

MATING SYSTEM IN ISOLATED STANDS OF EUROPEAN BEECH (*FAGUS SYLVATICA* L.)

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ABSTRACT

Three relatively isolated stands and 9 allozyme loci (*Got-B*, *Idh-A*, *Lap-A*, *Mdh-B*, *Mdh-C*, *Mnr-A*, *6-Pgdh-A*, *Pgi-B* and *Pgm-A*) were used to study the mating system in European beech (*Fagus sylvatica* L.). Multilocus outcrossing rates for the three stands were high ($t_m = 1.015-1.025$), but did not differ significantly from 1. According to paternity analysis, the maximum selfing rates ranged from 5.6 % to 12.9 % while the most likely selfing rate ranged from 1.2 % to 3.7 %. No evidence of biparental inbreeding was found. Mating system parameters in two different years showed little difference. These results indicate that European beech within the isolated stands is predominantly outcrossed but shows part of self-fertilization. The proportion of self-fertilization should be considered for natural regeneration and for effective and representative seed collections.

Key words: allozyme, mating system, outcrossing rate, selfing, *Fagus sylvatica* L.

INTRODUCTION

The mating system of a species is an important determinant of its genetic structure and evolution (ALLARD 1975; BROWN 1979; CLEGG 1980; HAMRICK 1989; MERZEAU *et al.* 1994). Detailed knowledge of the mating system is necessary to understand the distribution of genetic variation within and among individuals, gene flow within and between populations, and the resultant substructuring of populations (BOSHIER *et al.* 1995). Information on mating system is also of practical importance to the success of breeding programs in forestry. Knowledge of mating system could be used to estimate the minimum population sizes for conservation areas as well as minimum population densities in natural and managed forests (STACY *et al.* 1996).

Estimation of mating systems in conifer have often been reported (E.g., EL-KASSABY & RITLAND 1986; MORGANTE *et al.* 1991; XIE *et al.* 1991; EL-KASSABY & RITLAND 1998). However, temperate angiosperm trees have only poorly represented in the plant mating system literature (BACILIERI *et al.* 1996; MÜLLER-STARCK 1996; ROSSI *et al.* 1996; GODT & HAMRICK 1997; GEHLE 1999).

European beech (*Fagus sylvatica* L.) is a monoecious and wind-pollinated species, characterized by the possibility of self-fertilization but generally showing high outcrossing rates (MERZEAU *et al.* 1994; MÜLLER-STARCK 1996; ROSSI *et al.* 1996). But till now, little is known about the temporal variation of mating system.

In addition, more evidence is required to explore the level of inbreeding in European beech.

In this study, three isolated stands and seed samples of two years were used to characterize the mating system. The objectives of this study are to characterize (1) the outcrossing rate based on a mixed-mating model; (2) the selfing rate using paternity analysis and (3) the temporal variation of mating system parameters.

MATERIALS AND METHODS

Seed materials and stands information

Three relatively isolated stands were used in this study (Table 1). Stand 34B₁ and 10A₂₁ are located in the forest district of Escherode. Another stand 100C is located in the Solling, which is in the area of a research project of the Forest Ecology Center (University of Göttingen). Stand 34B₁ is mixed with spruce, other two stands are pure beech stands. Seeds in two different years (1994 and 1998) were collected for stand 10A₂₁ (the seeds of stand 34B₁ and 100C were collected in 1998). Seeds were sampled on the ground around each adult tree at a radius of 3 m within three circles, which were 40 cm in diameter and located north, southwest and southeast of the stem at angles of 120°. All of the seeds encountered in each circle were sampled. All of the trees within the stands were tagged, and the location of each tree was mapped.

Table 1. Description of the beech stands in the forest district of Escherode and Solling, Northern Germany.

Stand	34B ₁	10A ₂₁	100C
Age	150	180	190
Area	50 m × 70 m	60 m × 130 m	120 m × 160 m
Altitude	530	500	370
Distance to nearest beech stand (m)	300	140	500
No of adult trees	24	70	99
No of seeds	-	1699	-
No of seeds	511	844	1954

Table 2. Enzyme systems and enzyme coding gene loci.

