 and 1999. Seeds were genotyped by the multilocus-genotype method. Bendixen 2001.*

pollen. The minimum of wind pollination was estimated at 2.8% with a maximum estimate at 4.7%. The results indicate that wind pollination occurs to a low extent in *A. campestre.*

Since there were no seeds in trees 3 and 14 following paper bag isolation, no selfing had occurred in these 2 trees, while selfing might have occurred in 8.4% of flowers in tree No 1. Selfing was estimated at 2.5% following the analysis of 480 flowers.

494 flowers from one tree were included in the study of asexual reproduction and 104 seeds were harvested. All of them lacked an embryo, which suggests that asexual reproduction is at most rare in *A. campestre*.

The study of mating distance between parents in the Forest Botanical Garden comprised 15 trees and 578 seeds in 1998 and 24 trees and 708 seeds in 1999. The corresponding figures for the Gartetal population were 50 trees and 1,500 seeds. Seeds were genotyped by the multilocus method. Fig. 39-40 reveal that the majority of matings took place within short distances in both populations. In Gartetal 75% of the matings occurred with pollen from the 6 nearest neighbors. More than half of the matings took place within a distance of 30 meters in Gartetal. In the Forest Botanical Garden 29.1% and 51.7% of the matings took place within a distance of 20 meters in 1998 and 1999. It was shown that 84 of the

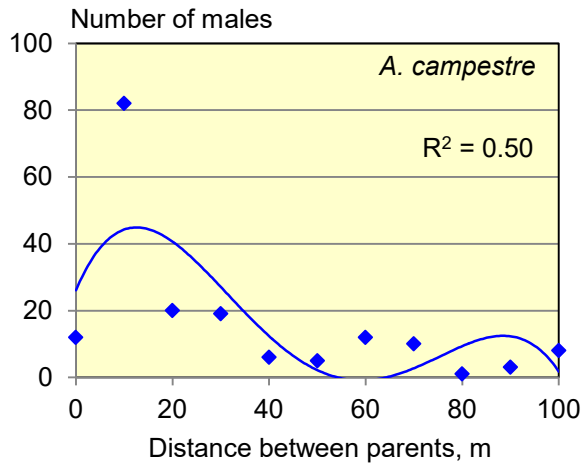


Figure 40. The relationship between distance of A. campestre *parents in successful matings in Gartental in year 1998. Seeds were genotyped by the multilocus genotype method. Bendixen 2001.*

1,500 Gartetal seeds (5.6%) had external male parents. The corresponding percentages for the Forest Botanical Garden were 7.4% and 9.2% (1998 and 1999).

Of the seeds collected in 1998 in the Forest Botanical Garden, 53 fatherhoods could unequivocally be determined and the corresponding number of seeds from 1999 was 58 seeds. Fig. 41 reveals that there was a large variation in pollination success among the trees. A large variation between years is also visible, as well as substantial differences in selfing among the trees.

Seeds were collected from 2–3 parts of the tree crown in 31 trees to test the homogeneity in tree crowns. Only in 3 of the 31 trees were there proven differences between parts in the crown.

There are several reasons for large variation from random mating:

- Variation in the frequency of female and male flowering
- Phenological differences – variation in overlapping of receptivity and pollen dispersal
- Distances among the trees
- Pollinator preferences of female flowers
- The ambient conditions, weather and soil conditions

From this investigation it was clearly shown that mating was far from random.

As regards seed collection it was stressed that it is important to try to encompass as much genetic variability as possible in the seeds collected.

No discussion of the demand for genetic variability in different types of populations was carried out. It is certainly recommended that the breeding and gene conservation populations should have large variability. For production populations such a broad variability is usually not needed.

Summary. An impressive amount of data from 2 planted populations in central Germany. Large phenological difference was noted among trees and between years. Most successful pollinations occurred within short distances in the 2 plantations, up to 30 meters. Selfing occurred in low frequency, never above 10%. Similarly, long distance pollination occurred in low frequency.

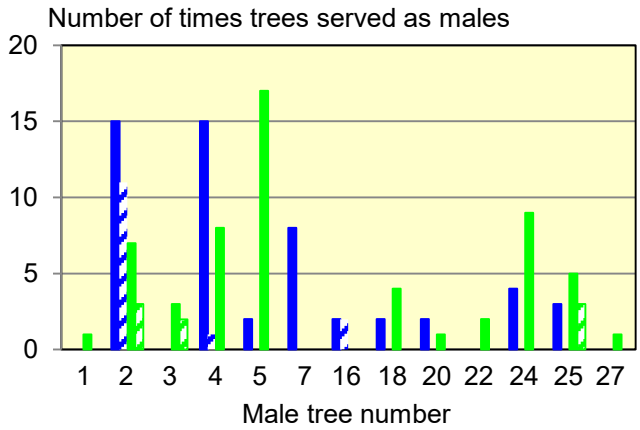


Figure 41. The number of times an A. campestre *tree in the Forest Botanical Garden served as pollen donor in years 1998 (blue) and 1999 (green). Striped columns show the numbers of selfing in all cases. Seeds were genotyped by the multilocus genotype method. Bendixen 2001.*

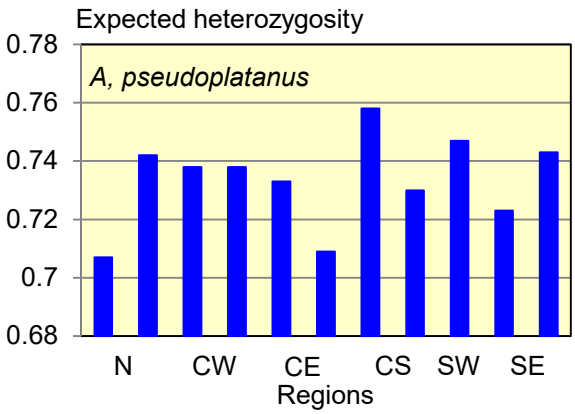


Figure 42. Expected heterozygosity in material from various provenance regions of A. pseudoplatanus *in Germany. N = North, CW = Central West, CE = Central East, CS = Central South, SW = South West, SE = South East. Neophytou et al. 2019.*

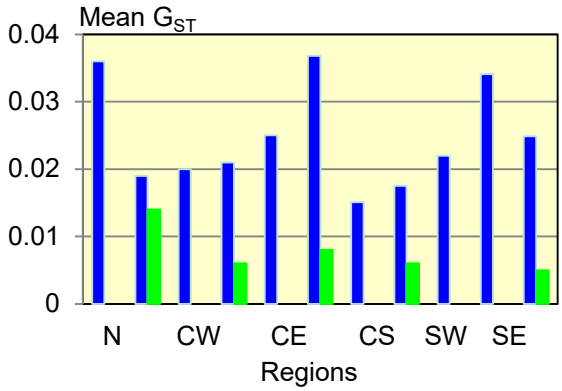


Figure 43. Mean G_{ST} (blue columns) estimated for material from various provenance regions of A. pseudoplatanus *in Germany. Green columns refer to G_{ST}s within N, CW, CE, CS, and SE regions. N = North, CW = Central West, CE = Central East, CS = Central South, SW = South West, SE = South East. Neophytou et al. 2019.*

To get an understanding of the genetic differentiation in *A. pseudoplatanus,* Neophytou et al (2019) genotyped 1,033 German plus trees of *A. pseudoplatanus*. In addition, 12 trees from neighboring countries were included. The plus trees were scattered all over Germany, some growing outside the natural range of this species. To get some understanding of possible geographic differentiation the trees were pooled into 11 provenance regions in Germany. Eleven microsatellite loci as well as 2 haplotypes were studied. Bayesian clustering according to STRUCTURE was applied.

