

## Inferences on the Reproductive System of *Cunninghamia lanceolata*

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### ABSTRACT

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Ten-locus genotypes of endosperm and corresponding embryo of two provenance seed samples of *Cunninghamia lanceolata* were studied in an attempt to describe predominant characteristics of the reproductive system as realized in the respective populations. The empirical genotypic structures were compared with three types of reference structures: Hardy-Weinberg; multiplicative; and inbreeding. Strong deviations from the hypothesis of random fusion of gametes are obtained. This phenomenon cannot be explained by assuming sexually asymmetrical fertility selection. Results clearly indicate that inbreeding is the most prominent component of the underlying reproductive conditions in both seed samples. Of the additional phenomena involved, the most probable is viability selection. Some general consequences of these results are discussed.

### INTRODUCTION

In various tree species, deviations from random mating of genotypes or from random fusion of gametes were proven to occur in natural populations as well as in certain breeding populations such as seed orchards. In many cases, this phenomenon was verified by means of a comparison between the genetic structures of parental and offspring populations (e.g. Shen et al., 1981; Yeh et al., 1983; Müller-Starck et al., 1983; King et al., 1984; Cheliak, 1985; Yazdani et al., 1985). Most of the studies revealed such non-randomness by estimating particular components of the mating system, such as the probabilities of self- or cross-fertilization (for references see, e.g., El-Kassaby and White, 1985; Rudin, 1986). Consequently, it can be expected that deviations from random processes in reproduction are the rule rather than the exception in forest tree populations.

The present study deals with Chinese fir (*Cunninghamia lanceolata* Hook.),

a coniferous species which is widespread from the central to the southeastern part of China. Chinese fir is a fast-growing species of substantial economic importance. It is most common under artificial regeneration in silvicultural management which favours monospecies stands with short-rotation cycles (20–30 years). Under natural conditions, Chinese fir is associated to some extent with *Sassafras* species and *Pinus massoniana* Lamb.

The results of a ten-locus inventory of seed samples from two provenances of *C. lanceolata* (Müller-Starck and Liu, 1989) are used to attempt a preliminary characterization of components of the realized reproductive system. Herein, reproduction is considered as the fertility of the respective parental population, the mode of fusion between gametes (mating system) and the viabilities until census. Inferences of the fertilities of the parental genotypes are not possible, because this information cannot be verified. Nevertheless, the form of sexually asymmetrical fertility selection (Ziehe and Gergorius, 1981; Ziehe, 1982a) is traceable by the study of offspring populations alone (Müller-Starck, 1982a; Ziehe, 1982b; Müller-Starck and Ziehe, 1984). Main emphasis will be on the question of to what extent deviations from random fusion of gametes occurred in the formation of the two seed samples. The phenomena responsible for the detected deviations will be tentatively described by means of a systematic comparison of the empirical genotypic structures with selected reference structures.

The study of the mating system will focus on the most-frequent reason for deviations from the random fusion of gametes, i.e. the occurrence of inbreeding. Several authors have developed models or have estimated coefficients of inbreeding in forest tree populations (e.g. Gregorius, 1975a,b; Gregorius and Müller (-Starck), 1975; Müller (-Starck), 1976, 1982b). Many studies have described adverse effects of inbreeding on viability parameters and metric characters (e.g. Franklin, 1970; Gansel, 1971; Eriksson et al., 1973; Andersson et al., 1974; Plym-Forshell, 1974; Sorensen and Miles, 1974; Kriebel, 1975; Libby et al., 1981; Park and Fowler, 1983; Griffin and Lindgren, 1985; Geburek, 1986). Since inbreeding is a consequence of mating among relatives, its most severe form is self-fertilization. In conifers, as opposed to angiosperm tree species, self-fertilization cannot be prevented by prezygotic incompatibility (sporophytic or gametophytic). The remaining means of reducing offspring from self-fertilization, i.e. zygote elimination, may vary in its effectivity among the various coniferous species. To our knowledge, inbreeding has not yet been studied by enzyme gene markers in *C. lanceolata*.