Enzyme systems	E.C.No	Gene loci	Buffer system
Glutamate oxaloacetate transaminase	2.6.1.1	<i>Got-B</i>	Ashton
Isocitrate dehydrogenase	1.1.1.42	<i>Idh-A</i>	TC
Leucine aminopeptidase	3.4.11.1	<i>Lap-A</i>	TC
Malate dehydrogenase	1.1.1.37	<i>Mdh-B, Mdh-C</i>	TC
Menadion-Reduktase	1.6.99.2	<i>Mnr-A</i>	Ashton
6-Phosphogluconate dehydrogenase	1.1.1.44	<i>6-Pgdh-A</i>	TC
Phosphoglucose isomerase	5.3.1.9	<i>Pgi-B</i>	Ashton
Phosphoglucomutase	2.7.5.1	<i>Pgm-A</i>	Ashton

TC-buffer: Tris citric acid buffer pH 7.8; Ashton-buffer: pH 8.6.

Electrophoresis

Nine enzyme-coding gene loci were utilized for multilocus genotyping (*Got-B*, *Idh-A*, *Lap-A*, *Mdh-B*, *Mdh-C*, *Mnr-A*, *6-Pgdh-A*, *Pgi-B* and *Pgm-A*). Genetic control and mode of inheritance of the respective enzyme systems were verified previously (MÜLLER-STARCK & STARKE 1993). Enzymes were separated by standard horizontal starch gel electrophoresis. For survey of enzyme systems and gene loci see Table 2.

Data analysis

The fixation index for a single locus is estimated according to the following equation.

$$F = 1 - \frac{\sum_{i < j} p_{ij}}{1 - \sum_i p_i^2}$$

where F is the fixation index for single locus. p_{ij} and p_i are genotype frequency and gene frequency of adult stand or seed generation (HATTEMER *et al.* 1993).

Within stand, multilocus genotype exclusion method was used to identify seeds, which carry at least one of

two alleles at any locus also carried by the adult tree. The adult tree under which the seed was sampled was regarded as seed tree. Then the seeds of the seed tree were assumed to be either the result of selfing (s) or random outcrossing (t), according to the mixed-mating model of BROWN and ALLARD (1970). Population multilocus outcrossing rate (t_m) was estimated using the multilocus procedure of RITLAND and JAIN (1981). The MLTR program of RITLAND (1996 version 1.1) was used for the computation of single locus (t_s) and multilocus outcrossing rates (t_m). All variances were estimated using 100 bootstraps.

One seed was considered to originate from self-fertilization if none of all alleles in multilocus genotype was different from the seed tree. This leads to the maximum selfing rate (s_{max}) or potential selfing rate based on the simple paternity exclusion method (ELLSTRAND 1984; HAMRICK & SCHNABEL 1985). According to the most-likely method, the seed was regarded as self-fertilization (s_{ml}) if the seed tree is the first most likely pollen donor (MEAGHER 1986; MEAGHER & THOMPSON 1987; DEVLIN *et al.* 1988; ROEDER *et al.* 1989). s_{max} and s_{ml} were estimated with help of CERVUS program of MARSHALL *et al.* (1998 version 1.0).

Table 3. Observed fixation index (F) and the results of X^2 -tests.

Stand	Stand 34B ₁		Stand 10A ₂₁			Stand 100C	
	Adult	S98	Adult	S94	S98	Adult	S98
N ⁺	24	511	70	1699	844	99	1954
<i>Gor-B</i>	0.26	0.01	0.16	0.08***	0.08*	-0.08	0.07***
<i>Idh-A</i>	-0.13	-0.09*	0.19	-0.03	-0.03	0.01	-0.02
<i>Lap-A</i>	0.10	0.03	0.02	0.03*	0.06**	0.20**	0.03*
<i>Mdh-B</i>	0.02	0.04	0.18*	0.30***	0.21***	0.07	0.12***
<i>Mdh-C</i>	-0.13	0.09*	0.22	0.02	0.04	0.14	-0.03
<i>Mnr-A</i>	-0.09	-0.11*	-0.03	-0.04	-0.02	-0.05	-0.03
<i>6-Pgdh-A</i>	-0.07	-0.04	0.17	0.01	-0.05	0.10	0.02
<i>Pgi-B</i>	0.00	0.00	0.00	0.00	-0.01	-0.03	-0.01
<i>Pgm-A</i>	0.11	0.16***	0.17	-0.01	0.02	0.09	0.04*
Mean	0.01	0.01	0.12	0.04	0.03	0.05	0.02

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. N refers the no. of the trees or seeds.