The expected heterozygosity was high (Fig. 42) and the number of effective alleles was with one exception (3.71) between 4 and 5. One of the 2 haplotypes occurred mainly in the eastern part of Germany. The other haplotype occurred all over Germany and was the only one in northwestern Germany. With respect to differentiation, both haplotype and microsatellite data indicated a differentiation between east and west in Germany. It was suggested that these results reflected the existence of 2 refuges during the latest glaciation.

Generally the G_{ST} estimates were low. Since the trees used in this investigation were plus trees and thus selected based on the same selection criteria, the differentiation among regions may be lower than in a study of Mendelian populations from different regions in Germany. It was stated that the differentiation was larger in southern Germany than in northern Germany. This was attributed to constraints to gene flow owing to the hilly and mountainous landscape in southern Germany, regions CE–SE. To get some information on this differentiation, we have illustrated the mean G_{ST}s for all regions in Fig. 43. Besides, we have illustrated the G_{ST}s for differentiation in various parts of Germany, N, CW, CE, CS, and SE. As seen from this figure the differentiation within the hilly and mountainous regions, CE, CS, and SE was low. Thus, there was limited support for the statement of higher differentiation in southern Germany.

Summary. More than 1,000 German *A. pseudoplatanus* plus trees originating from all over the country were genotyped by 11 microsatellite loci and 2 haplotypes. High estimates of expected heterozygosity were noted. The trees were allocated to 11 geographic regions and the mean G_{ST}s for each region did not exceed 0.04. Since plus trees were selected, the genetic variability might be reduced and differentiation less than in randomly selected trees.

1.2.2 Sexual morphs

In a series of papers Gleiser et al. (2008a, 2008b, and 2018) reported studies of flowering and mating patterns in a population of *A. opalus* in southeastern Spain.

In the Gleiser et al. 2008a paper the evolution of gender dimorphism in a heterodichogamous *A. opalus* population located at latitude 38.67°N, longitude 0.50°E and altitude around 1,300 masl was studied. Four morphs were identified among the trees: male, protandrous, protogynous, and non-flowering trees. Protandrous means that male flowering occurs first, followed by female flowering. Protogynous means that female flowering occurs first, followed by male flowering. Samplings of the morphs were:
in 2002 10 males, 5 protandrous, and 10 protogynous trees
in 2003 26 males, 13 protandrous, and 19 protogynous trees
The number of inflorescences was counted on some branches in different orientations and then multiplied by the number of branches of the tree. Sampling was carried out every 2–11 days, depending on rate of development.
During years 1999–2002 the sexual expression was followed in 44 trees. In years 2003–2004 100 trees were followed.
The hypothesis that the seed weight drops over time was tested in 21 protandrous trees and 6 protogynous trees.
The prospective gender of individuals and morphs in the sampled material was estimated by accounting for their sex allocation, their time-dependent mating opportunities, and the possible time-dependent reduction in female fitness over the course of the reproductive season. The following formula was used to estimate the equilibrium frequencies of the morphs:
$f'_i = f_i w_i / \Sigma f_j w_j$
in which f_i and f'_i are the frequency of the ith phenotype in generations t and t + 1, w_i and w_j are the fitnesses of the individual j and morph i.
A sample of 50 males, 12 protandrous, and 62 protogynous trees were included in the study of male functional gender by paternity analysis.

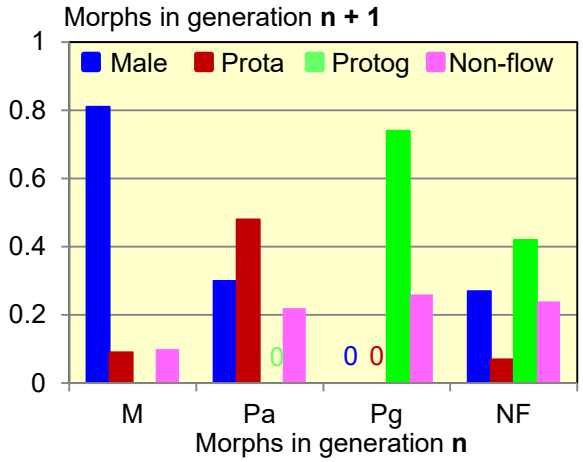


Figure 44. The fraction of morphs in generation n +1 for the 4 morphs male (M), protandrous (Pa), protogynous (Pg) or non-flowering (NF) based on a 6-year survey of flowering in a southeastern Spanish A. opalus *population. Gleiser et al. 2008a*

Three methods were used for this analysis:
Categorical likelihood-based paternity analysis
Non-spatial Bayesian method of fractional paternity inference
The PatQuest version 4.0 program, in which distances between females and males are considered.
Six microsatellite markers were used in the paternity analysis. Fig. 44 reveals that the morph remained fairly stable in the male and protogynous trees. There was no transition to protandrous or males in the consecutive generation. Only 24% of the non-flowering trees remained non-flowering in the consecutive generation.
Seed weight showed a significant dependence on initiation time of fruit development. It should be noted that fruit initiation occurred late in the protandrous trees, accompanied by low fruit weights. The longer time series of seed weight in protogynous trees clearly showed a decrease over time.
Prospective functional gender. In year 2002 and 2003 the total number of male flowers was:

	Males	Protandrous
2002	2,700	19,100
2003	31,300	12,900

For both years it was confirmed that the protandrous trees were specialized males and the

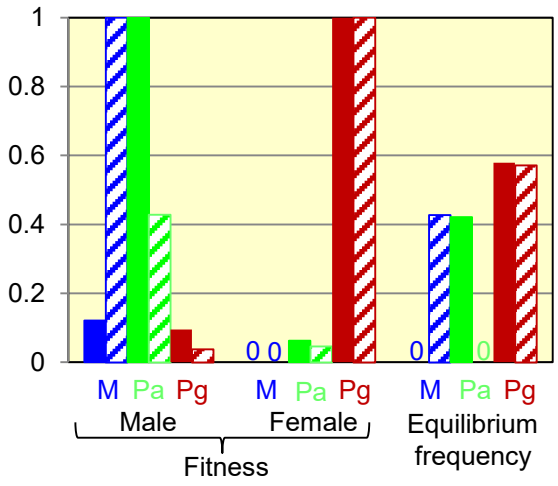


Figure 45. Male and female prospective fitness based on data from years 2002 (filled) and 2003 (striped) for male (M), protandrous (Pa), and protogynous (Pg) A. opalus *trees growing in southeastern Spain. The morph with highest fitness is set at 1.0. The equilibrium frequencies are shown in an analogous way. They were estimated under the assumption of a linear decrease of seed viability over time. Gleiser et al. 2008a.*

protogynous trees were specialized females. The prospective functional femaleness of the protandrous trees was 0.01 and 0.10 in years 2002 and 2003 while the corresponding estimates for the protogynous trees were 0.81 and 0.95. It was also shown that sex expression was not related to tree size, whether size was based on the largest stem or based on the sum of the 3 largest stems.