### *Problems involved*

The available seed samples can allow only a tentative and preliminary description of predominant characteristics of the reproductive system as it was realized in a certain set of *C. lanceolata* populations during one reproductive

period. The most severe limitation to continuing interpretations is the lack of information about the genetic structure of the parental populations. Furthermore, the degree to which each of the two provenance samples represents an entire provenance cannot be predicted. This aspect is not of particular concern in the present study: Populations within a provenance generally cannot be expected to be genetically homogeneous, so that samples from different locations should reflect interpopulational genetic variation. In the present case, it is known that the samples originate from collections in several stands in 1985. The calculation of the genetic diversities among the female and the male successful gametes (Müller-Starck and Liu, 1989) revealed high values for both types, so that a concentration of the collection on only a few maternal trees is not indicated. In this sense, the available seed sample may be accepted as representing genetically the stands being harvested but not the entire provenance gene pool.

Some of these drawbacks may be overcome by studying additional seed samples from several locations within each provenance and from different reproductive periods. But it has to be taken into account that even in the case of a well-defined parental population, substantial genetic variation can be expected among the offspring populations which originate from open pollination in different reproductive periods. This was shown, for instance, by Müller-Starck et al. (1983) and Müller-Starck (1985) in Scots-pine seed orchards for the all-orchard offspring and the reproductive success of single clones in different temporal and spatial environments. Consequently, it must be kept in mind that, in the present study, interpretations regarding any characteristics of reproduction concern only the available offspring populations and one reproductive period.

## MATERIAL AND METHODS

### *Seed samples*

The seed samples were supplied by the Forestry Department of Sichuan Agricultural University, Yaan. The seeds originate from the district of Hungya in west-central China and the district of De-Chang in southwestern China. Both samples were drawn randomly from official provenance collections, each of which originate from mixtures of crops from several stands of *C. lanceolata*. All available seeds were used in this study (151 seeds for the first provenance and 114 seeds for the second).

### *Genotyping*

The genotype of each seed was determined by separate analysis of its haploid endosperm and diploid embryo. Ten loci were scored simultaneously by means of horizontal starch gel electrophoresis: GDH-A; GOT-A,B,C; IDH-B; 6PGDH-A,B; PGI-A; SKDH-A,B. For genetic control, inheritance, linkage relationship

and details on the genotyping of the two seed samples see Müller-Starck and Liu (1988, 1989).

## RESULTS AND DISCUSSION

The only utilizable information is the mode by which the empirical genotype frequencies are derived from the underlying allele frequencies; the results of statistical comparisons between the empirical genotypic structures and selected reference structures serve as criteria in the characterization of the realized reproductive system. These references are the Hardy-Weinberg structure, the multiplicative structure, and the inbreeding structure.

### *Hardy-Weinberg structure*

This reference structure represents the hypothesis of random fusion of gametes by excluding asymmetrical association ( $p_i^{\text{♀}} = p_i^{\text{♂}}$  for all  $i$ ). Consequently, this standard is an indication for only that part of the reproduction which refers to the mating system, and cannot be used as a reference for monitoring fertility or viability selection.

The conformity of the empirical genotypic structure at each locus (female and male contributions unordered) to the expected Hardy-Weinberg structure was tested within each sample using the log-likelihood ratio, or  $G$ -test.

The obtained  $G$ -values, which are presented in Table 1, indicate significant

TABLE 1

Statistical comparison between the observed genotypic structures and each of three hypothetical structures (Hardy-Weinberg, multiplicative, inbreeding)

Gene locus	G-values					
	Hardy-Weinberg		Multiplicative		Inbreeding	
	Hungya	De-Chang	Hungya	De-Chang	Hungya	De-Chang
GDH-A	15.160***	49.424***	15.160***	49.774***	0.000	3.640
GOT-A	18.277**	11.504**	18.274**	11.499*	4.011	4.937
GOT-B	17.583**	14.778**	17.764**	14.778**	5.815	4.725
GOT-C	16.153*	16.057**	17.804**	18.442**	15.427*	3.684
IDH-B	4.521	23.761***	4.761	25.969**	3.854	4.660
6PGDH-A	16.009	13.392*	21.295	13.344*	10.046	-
6PGDH-B	1.276	11.926	1.188	11.852	-(+)	7.711
PGI-A	28.216	28.052**	34.142	32.084**	19.168	23.217*
SKDH-A	43.128***	24.932	52.525**	26.807	30.516*	10.904
SKDH-B	51.738***	21.500**	58.297***	25.486***	0.914	7.139

Significance levels are 0.05 (\*), 0.01 (\*\*), 0.001 (\*\*\*).