RESULTS

Fixation index

The observed fixation indices for three stands (adult trees and seeds from two years) were shown in Table 3. Parts of these values were significant indicating a deviation from random mating. Two loci (*6-Pgdh-A* and *Pgi-B*) showed no difference from Hardy-Weinberg structure in all of the samples. The mean single-locus F -values indicated a weak overall excess of homozygotes. Most estimates of F calculated from adult trees were not significantly different from zero in all stands.

Outcrossing rate

Multilocus and mean single-locus estimates of outcrossing rates based on MLTR program were presented in Table 4 along with standard errors for each based on 100 bootstraps. The adults for which more than 12 seeds were analyzed were used to estimate the multilocus and mean single-locus outcrossing rates. The outcrossing rates were all larger than 1. However, the multilocus outcrossing rate (t_m) was not significantly different from unity.

Maximum selfing rate and most likely selfing rate

The maximum and the most likely selfing rates as well as the average percentage of empty seeds (Pes) for

three stands (only seed samples in 1998) were presented in Table 5. The maximum selfing rates ranged from 5.6 % to 12.9 %, whereas the most likely selfing rate ranged from 1.2 % to 3.7 %. The results based on the seeds produced in two years in stands 10A₂₁ showed only slight differences.

DISCUSSION

Fixation index

Inbreeding is the likely cause of positive F -values only if similar positive values are observed at most loci. The heterogeneity of fixation indices implied no evidence for a strong influence of inbreeding on the genotypic structures of these isolated beech stands. Moreover, significant negative F -values at *Idh-A* and *Mnr-A* were found in this study. These results are consistent with the reports that no evidence for an inbreeding structure was revealed by the F -values in European beech (MERZEAU *et al.* 1994; MÜLLER-STARCK 1996; ZIEHE *et al.* 1998). The significantly positive F -values at several loci and average positive fixation indices of single loci implied presence of selfing, assortative mating and/or selection. There are exceptionally large F -values at some gene loci such as *Lap-A* but these are more probably due to early viability selection (TUROK & HATTEMER 1995; MÜLLER-STARCK 1996; ZIEHE *et al.* 1998; WANG 2001). Another reason of variation in the fixation indices in different life-cycle phases was observed, indicating possible presence of selective processes between seed set and sexual maturity (ROSSI *et al.*

Table 4. Single-locus (t_s) and multi-locus (t_m) estimates of outcrossing rate.

Stand	Stand 34B ₁	Stand 10A ₂₁	Stand 100C
Year	98	94	98
No of trees	17	14	16
No. of seeds	270	364	220
t_m (SE)	1.015 (0.026)	1.025 (0.032)	1.018 (0.028)
t_s (SE)	1.104 (0.033)	1.082 (0.044)	1.061 (0.036)

t_m is the multilocus outcrossing rate, t_s is the mean single locus outcrossing rate and SE is the standard error.

Table 5. Maximum selfing rate and most likely selfing rate.

Stand	Year	No. of seeds	Number of seeds possibly selfing	s_{max} (%)	No. of seeds most likely selfing	s_{ml} (%)	Pes (%)
Stand 34 B ₁	1998	289	17	5.9	5	1.7	23.6
Stand 10 A ₂₁	1994	680	38	5.6	8	1.2	
	1998	366	24	6.6	9	2.5	30.6
Stand 100 C	1998	1,383	179	12.9	51	3.7	21.4

1996). The exceptionally large values of F in *Lap-A* may also be due to the presence of a null allele, however, such situation is not confirmed in several studies of European beech (TUROK & HATTEMER 1995; MÜLLER-STARCK 1996; WANG 2001). In addition, assortative mating was found at gene loci *Lap-A* and *Mdh-B* within stand 10A₂₁ and 100C (WANG 2001).

Outcrossing rate and selfing rate

All of the multilocus estimates of outcrossing rates for the three stands based on MLTR program were larger than 1 but did not differ significantly from 1. Those high outcrossing rates in more or less isolated stands of European beech suggested wide dispersal of pollen. MERZEAU *et al.* (1994), in natural populations of beech, estimated very high values of outcrossing rates, ranging from 0.94 to 1. ROSSI *et al.* (1996) reported high values of outcrossing rates ranging from 0.94 to 0.98 in two Italian beech populations. In present study, the result $t_m < t_s$ could not be interpreted by inbreeding. When there is inbreeding in addition to selfing, the multilocus estimates of t_m are expected to be higher than the mean of the single-locus estimates t_s (SHAW *et al.* 1981).