The protogynous trees showed the highest female fitness both years while the maximum male fitness differed during the 2 years (Fig. 45). It was noted that the equilibrium frequencies of the protogynous trees were more or less identical in both 2002 and 2003, while there was a large shift as regards male fitness between the 2 years. It was pointed out that seed weight had limited effect on equilibrium frequencies.

Of the 240 seeds with an identified male parent, 105 seeds were sired by males, 46 by protandrous parents, and 80 by protogynous parents. The relative success of the 3 morphs is illustrated in Fig. 46. These estimates were obtained after correction for the unbalanced

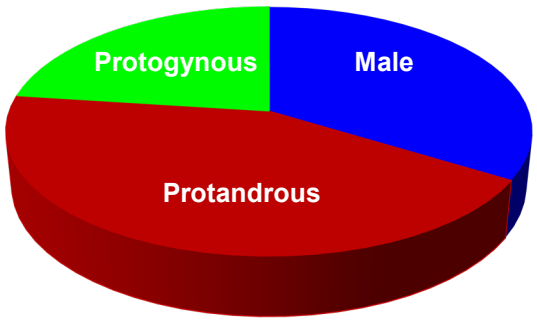


Figure 46. Relative siring success of male (blue), protandrous (brown), and protogynous (green) from an A. opalus *population growing in southeastern Spain. The figures were corrected for the difference in number of the 3 morphs in the population. Gleiser et al. 2008a.*

number of sires. The protandrous trees were most successful in siring. Some gender switch was noted for males and protandrous trees, while the protogynous trees remained protogynous. No matings within the protandrous trees were observed, in contrast with 21% matings within protogynous trees.

Summary. The study of the development of morphs over a 6-year period showed that the male and protogynous morphs were most stable over time, while protandrous and non-flowering morphs were much less stable. As expected, the prospective femaleness was highest in protogynous trees and very low in protandrous trees. For males and protandrous trees, the maximum male fitness differed between the 2 years of study. In contrast, female fitness was highest in protogynous trees both years. It is premature to draw any far-reaching conclusion about the long-term evolution of morph fitness.

The question as to whether the 3 different morphs (male M, protandrous PA, and protogynous PG) in *A. opalus* differ in male fitness was addressed by Gleiser et al. (2008b). This investigation was carried out in the same population as in the above paper. In addition, the frequency of protandrous trees in 6 other *A. opalus* populations from southeastern Spain was reported.

Prior to anthesis 12 PG trees were selected for a study of wind pollination. One to 3 inflorescen-

ces per tree were enclosed in bags that excluded pollinators but allowed pollen penetration into the bags. Emasculation of male flowers in the isolation bags had taken place. Controls were also labelled for estimation of open-pollination. After harvest, the percentage of viable seeds was recorded.

Pollination rates among the 3 morphs were assessed in 7 M, 5 PA, and 10 PG trees. Number of pollinators was recorded during 2 minutes at 10.00–14.00 on sunny days. The recordings were repeated every 4–5 days during the flowering period. In addition, the number of male flowers releasing pollen from the selected trees was recorded.

The siring success was studied in 12 PG trees, in which flowers were isolated in pollen-proof bags. Males in the bags were emasculated to prevent selfing. Flowers were artificially pollinated by brushing with pollen from one of the 3 morphs. Owing to phenological constraints only 5 PG trees could be used as pollinators. The proportion of seeds pollinated by each of the 3 morphs was recorded. Two controls were included, bagged flowers without an artificial pollination and an emasculation of male flowers within the bags to detect any apomixis.

Pollen competition was studied by mixed pollination with 3 pairwise combinations of the 3 morphs. Fruits were harvested at the end of the ripening season. They were genotyped with 5 microsatellite markers. In all, 101 seeds could be genotyped and paternity identified. For each cross the genetic distance between the 2 parents was estimated. After germination the seedlings were grown in containers in a greenhouse for 3 growth periods.

In the 7 populations used for estimation of the 3 morphs, the PG and M morphs were most frequent, with a low percentage of PA trees, never above 12%.

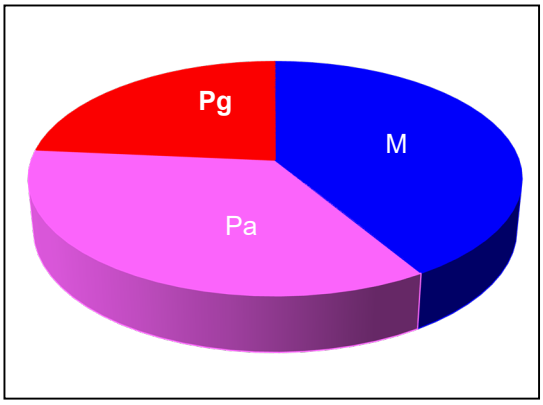


Figure 47. Relative number of visits by pollinators to male (M), protandrous (Pa), and protogynous (Pg) A. opalus *trees growing in a southeastern Spanish population. Gleiser et al. 2008b.*

In the pollinator-exclusion experiment only 0.3% viable seeds were noted from the bagged inflorescences. This means that wind-pollination is rare in this species. In the open-pollinated treatment 13% viable seeds were found. The pollinator (mainly bumble bees and honey bees) visits to the M and PA trees were much more frequent than visits to the PG trees (Fig. 47). The differences between M and PG as well as PA and PG were significant. These differences were attributed to fewer pollinators available at the time for pollen dispersal of the PG trees.

The percentages of seeds sired by the 3 morphs were almost the same, 46.0–48.0. However, the number of seedlings raised from the competition experiment varied dramatically (Fig. 48) which means that the the competition between protandrous and protogynous pollen based on a low number of seedlings suffers from a great imprecision. No effect of relatedness on siring success could be discerned. Apomixis was more or less absent in the siring success experiment.