(+) Negative average coeff. of inbreeding.

deviations of the empirical from the hypothetical genotypic structure for the majority of the gene loci. This result holds for both samples, although the ranking of the loci according to the amount of deviation differs. From this, it can be stated that the empirical genotype frequencies cannot be explained by the assumption of exclusively random fusion of gametes. The obtained deviations are so substantial that any assumptions on a possible masking of actual random mating among gametes by viability selection prior to the census stage appear to be unrealistic.

*Multiplicative structure*

Under this structure, random association of gametes is extended to encompass sexual asymmetries as opposed to the required averaging of the female and the male gametic frequencies in the case of Hardy-Weinberg structure (multiplicative structure:  $p_i^{\text{♀}} p_j^{\text{♂}} \cdot N$  for  $i, j = 1, \dots, k$ , with  $k = \text{number of alleles}$ ; Ziehe and Gregorius, 1981, Ziehe, 1982a). Consequently, sexually asymmetrical fertility selection which results in  $p_i^{\text{♀}} \neq p_i^{\text{♂}}$  for at least one  $i$  is a part of this type of genotypic reference structure.

To verify the occurrence of sexual asymmetries, the empirical frequencies among the female and the male gametic contributions to the embryos were compared statistically by means of a  $k \times 2$  chi-square test of homogeneity. Significant deviations were obtained in 2 out of 20 tests (10 loci for each of two samples); deviations at the level  $0.05 \leq P < 0.10$  occurred in two additional cases (GOT-C<sub>1</sub>, IDH-B<sub>2</sub>). The significant cases are presented in Table 2.

These results support the assumption of sexual asymmetries, although this phenomenon seems to have only marginal significance. This statement is also supported by the fact that statistically significant deviations generally are more

TABLE 2

Statistical comparison of the observed allele frequencies<sup>a</sup> among the female and the male gametic contributions to the embryos of the provenance samples Hungya and De-Chang

Provenance	Gene locus	Sample size	Sex	Allele frequency					$\chi^{2b}$
				0	1	2	3	4	
Hungya	IDH-B	151	♀	2	5	128	16	-	6.162*
		151	♂	-	17	125	8	1	
De-Chang	SKDH-B	114	♀	4	78	-	32	-	5.992*
		114	♂	6	91	2	15	-	

<sup>a</sup>Frequencies less than 4 are pooled.

<sup>b</sup>\*Significance level 0.05 (\*).

pronounced between the two seed samples (see Müller-Starck and Liu, 1989, table 4) than between the female and the male gametic contributions within each seed sample. The conformity of the empirical genotypic structure at each locus to the respective multiplicative structure was checked by the log-likelihood or *G*-test of homogeneity. The results given in Table 1 are surprisingly similar to the corresponding *G*-values of the Hardy-Weinberg structures. It is clearly indicated that, in the present case, the acceptance of sexually asymmetrical fertility selection in combination with random association of gametes does not suffice to obtain any better conformity of empirical and reference structure.

### *Inbreeding structure*

Recalling the Hardy-Weinberg and multiplicative structures, it is obvious that a considerable part of the deviations of the empirical structures from these references traces back to a surplus in the observed frequencies of homozygotes. This is indicated for all loci except 6PGDH-B in Hungya and 6PGDH-A in De-Chang. To illustrate this phenomenon and the variation between the loci, the absolute numbers of homozygotes among the empirical and the expected numbers under the corresponding multiplicative structures together with the ratios between them are surveyed in Table 3. These ratios vary between 0.992 and 1.538 in the case of Hungya and between 0.955 and 1.391 in De-Chang. The surplus of homozygotes in most cases affects the different alleles at one locus to a similar extent. Deviations from this are particularly evident for SKDH-B in Hungya (ratio  $65/48.3=1.346$  for allele 1 and  $38/21.5=1.767$  for