It was observed that the maximum selfing rate (s_{max}) as inferred from paternity analysis ranged from 5.6 %

to 12.9 % for the three stands. MÜLLER-STARCK (1996) found maximum selfing rates of 2.2 %, 5.6 % and 6.6 %, respectively, for three seed trees and suggested that selfing may be explained as one of the important causes of empty seeds in beech. In the present study the percentage of empty seeds ranged from 21.4 % to 30.6 % among the three stands. WERDER (2000) reported a maximum selfing rate of 13 % in European beech. In the present study, the most likely selfing rate (s_{ml}) on the basis of most likely paternity analysis ranged from 1.2 % to 3.7 % which indicated that 1.2 % to 3.7 % of pollen possessed highest probability of fertilizing on ovum of the same individual.

The estimates of outcrossing rate and selfing rate indicate that European beech within isolated stands is predominantly outcrossed but shows part of self-fertilization. This is consistent with other studies in European beech and several other temperate angiosperm tree species (MERZEAU *et al.* 1994; BACILIERI *et al.* 1996; MÜLLER-STARCK 1996; ROSSI *et al.* 1996; GODT & HAMRICK 1997).

Generally, all of the three parameters (t_m , s_{max} and s_{ml}) show the similar result that European beech is predominantly outcrossed. However, s_{max} indicates the potential value of self-pollination and it is calculated directly from the number of possible self-fertilized seeds while s_{ml} reflects the proportion of seeds when the

seed tree is the first most likely pollen donor. t_m is estimated based on maximum likelihood method and should be closer to the most likely selfing rate (s_{ml}) according to this point.

Temporal variation of mating system parameters

For stand 10A₂₁, seeds were sampled in two years of abundant flowering. According to *t*-test, the difference between the single loci fixation indices of two years was not significant. Furthermore, multilocus outcrossing rates (t_m) in stand 10A₂₁ showed no difference between two years. In addition, the maximum selfing rate (s_{max}) and the most likely selfing rate (s_{ml}) indicated little difference between two years. Few studies were done to compare the mating system realized in different years. MORAN and BROWN (1980) found that outcrossing estimates were highest in the oldest of three seed crops in *Eucalyptus delegatensis*. BROWN *et al.* (1985) reported temporal variation in outcrossing rate in one population of *Eucalyptus stellulata* and showed that the outcrossing rate in one of four years was above the average of four years. CHELIAK *et al.* (1985) found that there was an approximately linear increase in the apparent selfing rate from the oldest (1975) to the newest (1978) crop in the cones of a natural population of jack pine and explained these changes by selection against selfed zygotes. PERRY and DANCİK (1986) did not find significant temporal variation in lodgepole pine. BACILIERI *et al.* (1996) reported multilocus outcrossing rate (t_m) of two years in sessile oak, which were 0.995 and 1.009, respectively. SPROULE and DANCİK (1996) showed that there were no significant differences in outcrossing estimates among populations or between years in black spruce. BURCZYK (1998) studied the mating system variation in a scots pine clonal seed orchard and found that population multilocus estimates of three years exhibited a decreasing trend (0.976, 0.966 and 0.962, respectively), but the variation was not significant. It was reported that temporal variation of outcrossing rate might result either from different pollination patterns or from the time elapsed since fertilization, if seed crops of different age were analyzed at one and the same time (MITTON 1992).

Concluding remarks

In summary, the results indicate that European beech within the isolated stands is predominantly outcrossed, but shows part of self-fertilization. No evidence of inbreeding was found within the three stands. Mating system parameters in two different years showed little

difference. Selfing may be one of the important factors, which cause empty seed. The proportion of self-fertilization should be considered for decisions on where and when to harvest seed and in the establishment of seed production stands. Effective and representative seed collections for ex situ conservation or for reafforestation and breeding demand knowledge of genetic base being sampled.