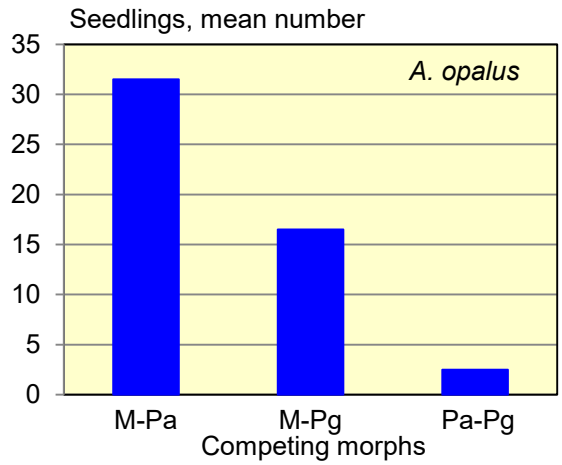


Figure 48. Mean number of seedlings in the competition experiment. M-Pa stands for pollen competion between male and protandrous morphs, M-Pg and Pa-Pg are the 2 other types of competition. Gleiser et al. 2008b.

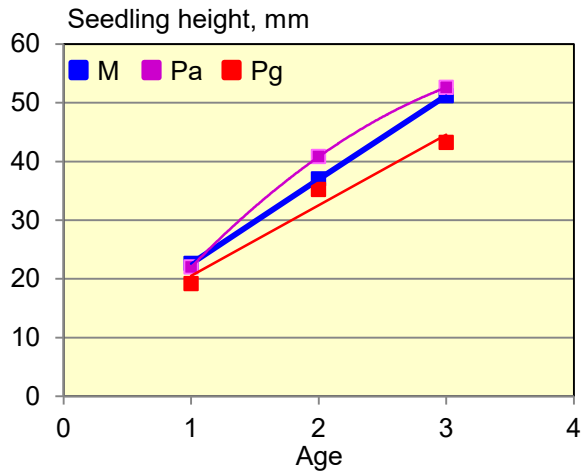


Figure 49. Seedling height at ages 1–3 of progenies after artificial pollination with 3 types of father, male (M blue), protandrous (Pa purple), and protogynous (Pg red) in A. opalus *trees growing in a southeastern Spanish population. Gleiser et al. 2008b.*

The most remarkable result of the seedling growth of the progenies was the poor growth, only slightly more than 5 cm growth in 3 seasons (Fig. 49). No comment on this was presented. A more or less linear growth was noted for the 3 types of progeny. It was stated that the mechanisms behind the inferior growth of the Pg progenies were unknown. We assume that it is likely that the poorer growth of the Pg progenies originates from the late pollination with Pg pollen. This has caused a shorter growth period of the seeds and consequent lower seed weights. This in turn is reflected in poorer growth, which is a purely maternal effect.

Summary. The most spectacular result in this investigation was the poor growth of all 3 types of seedlings. Competition between the morphs in the mixed pollination treatments did not play any great role in siring success. Wind pollination does not play any role in siring of *A. opalus*. Fewer pollinators visited the Pg trees, probably owing to lower activities of pollinators at pollen release from Pg trees.

The hypothesis that phenological match governs the effective pollen transfer between trees in the heterodichogamous *A. opalus* was tested by Gleiser et al. (2018).

Three types of trees were identified:

Males	M
Protandrous	Pa
Protogynous	Pg

These 3 types of trees can all serve as pollinators and contribute to the progeny by siring. Offspring were genotyped with 6 polymorphic microsatellite markers.

Intuitively, siring success is dependent on:

1. overlapping of pollen dispersal and female receptivity, i.e. flowering phenology of the tree
2.. fecundity: for which tree size was used as a proxy
3. distance between the mates

The overlap in phenology between receptivity of protogynous trees and pollen dispersal of males + protandrous trees was more than 3.5 times larger than the male and female phases in the protogynous trees (Fig. 50). This difference could not be attributed to difference in tree size of the 3 morphs. The Pg trees spread their pollen over much longer distances than the M/Pa trees. It is likely that this could be attributed to the late pollen dispersal of the Pg trees at a time when

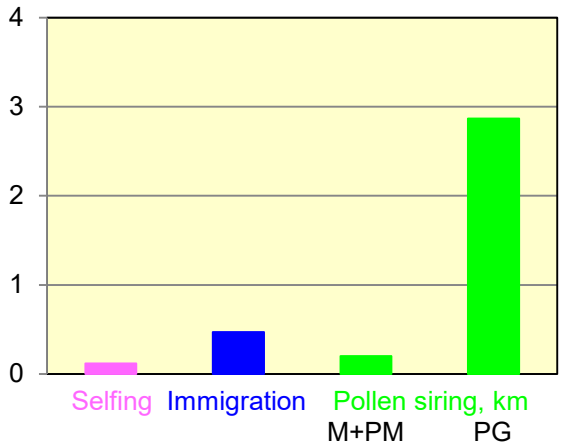


Figure 50. Selfing rate, immigration rate, as well as siring distances in km for males and protandrous males (M+PM), and protogynous trees (PG), respectively. A population of A. opalus *in southeastern Spain was studied. Six polymorphic microsatellite markers were analyzed. Gleiser et al. 2018.*

there were fewer receptive Pa trees. It should be noted that the morphs were distributed in a random pattern in the studied population. In contrast, there was a genetic structuring in the populations, probably caused by limited seed dispersal.

Gleiser et al. tested 8 combinations of the 3 variables listed above for 1–3 variables in each model. The model containing all 3 variables had the highest fit to obtained data.

A substantial immigration into this population took place, 47% .

Summary. Overlapping of receptivity and pollen dispersal, fecundity, and spatial difference between mates had the greatest impact on siring success. Immigration was estimated at 47%.

A detailed study of flowering of 74 *A. pseudoplatanus* trees in a deciduous tree stand in the neighborhood of Leipzig, Germany, was carried out by Tal (2009). Sexual morphs and flowering morphology were observed at 2–3 positions in the crown in 2–3 branches. The number of flowers in the different phases was recorded in 37 protandrous and 13 protogynous trees. The functional femaleness was calculated as F(F +MxE), in which F and M are the mean of flower number and E is the ratio F/M of all trees. Primack´s (1980) index was calculated according to Σa/b/[n(n–1)/2], *in which the percent of overlap for each pair is taken as the ratio between the duration of their common flowering a, and the shorter flowering duration of the two b, and n is the number of trees*. The number of germinating pollen grains on the stigmas, the number of pollen tubes within the stigmatic lobes, and the number of pollen grains in the style were recorded. This investigation was carried out from a crane at canopy top level. Insects in 31 samples from inflorescences in 13 trees were identified. Of these 31 samples, 18 were at female receptivity.

Five sexual morphs of the trees were found with phases:

Female–male
Female–male–male
Male–female
Male–female–male
Male

In the morphs with 3 phases a clear pause between phases 2 and 3 with neither female nor male flowers occurred.

The majority of trees belonged to the male-female-male morph and only one tree was purely male flowering (Fig. 51). The Primack index was almost identical for phases 1 and 2, 0.58 and 0.57. This means that there was a fairly large overlap between female receptivity and pollen dispersal.