TABLE 3

Comparison of the observed and the expected (multiplicative structure) frequencies of homozygotes among the samples of Hungya and De-Chang

Gene locus	Hungya ( <i>n</i> = 151)			De-Chang ( <i>n</i> = 114)		
	Abs. frequencies		Ratio	Abs. frequencies		Ratio
	Obs.	Exp.	Obs./Exp.	Obs.	Exp.	Obs./Exp.
GDH-A	123	108.0	1.139	96	69.0	1.391
GOT-A	142	136.6	1.040	111	109.1	1.017
GOT-B	98	84.9	1.154	82	73.4	1.117
GOT-C	74	68.6	1.079	65	50.5	1.287
IDH-B	110	107.4	1.024	87	73.1	1.190
6PGDH-A	72	67.3	1.070	53	55.5	0.955
6PGDH-B	132	133.0	0.992	104	102.4	1.016
PGI-A	92	84.7	1.086	61	58.1	1.050
SKDH-A	72	60.9	1.182	89	81.3	1.095
SKDH-B	108	70.2	1.538	79	66.7	1.184

allele 3) and for GDH-A in De-Chang (ratio 20/7.1 = 2.817 for allele 3 and 75/61.9 = 1.212 for allele 4). Please note that the Hardy-Weinberg structure results in a slightly greater (max. 1.3%) or equal proportion of homozygotes than the multiplicative structure. The trend in favour of the homozygotes supports the assumption that at least part of the significant deviations from the random association are at least partly due to inbreeding.

The inbreeding hypothesis can be tested by comparing the observed genotype frequencies with Wright's inbreeding structure. Given an inbreeding coefficient  $F$  between 0 and 1, with  $F = 1 - (1 - \sum_i P_{ii}) / (1 - \sum_i p_i^2)$ , the inbreeding structure is derived from the following standard equations, which evaluate the expected relative frequency of each genotype ( $P_{ii}^I, P_{ij}^I; I = \text{inbreeding}$ ):

$$P_{ii}^I = p_i F + p_i^2 (1 - F) = p_i^2 + p_i F (1 - p_i) \quad \text{and} \quad (1)$$

$$P_{ij}^I = 2p_i (1 - F) p_j = 2p_i p_j - 2p_i p_j F \quad (2)$$

Deviations from the inbreeding structure can be detected in detail if coefficients of inbreeding are estimated for single homozygotes and heterozygotes at each gene locus (H.R. Gregorius, personal communication, 1988). By this, it is taken into consideration that other phenomena, such as assortative mating (e.g. genotype-dependent variation in the annual period of flowering), may be the reason why the surplus of homozygotes does not affect each allele to the same extent. For each locus, the coefficients of inbreeding for each homozygote ( $F_{ii}$ ) and each heterozygote ( $F_{ij}$ ) are estimated by the following equations:

$$F_{ii} = (P_{ii} - p_i^2) / p_i (1 - p_i) \quad \text{and} \quad (3)$$

$$F_{ij} = (2p_i p_j - P_{ij}) / 2p_i p_j = 1 - (P_{ij} / 2p_i p_j) \quad (i \neq j) \quad (4)$$

where  $P_{ii}, P_{ij}$  (unordered) are the empirical genotype frequencies and  $p_i^2, 2p_i p_j$  the corresponding Hardy-Weinberg frequencies. An inbreeding structure is realized only if all  $F_{ii}$  and  $F_{ij}$  are identical and positive.

Analogously to the other reference structures, the conformity of the empirical structure and the inbreeding structure was tested for each gene locus by means of the  $G$ -test of goodness of fit. The results, which are included in Table 1, clearly demonstrate that the inbreeding structure is the only reference with substantial increase of conformity to the observed structures. In contrast to the other reference structure, in Hungya only two gene loci (GOT-C, SKDH-A) and in De-Chang one locus (PGI-A) still indicate significant deviations.