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REFERENCES

- ALLARD, R.W. 1975: The mating system and microevolution. *Genetics* **79**: 115–126.
- BACILIERI, R., DUCOUSSO, A., PETIT, R. J. & KREMER, A. 1996: Mating system and asymmetry hybridization in a mixed stand of European oaks. *Evolution* **50**: 900–908.
- BOSHIER, D.H., CHASE, M.C. & BAWA, K.S. 1995: Population genetics of *Cordia allodora* (Boraginaceae), a neotropical tree. 2. Mating system. *Am. J. Bot.* **82**: 476–483.
- BROWN, A.H.D. 1979: Enzyme polymorphism in plant populations. *Theor. Popul. Biol.* **15**: 1–42.
- BROWN, A.H.D. & ALLARD, R.W. 1970: Estimation of the mating systems in open-pollinated maize populations using isoenzyme polymorphisms. *Genetics* **66**: 133–145.
- BROWN, A.H.D., BARRETT, S.C.H. & MORAN, G.F. 1985: Mating system estimation in forest trees: models, methods and meanings. *In*: Population Genetics in Forestry. (ed. H.-R. Gregorius). Lecture Notes in Biomathematics, Vol. 60. pp.32–49. Springer-Verlag Berlin, Heidelberg, New York, Tokyo.
- BURCZYK, J. 1998: Mating system variation in a Scots pine clonal seed orchard. *Silvae Genet.* **47**: 155–158.
- CHELIAK, W.M., DANCİK, B.P., MORGAN, K., YEH, F.C.H. & STROBECK, C. 1985: Temporal variation of the mating system in a natural population of jack pine. *Genetics* **109**: 569–584.
- CLEGG, M. T. 1980: Measuring plant mating systems. *Bioscience* **30**: 814–818.
- DEVLIN, B., ROEDER, K. & ELLSTRAND, N.C. 1988: Fractional paternity assignment: theoretical development and comparison to other methods. *Theor. Appl. Genet.* **76**: 369–380.
- EL-KASSABY, Y.A. & RITLAND, K. 1986: The relation of