The estimated numbers of flowers were around 800 in the protogynous trees and around 2,900 in the protandrous trees. Strangely, the highest

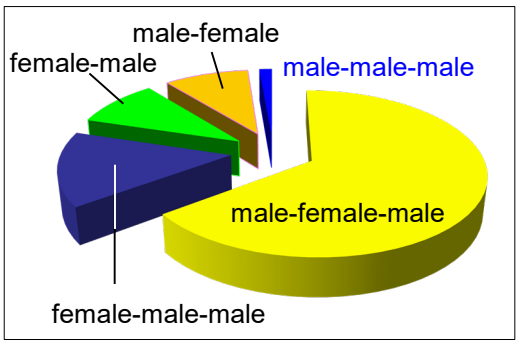


Figure 51. The percentage of flowering morphs among 74 A. pseudoplatanus *trees in a stand close to Leipzig, Germany. The morphs represent the sequence of appearance of female and male flowers. Tal 2009.*

flowering estimate in the protogynous trees was the male 1 phase (Fig. 52). Moreover, the number of female flowers was higher in the protandrous trees than in the protogynous trees.

There was a clear difference in the numbers of germinating pollen on the stigmas of the protogynous trees from the numbers on the protandrous trees (Fig. 53). There was no female flowering in the protogynous trees at the late observation dates. There was one exceptional protandrous tree at day 33 with 14 germinating

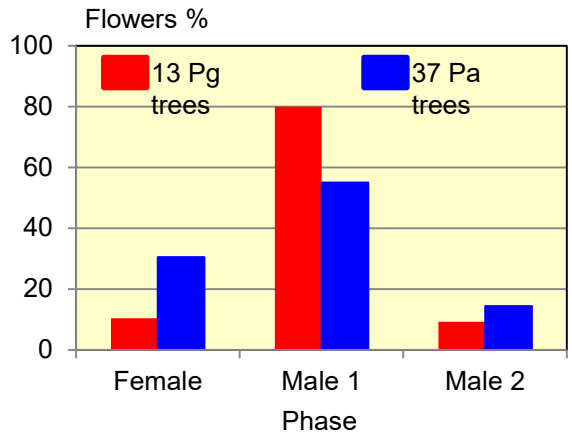


Figure 52. The percentage of female flowers and the percentages of the 2 phases of male flowers in 13 protogynous and 37 protandrous A. pseudoplatanus *trees in a stand close to Leipzig in Germany. The total number of flowers in protogynous trees was around 800 and the corresponding figure for the protandrous trees was around 2,900. The figures were read in Fig. 2 of the paper. Tal 2009.*

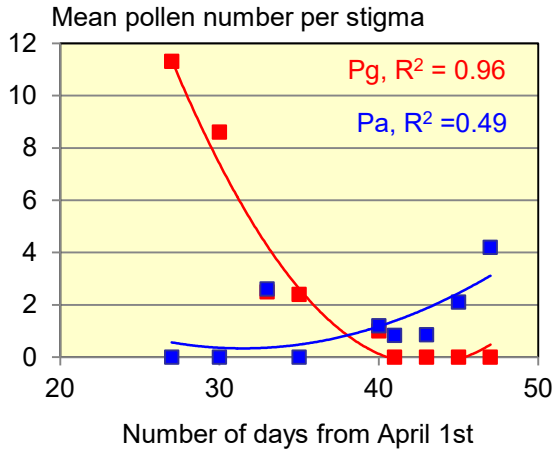


Figure 53. The relationship between date and mean number of germinating pollen per stigma in 7 protogynous (Pg) and 21 protandrous (Pa) A. pseudoplatanus *trees in a stand close to Leipzig, Germany. The figures were derived from Fig. 5 in the paper. Tal 2009.*

pollen grains. If this outlier tree is omitted from the binominal relationship, the R^2 increases to 0.88.

The occurrence of trips per inflorescence declined from the first observations in late April until May 18 (Fig. 54). Trips were brooding in the maple flowers. Larval trips appeared at May 4 and reached a peak on May 10. The relationship between number of adult trips per inflorescence and the number of stigmas with pollen per sampling date was significant. However, the degree of explanation was only 28%. Even so, trips were probably the most important pollen vector. Two other insect species, *Epuraea melanocephala* and *Ceranisus pacuvius*, were found in the inflorescences, but at low frequency.

The number of fruits per tree was much larger in the protandrous than in the protogynous trees (Fig. 55). However, the number of seeds was much larger in the protogynous trees than in the protandrous trees. One explanation for this was the earlier fertilization in the protogynous trees, which gave them a longer period for ripening than the later fertilization in the protandrous trees. The ratio seed/fruit was significantly correlated with the percentage of pollen on stigmas, $R^2 = 0.48$.

It was hypothesized that the morph was geneti-

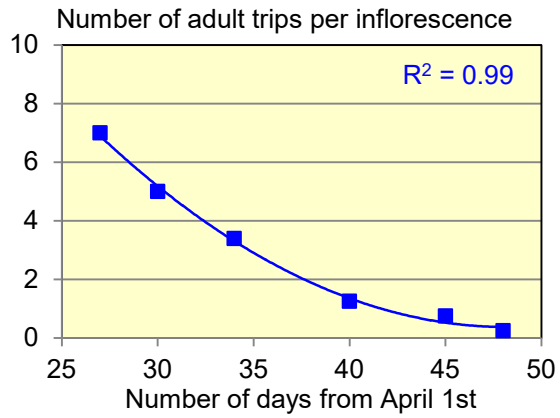


Figure 54. The number of trips per inflorescence in years 2004 and 2005 of protandrous and protogynous A. pseudoplatanus *trees in a stand close to Leipzig. The figures were read from Fig. 6 in the paper. Tal 2009.*

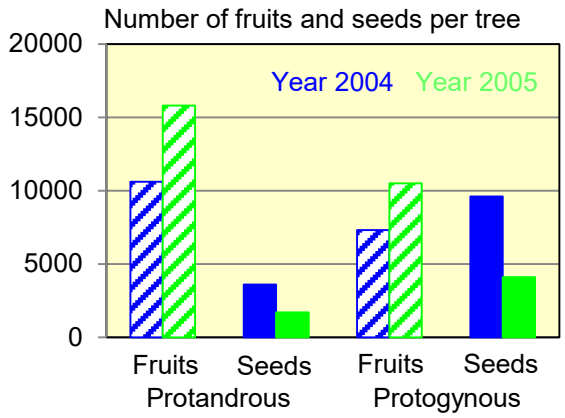


Figure 55. The number of fruits and seeds per tree in years 2004 and 2005 of protandrous and protogynous A. pseudoplatanus *trees in a stand close to Leipzig. Tal 2009.*

cally regulated for the following reasons:

No tree switched morph during the 2-year study

The morphs differed in floral structures

The pollination within gender is more likely in protandrous than in protogynous trees owing to differences in phenology of the 2 morphs, which evolutionarily might lead to a larger ratio than 1.0 for protandrous/protogynous trees.

It was concluded that the present investigation did not allow a final proof of this hypothesis.