These results demonstrate that the realized mating system can be expected to favour inbreeding, although the heterogeneity among the gene loci with respect to conformity of empirical and inbreeding structures indicates interference by additional phenomena. As mentioned above, positive assortative mating can induce heterogeneities in the surplus of homozygotes as well as genotype-dependent differential self-fertilization. Furthermore, phenomena apart from the mating system can be involved, such as specific viability selection favour-

ing certain homozygotes (the percentage of previously removed empty seeds is not known) or an increase of homozygotes due to a mixing of seeds from different subpopulations ('Wahlund effect'; see Hattemer, 1982). To monitor in detail possible preferences in the association of alleles in the embryonic genotypes, the following equation, which is based on a concept of Gregorius and Hattemer (1987), was used for quantification:

$$U_{\varphi i: \delta j} = \frac{1}{2} P_{ij}^{\varphi \delta} / (2(\frac{1}{2} p_i^{\varphi} \frac{1}{2} p_j^{\delta})) = P_{ij}^{\varphi \delta} / p_i^{\varphi} p_j^{\delta} \quad (5)$$

with empirical relative frequencies  $P_{ij}^{\varphi \delta}$  for ordered genotypes and  $p_i^{\varphi}$ ,  $p_j^{\delta}$  for alleles among the female and the gametic contribution to the embryos ( $U_{\varphi i: \delta j} = U_{\delta j: \varphi i}$ ). The allelic preference parameter  $U_{\varphi i: \delta j}$  (or  $U_{\delta j: \varphi i}$ ) is equal to 1 in the case of random association of alleles. It indicates a negative preferential relationship for the range  $0 < U_{\varphi i: \delta j} < 1$ , no association for  $U_{\varphi i: \delta j} = 0$  and a positive preferential relationship for  $U_{\varphi i: \delta j} > 1$ . In Table 4 only those

TABLE 4

Allelic preference parameter  $U_{\varphi i: \delta j}$  for the most frequent alleles\* being associated in embryonic genotypes at five gene loci

Sample	Genotype (♀ ♂)	Freq.	$U_{\varphi i: \delta j}$
De-Chang	GDH -A <sub>3</sub> A <sub>3</sub>	0.175	2.808
	-A <sub>4</sub> A <sub>3</sub>	0.061	0.311
	-A <sub>3</sub> A <sub>4</sub>	0.088	0.449
	-A <sub>4</sub> A <sub>4</sub>	0.658	1.212
Hungya	SKDH -B <sub>1</sub> B <sub>1</sub>	0.423	1.323
	-B <sub>3</sub> B <sub>1</sub>	0.126	0.568
	-B <sub>1</sub> B <sub>3</sub>	0.113	0.552
	-B <sub>3</sub> B <sub>3</sub>	0.252	1.773
Hungya	GOT -C <sub>2</sub> C <sub>2</sub>	0.132	1.448
	-C <sub>3</sub> C <sub>2</sub>	0.126	0.798
	-C <sub>2</sub> C <sub>3</sub>	0.199	0.971
	-C <sub>3</sub> C <sub>3</sub>	0.351	0.988
De-Chang	PGI -A <sub>3</sub> A <sub>3</sub>	0.421	1.014
	-A <sub>4</sub> A <sub>3</sub>	0.228	1.055
	-A <sub>3</sub> A <sub>4</sub>	0.184	1.023
	-A <sub>4</sub> A <sub>4</sub>	0.096	1.026
Hungya	SKDH -A <sub>3</sub> A <sub>3</sub>	0.391	1.091
	-A <sub>4</sub> A <sub>3</sub>	0.073	1.027
	-A <sub>5</sub> A <sub>3</sub>	0.073	0.699

\*For allele frequencies see Müller-Starck and Liu 1989; for further explanation see text.

embryonic genotypes are considered whose absolute frequencies are greater than 5.

The first two gene loci in Table 4 (GDH-A, SKDH-B) are the above-mentioned ones, the alleles of which reflect the surplus of homozygotes to different extents. The following three loci (GOT-C, PGI-A, SKDH-A) are those which indicate significant deviations between the empirical and the inbreeding structures (see Table 1). In contrast to the latter, the first two loci can be expected to represent the unlisted 5 gene loci with respect to a substantial over-representation of homozygotes as compared to the Hardy-Weinberg and the multiplicative structure.