- outcrossing and contamination to reproductive phenology and supplemental mass pollination in a Douglas-fir seed orchard. *Silvae Genet.* **35**: 240–244.
- EL-KASSABY, Y.A. & RITLAND, K. 1998: Isozymes: Techniques, interpretation and application to forest genetics. *In: Forest Genetics and Tree Breeding*. (eds. A.K. Manda & G.L. Gibson). Pp 227–238. New Delhi: CBS Publishers & Distributors.
- ELLSTRAND, N.C. 1984: Multiple paternity within fruits of the wild radish, *Raphanus sativus*. *Am. Nat.* **123**: 819–828.
- GEHLE, T. 1999: Reproduktionssystem und genetische Differenzierung von Stieleichenpopulationen (*Quercus robur* L.) in Nordrhein-Westpfalen. Göttingen Research Notes in Forest Genetics 24, pp.144.
- GODT, M.J.W. & HAMRICK, J.L. 1997: Estimation of mating system parameters of *Albizia julibrissin* (Fabaceae). *For. Genet.* **4**(4): 217–221.
- HAMRICK, J.L. 1989: Isoenzymes and the analysis of genetic structure in plant populations. Pp 87–105. *In: Isoenzymes in Plant Biology*. (eds. D.E. Soltis and P.S. Soltis). Dioscorides Press. Oregon, USA.
- HAMRICK, J.L. & SCHNABEL, A. 1985: Understanding the genetic structure of plant populations. Some old problems and a new approach. *In: Population Genetics in Forestry*. (ed. H.-R. Gregorius). Lecture Notes in Biomathematics, Vol. 60. pp.50–70. Springer-Verlag Berlin, Heidelberg, New York, Tokyo.
- HATTEMER, H.H., BERGMANN F. & ZIEHE, M. 1993: Einführung in die Genetik für Studierende der Forstwissenschaft. J.D. Sauerländer's Verlag, Frankfurt am Main. Zweite, neubearb. und erw. Auflage, pp.492.
- MARSHALL, T.C., SLATE, J., KRUIK, L.E.B. & PEMBERTON, J.M. 1998: Statistical confidence for likelihood-based paternity inference in natural populations. *Mol. Ecol.* **7**: 639–655.
- Meagher, T.R. 1986: Analysis of paternity within a natural population of *Chamaelirium luteum*. 1. Identification of most-likely male parents. *Am. Nat.* **128**: 199–215.
- MEAGHER, T.R. & THOMPSON, E. A. 1987: Analysis of parentage for naturally established seedlings of *Chamaelirium luteum* (Liliaceae). *Ecology* **68**: 803–812.
- MERZEAU, D., COMPS, B., THIEBAUT, B. & LETOUZEY, J. 1994: Estimation of *Fagus sylvatica* L mating system parameters in natural populations. *Ann. Sci. For.* **51**: 163–173.
- MITTON, J.B. 1992: The dynamic mating systems of conifers. *New Forests* **6**: 197–216.
- MITTON, J.B. 1998: Allozymes in tree breeding research. *In: Forest Genetics and Tree Breeding*. (eds. A.K. Mandal & G.L. Gibson), pp. 239–249. New Delhi: CBS Publishers & Distributors.
- MORAN, G.F. & BROWN, A.H.D. 1980: Temporal heterogeneity of outcrossing rates in alpine ash (*Eucalyptus delegatensis* R.T. Bak.). *Theor. Appl. Genet.* **57**: 101–105.
- MORGANTE, M., VENDRAMIN, G.G. & ROSSI, P. 1991: Effects of stand density on outcrossing rate in two Norway spruce (*Picea abies*) populations. *Can. J. Bot.* **69**: 2704–2708.
- MÜLLER-STARCK, G. & STARKE, R. 1993: Inheritance of isoenzymes in European beech (*Fagus sylvatica* L.). *J. Heredity* **84**: 291–296.
- MÜLLER-STARCK, R. 1996: Genetische Aspekte der Reproduktion der Buche (*Fagus sylvatica* L.) unter Berücksichtigung waldbaulicher Gegebenheiten. Ber. Forschungszentrum Waldökosysteme, Reihe A, Bd. 135. Göttingen, Germany, pp.150.
- PERRY, D.J. & DANCİK, B.P. 1986: Mating system dynamics of lodgepole pine in Alberta, Canada. *Silvae Genet.* **35**: 190–195.
- RITLAND, K. 1996: Multilocus mating system program (MLTR version 1.1). Department of Botany, University of Toronto, Canada.
- RITLAND, K. & JAIN, S.K. 1981: A model for the estimation of outcrossing rate and gene frequencies using n independent loci. *Heredity* **47**: 35–52.
- ROEDER, K.M., DEVLIN, B. & LINDSAY, B.G. 1989: Application of maximum likelihood methods to population genetic data for the estimation of individual fertilities. *Biometrics* **45**: 363–379.
- ROSSI, P., VENDRAMIN, G.G. & GIANNINI, R. 1996: Estimation of mating system parameters in two Italian natural populations of *Fagus sylvatica*. *Can. J. For. Res.* **26**: 1187–1192.
- SHAW, D.V., KAHLER, A.L. & ALLARD, R.W. 1981: A multilocus estimator of mating system parameters in plant populations. *Proc. Nat. Acad. Sci. (USA)* **78**: 1298–1302.
- SPOURLE, A.T. & DANCİK, B. P. 1996: The mating system of black spruce in north-Central Alberta, Canada. *Silvae Genet.* **45**: 159–164.
- STACY, E.A., HAMRICK, J.L., NASON, J.D., HUBBELL, S.P., FORSTER, R.B. & CONDIT, R. 1996: Pollen dispersal in low-density populations of three neotropical tree species. *Am. Nat.* **148**(2): 275–298.
- TUROK, J. & HATTEMER, H.H. 1995: Gene resources in beech: which populations should be chosen? *In: Genetics and Silviculture of Beech* (ed. Madsen, S.F.) Proceedings from the 5th Beech Symposium of the IUFRO Project Group P1.10–00, 19–24 Sept. 1994, Møgenstrup, Denmark. Forskningsserien 11, Forskningscentret for Skov & Landskab, Hørsholm, pp. 210–225.
- WANG, K.S. 2001: Gene flow and mating system in European beech (*Fagus sylvatica* L.). Forstwiss. Dissertation, Universität Göttingen. Cuvillier Verlag, Göttingen, Germany, pp. 160.
- WERDER, H.V. 2000: Zertifizierung genetischer Eigenschaften forstlichen Saat- und Pflanzgutes auf der Basis etablierter Methoden der Populationsgenetik. Dissertation, Universität Göttingen, Germany. <http://webdoc.sub.gwdg.de/diss/2000/vwerder>.
- XIE, C., DANCİK, B.P. & YEH, F.C. 1991: The mating system in natural populations of *Thuja orientalis* Linn. *Can. J. For. Res.* **21**: 333–339.
- ZIEHE, M., STARKE, R., HATTEMER, H.H. & TUROK, J. 1998: Genotypische Strukturen in Buchen-Altbeständen und ihren Samen. *Allg. Forst- u. Jagdztg.* **169**: 91–99.