Many of the flowering characteristics of *A. pseudoplatanus* are regarded as adaptations to wind pollination. However, they may also be regarded as attractive to feeding and breeding trips and thus improve the fitness of the host tree.

Summary. The male-female-male morph was the dominating morph in a German *A. pseudoplatanus* stand close to Leipzig. The phase 1 percentage of the male flowering was dominating among the 3 phases. Noteworthy was the finding that the percentage of female flowering was larger in the protandrous than in the protogynous trees. The limited impact of male flowering phase 2 was evident. The mean number of germinating pollen grains on the stigmas dominated in the protogynous trees at the early sampling dates and declined sharply at the following sampling dates. There was a less pronounced upward trend in the protandrous trees. Trips were found to be the most important pollinator and their frequency was significantly related to the number of germinated pollen grains on the stigma.

1.3 Species differences

Six polymorphic microsatellite markers were used by Guarino et al. (2008) in their study of genetic diversity in 6 maple species from 5 regions in Campania. The species and number of populations included in this study are listed in Table 3.

The focus of the investigation was on species differences. Table 3 clearly shows that the material is far from balanced, which might influence the outcome of this investigation.

The observed heterozygosity varied in the range 0.30–0.60, while the range for expected heterozygosity was 0.40–0.70 (Fig. 56). For *A .campestre* and *A. monspessulanum* there was a pronounced difference between the 2 types of heterozygosity estimates with much lower observed heterozygosity. This suggests a considerable effect of genetic drift in these 2 species. This interpretation is supported by the high F_{IS} estimate, 0.60 for the 2 *A. monspessulanum* populations. The F_{IS} of *A. campestre* was also positive but rather modest, 0.14. It was stated that *no significant differences in expected heterozygosity were found among the* Acer *species in the five different areas of Campania (data not shown)*. This statement does not hold for the data presented in *Fig. 56*.

The F_{ST} estimates were, with one exception, mostly high and sometimes beyond the limit for F_{ST} (1.00, Fig. 57). This suggests that these estimates harbor large imprecision. This was not discussed. The low F_{ST} for the comparison *A. neapolitanum* and *A. obtusatum* was attributed to a difference between 2 alleles only. Since 19 populations were analyzed in both species this result cannot be attributed to low sample size. Morphologically, it is hard to separate these 2 species. With the exception of the discussed difference, the F_{ST} estimates were high, which suggests that gene flow has not prevented substantial differentiation among the 6 species. It is regrettable that F_{ST}s for differences within species within regions and among regions were not presented. A comparison of such estimates with among-species F_{ST}s would have enabled a deeper understanding of evolution of these maple species.

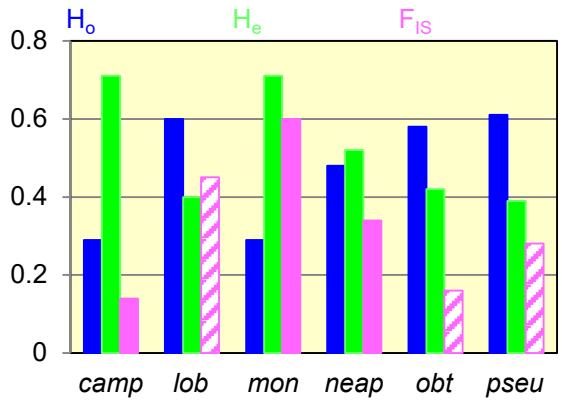


Figure 56. Observed, H_o, (blue) and expected heterozygosites, H_e, (green) as well as inbreeding coefficients, F_{IS}, (lilac) in 6 maple species from 5 regions in Campania, southern Italy. Striped columns refer to negative F_{IS} estimates. Six polymophic microsatellite loci were analyzed. camp = campestre, lob = lobelii, mon = monspessulanum, neap = neapolitanum, obt = obtusatum, pseu = pseudoplatanus. *For number of populations see Table 3. Guarino et al. 2008.*

Summary. Mostly low to moderate observed heterozygosity in the 6 species studied. The expected heterozygosity was much larger than the observed heterozygosity in *A .campestre* and *A. monspessulanum*. Half of the species had negative estimates of the inbreeding coefficient. A large surplus of homozygotes was noted for *A. monspessulanum*. The low F_{ST} for the comparison *A. neapolitanum* and *A. obtusatum* was attributed to a difference between 2 alleles only.

Table 3. The number of regions, populations, and total number of trees investigated in 6 maple species growing in the southern Italian province, Campania. Guarino et al. 2008.

Species	*Number of regions*	*Number of populations*	*Numberof trees*
A. campestre	5	19	533
A. lobelii	1	5	89
A. monspessulanum	1	2	48
A. neapolitanum	4	19	417
A. obtusatum	5	19	513
A. pseudoplatanus	1	4	91

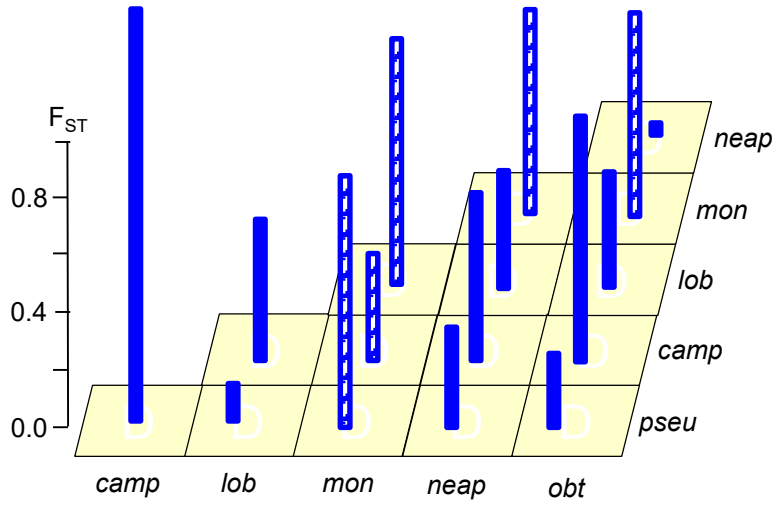


Figure 57. Pairwise F_{ST}s for 6 maple species from Campania in southern Italy analyzed by 6 polymorphic microsatellite markers. camp = campestre, lob = lobelii, mon = monspessulanum, neap = neapolitanum, obt = obtusatum, pseu = pseudoplatanus. A. monspessulanum *was represented by 2 populations only.* Guarino et al. 2008.

Gleiser and Verdú (2005) The authors followed 3 different paths to dioecy from:

heterodichogamous androdioecy
heterodichogamous trioecy
dichogamous subdioecy.

For definitions see Table 4. It was disclosed that dioecy is a derived state, which never had reversed. According to the authors this is in contrast to the situation in other species, in which androdioecy has evolved from dioecy. The authors claimed that dioecy was not evolved as a means of avoidance of inbreeding since dioecy exists in mainly nondioecious *Acer* species. Instead it was suggested that sexual specialization was selected for during the evolution of dioecy in this genus.