In the case of GDH-A and SKDH-B as well as the unlisted loci, a preferential association between alleles of the same type and not between different alleles is clearly indicated. According to the concept of  $U_{\varphi_i:\sigma_j}$ , the obtained values for the homozygotes correspond to the above ratios between empirical and expected genotype frequencies. The preference of an allele for its same type, which may not necessarily be identical by descent, is still recognizable in the case of GOT-C<sub>2</sub>, but not for GOT-C<sub>3</sub> and not for the loci PGI-A and SKDH-A, both of which reveal greater *G*-values (Table 1). Random association holds at least for the frequent alleles at PGI-A and for certain combinations at SKDH-A. Preferential association between different alleles is only indicated for SKDH-A<sub>5</sub><sup>♀</sup> A<sub>3</sub><sup>♂</sup>; here A<sub>3</sub><sup>♂</sup> shows a negative preference with A<sub>5</sub><sup>♀</sup> while it seems to be associated at random with its own type and with A<sub>4</sub><sup>♂</sup>.

These results can be interpreted to support the inbreeding hypothesis in combination with additional phenomena which increase or – in a very few cases – decrease the frequency of homozygotes. Phenomena such as species-specific assortative mating seem to have no or only marginal significance, because the remaining disparities between empirical and inbreeding structure appear in the samples at different loci. The Wahlund effect should not greatly affect the heterogeneity between the loci in the conformity with the inbreeding structure. More probable phenomena to complement the effects of inbreeding are environment-dependent viability selection and/or genotype-dependent differential self-fertilization.

#### CONCLUDING REMARKS

The tentative description of reproduction in *C. lanceolata* revealed stronger influences of the mating system than of other components of the reproductive system. It can be stated that the actual mating system results in substantial deviation from random fusion of gametes in favour of a system which appears to be dominated by inbreeding. The utilization of the three genotypic reference structures (Hardy-Weinberg, multiplicative, inbreeding) indicate this trend very clearly in both samples. However, it becomes evident that further processes are involved which increase or mask the tendency of a homozygote sur-

plus and thus result in the observed variation among the studied gene loci. The interpretations suggest the tentative acceptance of viability selection as the most probable phenomenon in addition to the monitored type of inbreeding.

Further studies are required to analyse in more detail whether that part of the surplus of homozygotes which is caused by inbreeding traces back primarily to self-fertilization or, to a larger extent, to a small inbreeding effective population size due to limited gene-flow. Self-fertilization should be involved, because the obtained variation in the ratio of homozygotes to heterozygotes among the gene loci conforms to the assumption of a genotypic-dependent variation in the clonal probabilities of self-fertilization.

The present study also attempted to extend the genetic characterization of seed samples to the essentials of the reproductive system, although no information about the genetic structures of the parental populations was available. It is self-evident that the resulting interpretations can hold only for the studied seed samples. However, the conformity of the revealed surplus of homozygotes in both seed samples is an indication that this phenomenon could be important in *C. lanceolata* populations. The same tendency was observed in another species of the family Taxodiaceae (*Sequoiadendron giganteum*; see Fins and Libby, 1982).

If the surplus of homozygotes is confirmed by other studies, the conclusion of small sizes of inbreeding-effective neighbourhoods (Gregorius, 1975a) is suggested. This can be a consequence of limited gene-flow via small-scale pollen dispersal (and/or limited seed dispersal in naturally regenerated populations) or of the formation of offspring from self-fertilization which exceeds by far the reciprocal value of the population size. The resulting inbreeding in seed samples is not necessarily disadvantageous as long as seed production is large enough and natural selection is strong enough to counterbalance it.

Techniques in silviculture should then avoid drastic manipulation of natural selection, as for instance in the case of the establishment of plantations with minimal numbers of plants per area. Neighbourhoods in forest stands – especially those from natural regeneration – should not be transferred to breeding populations, and the management of such populations should include concepts for the avoidance of inbreeding.

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