Li et al. (2005) used 2 regions, *psbM-trnD* and *nrnD-trnT,* in the chloroplast genome for a phylogenetic study of *Acer* species.

Three methods were used in the phylogenetic analyses:

Neighbor-joining
Maximum parsimony
Maximum likelihood

As regards the European maples the 3 methods gave the same result, i.e. a close relationship between *A. platanoides* and *A. campestre,* which were most separated from *A. pseudoplatanus* while *A. opalus* took an intermediate position.

In total 606 ITS (Internal Transcribed Spacer) clones were used by Grimm et al (2006) for a study of relationships of 81 species and subspecies of *Acer*. The analysis of relationships was carried out with maximum likelihood, split graphs and motif analysis. It is sometimes suspected that ITS grouped analysis does not give

Table 4. The 3 sexual morphs used as starting morph in the analysis of evolution toward dioecy and the definition of these 3 morphs in the paper by Gleiser and Verdú 2005.

Sexual morph	*Definition*
heterodichogamous androdioecy	Males (in low frequency) and bisexual individuals; the bisexuals are heterodichogamous (two dichogamous reciprocal morphs, protandrous and protogynous
heterodichogamous trioecy	Males (in increasing frequencies) and females (in various frequencies), and heterodichogamous bisexuals
Dichogamous subdioecy	Mainly unisexual individuals (males and females), and dichogamous bisexuals in low proportions.

as reliable results as phylogeny within genera. Since the sequences studied largely grouped by species in the accessions analyzed it was interpreted as good reliability of ITS for phylogeny studies. Furthermore, the occurrence of polyploidy in *Acer* did not have any great impact on the ITS analysis. The data obtained agreed fairly well with the morphology classification with its 16 sections of the genus *Acer*.
Split-based networks, ITS motif analysis, and morphology were used by Grimm et al. (2007) to trace the evolutionary history of section *Acer* in the genus *Acer*. The cuticle structure observed by scanning electron microscopy was used as a morphological character. Three major radiations in section *Acer* were identified and 7 subsections were observed. Two species reviewed by us were included in the Grimm et al. paper, *A. opalus* and *A. pseudoplatanus*. Considering all variables analyzed they were distantly related. *A. pseudoplatanus* was the only polyploid species in the *Acer* section.

Renner et al. (2007) studied the phylogeny of 56 *Acer* species and especially the evolution of sexual morphs. The following morphs were included:

Dioecy
Monoecy with dichogamous and duodichogamous flowering
Monoecy with heterodichogamous flowering
Labile sex expression, in which sex is regulated by ambient conditions

In all, 6,600 nucleotides of chloroplast introns, spacers, and a protein-coding gene were used in the analysis of 56 species. They identified 15 transformations, 5 of them concerning a change from monoecy-cum-duodichogamy to dioecy. Transformations from dioecy to other morphs were reported to be rare. Based on the species with labile sexual morph expression it was suggested that ability to change sexual morph might be a heritable strategy.

The internal transcribed spacers ITS1 and ITS2 of the nuclear-encoded 35S rDNA cistron were used by Grimm and Denk (2014) for genotyping of 51 *A. campestre* and 27 trees from other maples to identify species relationships. The *A. campestre* trees were samples from the main distribution area of this species in Europe.
In all, 9 different ITS genotypes were identified. Specific ITSs were found for trees originating from northeastern Turkey and the adjacent region of Armenia and Georgia. The difference in ITS between trees from this region and the trees from the main distribution area in Europe was of a magnitude comparable to species differentiation. Therefore, it was suggested that these trees represent one species, *A. orthocampestre*. However, there was no morphological separation of this species from *A. campestre*.
The probable evolutionary pathways of *A. campestre* from its origin in Southeastern Europe to other areas of Europe were presented.

1.4 Marker development

Konnert et al. (2001) reported on isozyme development and inheritance in *A. pseudoplatanus*. They analyzed 11 enzyme systems with 25 loci, of which 17 could be used for genetic studies.

Pandey et al. (2004) selected 24 simple and noninterrupted sequences for microsatellite development in *A, pseudoplatanus*. Eight primer pairs had reproducible, easily scorable bands. These microsatellites were used for an analysis of 96 trees growing close to Göttingen, Germany. The number of alleles per locus varied between 1 and 4 in this tetraploid tree. A cross-species amplification with 21 other *Acer* species showed that these loci could be used in various population genetics studies.

Segarra-Moragues et al. (2008) isolated and characterized 8 microsatellites in *A. opalus*. In all, 184 clones were isolated, 89% of which contained microsatellite sequences. Primers were designed for 27 clones, of which 10 primer-pairs produced clear amplicons. However, 2 of them produced complex banding patterns and were excluded. The remaining 8 microsatellites were tested in 142 trees with respect to Hardy-Weinberg equilibrium and linkage equilibrium between pairs of loci. Two loci were found to be

linked. The range of alleles in the loci was 5–18. The heterozygosity mean value was estimated at 0.64.

The microsatellites were tested in 8 other maple species. Two loci were amplified in all 8 species tested. The strongest agreement was noted for the closely related *A. monspessulanum*.

2. Genetic conservation and breeding

Nagy and Ducci (2004) presented the suggestions for genetic conservation of *A. campestre* in the series of technical guidelines for genetic conservation of forest trees published by EUFORGEN. The objective of the EUFORGEN network is to identify minimum genetic conservation requirements in the long term in Europe, in order to reduce the overall conservation cost and to improve the quality of standards in each country. It was stated that this species is not endangered and that few genetic studies had been carried out at the time of this publication. It was suggested that gene conservation should be carried out according to the multiple population breeding system (MPBS) suggested by Namkoong (1984) and further outlined by Eriksson et al. (1993). The 30 in situ subpopulations (called core populations in this paper) should cover the current distribution area of this species and encompass marginal populations. If possible joint conservation with other deciduous trees should take place. *Ex situ* collections with material containing special features might complement the *in situ* subpopulations.

The objective of the genetic conservation of *A. pseudoplatanus* is the same as for *A. campestre* (Rusanen and Myking 2003). It was stated that there are no threats to this species. As in other species marginal populations might experience a risk. In agreement with the suggestions for *A. campestre* a low-intensity in situ conservation was recommended. A minimum of 20 subpopulations covering the existing distribution area of this should be included in the MPBS conservation method. Each subpopulation should have 50 flowering and seed-producing trees. It was pointed out that marginal areas should be included in the conservation efforts. If possible a joint conservation with other deciduous trees could be carried whenever possible. Supplemental ex situ conservation was also an option to consider especially if seeds for reforestation were an additional objective for conservation. A broad genetic variability should be aimed at in each subpopulation. Finally it was stated that secondary breeding activities for timber improvement are also conceivable.

A breeding program for *A. pseudoplatanus* was initiated in Germany (Jánosi et al. 2017) to mitigate the negative effects of global warming. This species' limited demand for specific soil conditions is an advantage in the efforts to mitigate effects of global warming. Three elevational zones were identified, < 200 masl, 200–500 masl, and 500–800 masl. For each zone, phenotypic selection of around 300 plus trees was aimed at. The selection of the plus trees was based on superior quality, growth, and vitality. In total, 896 plus trees were selected mainly in approved seed tree stands. Additional plus trees were selected in seed orchards, clone archives and progeny trials. Twigs were collected for grafting of 750 of the 900 plus trees, which was accomplished in 2016. In all, 12,460 grafts were obtained in 2016. They were planted in seed orchards and clone archives. In the future, these clones will be evaluated in progeny trials.

3. Discussion and Conclusions

We have classified the reports found in our search for recent genetic studies on 4 European maple species (Fig. 58). The largest number of studies concerned population diversity as revealed by markers. The ultimate objective was to get information for sampling of populations for genetic conservation. A similar objective could apply to studies on metric traits including the possibilities of populations to mitigate the effects of climatic change (e.g. Vitasse et al. 2009a and b). Four papers treated evolutionary aspects of sexual morphs in *A. opalus and A. pseudoplatanus* (Gleiser et al. (2008a, 2008b, and 2018, Tal 2009). Two popular science papers on genetic conservation (Rusanen and Myking 2003, Nagy and Ducci 2004) and an outline of breeding efforts for *A. pseudoplatanus* in Germany (Jánosi et al. 2017) have been published. Several studies included populations from widely varying latitudes or altitudes.

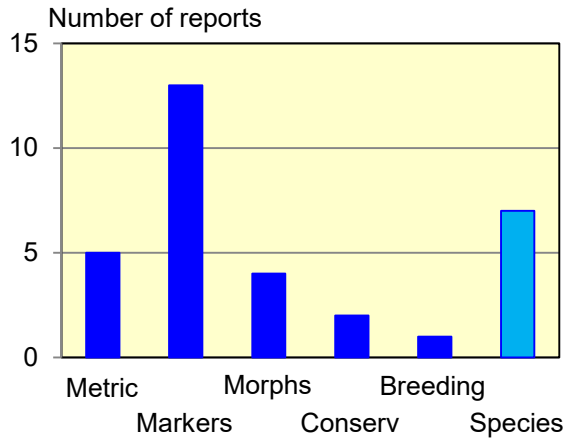


Figure 58. Number of publications treating different topics in our review of recent genetic research in 4 European maple species. Differences among species are only briefly treated.

Scattered distribution, low number of trees per population, and insect pollination of maples are expected to result in some inbreeding and large among-population differentiation owing to genetic drift and local adaptation (cf Eriksson et al. 2014). Significant variation among populations was revealed in most studies. However, their differentiation estimated as F_{ST} or G_{ST} was in many cases surprisingly low for such wide geographic distances (e.g. Ducci et al. 2009) and large ranges of elevation (e.g. Kvesic et al. 2020). Generally the within-population diversity was large (e.g. Lazic et al. 2022). The human impact on *A. campestre* in Italy might be one explanation for the limited population differentiation between geographically isolated *A. campestre* populations (Ducci et al. 2009). Another reason might be that differentiation estimated by markers is less than differentiation in quantitative characters (cf. Lewontin 1983). The large variation among marginal *A. platanoides* populations in Finland was one exception to the limited among-population differentiation found in other studies (Rusanen et al. 2000). The hypothesis that marginal populations are less diverse than central populations was tested in one case, but had to be rejected (Rusanen et al. 2003). In an investigation of NW Italian *A. pseudoplatanus* populations, the heterozygosity increased with age while the inbreeding coefficient decreased with age (Beletti et al.2007). These findings were attributed to selection against homozygotes. Genetic and geographic relationships were found in some cases but the relationships explained a minor part of the variation (e.g. Lazic et al. 2022, 6%, Wahlsten et al. 2023, 4%).

A large impact on the mating pattern in populations with contrasting number of trees per hectare was observed (Pandey et al. 2012). Usually, the distance between mates was limited (e.g. 40 m, Bendixen 2001). Wind pollination was tested following isolation with insect screens and was found to be of limited importance (Bendixen 2001, <3%).

Two of the ´metric´ studies concerned the effect of climatic or nutrient conditions on juvenile plant growth (Black-Samuelsson and Eriksson 2000, Eriksson et al. 2003). These 2 papers were the only ones reporting both among- and within-population diversity. The family variance components were stronger than the family x treatment interaction variance. The large family variance components suggest that there are good prospects for mitigation of effects of global change. Two metric *in situ* studies of phenology variation of *A. pseudoplatanus* populations along mountain slopes revealed clinal variation (Vitasse et al. 2009a and b). Different effects on shoot growth and photosynthesis following *Aceria macrorhynchus* feeding on 3 morphs of *A. opalus* were observed.

As expected, owing to the limited economic importance of *Acer* species, the papers we review are little concerned with genetic improvement by breeding. A multiple population breeding system, as conceived by Namkoong (1984) has been suggested for the genetic conservation of both *A. campestre* (Nagy and Ducci 2004) and *A. pseudoplatanus* (Rusanen and Myking 2003). In addition, a German breeding program is under way for *A. pseudoplatanus* to counteract the effects of global warming (Janosi et al. 2017). Neophytou et al. (2019) reported low variation among 6 regional groups of the 1,100 selected plus trees in Germany. The limited variation was attributed to the same selection factors being applied independently of the geographic origin of the plus trees.

Of considerable general interest are the sexual morphs of *Acer* species: how and why did they evolve, and why are they maintained? Does the occurrence of morphs reflect pathways to dioecy (see Gleiser and Verdú 2005)? Currently there are no clear answers to these questions. Gleiser et al. (2008a) found for a population of *A. opalus* in southern Spain that over a six-year period, the male and protogynous morphs were most stable, while protandrous and non-flowering morphs were much less stable. Femaleness was highest in protogynous trees and very low in protandrous trees. Gleiser et al. (2008b) studied male fitness in the same population. They found that overlapping of receptivity and pollen dispersal, fecundity, and distance between mates had the greatest impact om male success. Tal (2009) studied flowering in 74 *A. pseudoplatanus* trees near Leipzig, Germany. He recognized 5 sexual morphs, each with 1, 2 or 3 phases: female-male, female-male-male, male-female, male-female-male, and male. In the morphs with 3 phases, a pause occurred between phase 2 and 3. Surprisingly, the percentage of female flowering was higher in the protandrous than the protogynous trees. Further research on these issues using molecular markers is presented in the sections Species differences and Marker development. It is hoped that these studies will be followed up, leading to a clearer picture of the evolutionary events.

To get satisfactory guidance for genetic conservation there is a great need for further studies on adaptive traits to confirm or reject the information on population differentiation based on markers.

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A tree avenue of *Acer platanoides* at Ultuna, Uppsala. Photograph Gösta Eriksson

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