Effects of nonrandom mating schemes to delay the inbreeding accumulation in cultured populations of coho salmon (*Oncorhynchus kisutch*)

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Abstract: Chilean salmon culture is based on a high degree of artificial selection, which has had the tendency to increase the inbreeding (F). Three types of nonrandom mating were evaluated to control the inbreeding in two best linear unbiased prediction selected coho salmon (*Oncorhynchus kisutch*) populations (even and odd). These included compensatory mating on the basis of breeding values (C), modified compensatory mating (C1) based on the family mean of breeding values, and mating that minimized the mean co-ancestry of the group selected (MC scheme). In the odd population, the MC scheme ($F = 2.0\%$) reduced the increase in inbreeding of the next generation by 50% and 46% when compared with random mating of selected individuals with sib mating restricted ($F = 3.9\%$) and with C ($F = 3.7\%$), respectively. In the even population, the MC scheme reduced the increase in inbreeding by 14% compared with C1 (9.7 versus 11.2). In both populations, the MC scheme also reduced variance in inbreeding (even, 59%; odd, 39%). Thus, the MC scheme was more efficient in reducing the increase and variance of inbreeding, thus limiting the expression of inbreeding depression. Although the MC scheme was more time consuming, we recommend this scheme to carry out crosses in each generation.

Résumé : La culture du saumon au Chili comporte une forte composante de sélection artificielle, ce qui a eu tendance à augmenter la consanguinité (F). Nous avons évalué trois types de croisements non aléatoires dans le but de contrôler la consanguinité dans deux populations de saumons coho (*Oncorhynchus kisutch*) sélectionnées par la méthode de la meilleure prédiction linéaire non biaisée (paire et impaire). Les trois types comprenaient le croisement compensatoire basé sur la valeur génétique (C), le croisement compensatoire modifié (C1) basé sur la valeur génétique moyenne de la famille et un croisement qui minimise la filiation commune moyenne du groupe sélectionné (MC). Chez la population impaire, le type MC ($F = 2,0$ %) réduit l'augmentation de la consanguinité de la génération suivante respectivement de 50 % et de 46 % par comparaison au croisement aléatoire d'individus sélectionnés (avec restriction de l'accouplement entre membres d'une même famille) ($F = 3,9$ %) et au croisement de type C ($F = 3,7$ %). Dans la population paire, le croisement de type MC réduit l'accroissement de la consanguinité de 14 % par rapport au croisement de type C1 (9,7 % plutôt que 11,2 %). Chez les deux populations, le croisement de type MC réduit aussi la variance de la consanguinité (paire, 59 %; impaire, 39 %). Le croisement de type MC est donc plus efficace pour réduire l'augmentation et la variance de la consanguinité et il diminue ainsi l'expression de la dépression de consanguinité. Bien que les croisements de type MC requièrent plus de temps, nous les recommandons pour effectuer les croisements dans toutes les générations.

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Introduction

Genetic improvement of fishes in aquaculture has recently benefited by incorporation of the "best linear unbiased predictor" (BLUP) (Henderson 1975) for breeding values when using the animal model for genetic evaluation (Gjoen and Gjerde 1998; Martínez et al. 1999). This procedure maximizes the correlation between the true and the predicted breeding values using information from all parents in the present generation and of preceding generations, as well as the individual's own data. This animal estimation produces a more exact estimation for the breeding value and increases the genetic response compared with other methods, e.g., phenotypic selection (Belonsky and Kennedy 1988). However, given that the animal model favours selection of related individuals, it also produces an increase in the rate of inbreeding and a long-term reduction in the genetic variance (Belonsky and Kennedy 1988; Quinton et al. 1992). There

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have been few empirical evaluations of the rate of inbreeding in fish populations subject to artificial selection. In rainbow trout (*Oncorhynchus mykiss*) populations, Su et al. (1996) estimated a rate of inbreeding of 1.3–1.7% per generation, whereas Pante et al. (2001*a*) for other populations found rates of inbreeding of 0.53–2% per generation. J.A. Gallardo et al. (unpublished data) recently found that two populations of coho salmon (*Oncorhynchus kisutch*) selected following an animal model gave inbreeding rates of between 1.05 and 2.37% per generation.

Limiting inbreeding in selection programs is important, as higher levels of inbreeding increase the probability of inbreeding depression. Estimation of inbreeding depression in fishes has consistently shown that consanguineous progeny have lower viability and less growth and also show lower resistance to infection by protozoans (Su et al. 1996; Pante et al. 2001*b*; Arkush et al. 2002).

Various methods have been devised to reduce tendencies towards an increase in the rate of inbreeding produced by artificial selection (i.e., BLUP or mass selection) while at the same time maintaining a high genetic gain (Villanueva et al. 1996; Meuwissen 1997; Wu and Schaeffer 2000). These include (*i*) BLUP estimations of breeding values with incremented heritabilities (Grundy et al. 1994; Wu and Schaeffer 2000), (*ii*) estimations using a suboptimal selection criterion, for example, giving a lower weighting to family information (Verrier et al. 1993; Wu and Schaeffer 2000), (*iii*) selection methods that manipulate the genetic contribution to the next generation of each candidate selected (Toro and Nieto 1984; Meuwissen 1997), (*d*) nonrandom mating schemes such as compensatory mating or those that minimize the average co-ancestry of the group selected (Toro and Perez-Enciso 1990; Caballero et al. 1996), and (*e*) mixed methods that used some preceding approaches simultaneously (Grundy et al. 1994; Sonesson and Meuwissen 2000). Regardless of which method is to be applied for selecting the reproducers for the next generation, the mating scheme among selected candidates is a determining factor in reducing the inbreeding rate, with random mating of selected individuals the least efficient (Grundy et al. 1994; Caballero et al. 1996; Sonesson and Meuwissen 2000). Practical considerations and reproductive restrictions may also limit the efficiency of these methods in reducing the rate of inbreeding (Meuwissen 1997; Fernández and Toro 1999). To date, few studies have evaluated the methods cited above (Sanchez et al. 1999; Weigel and Lin 2000), and none has been evaluated taking into account the characteristics of programs used in genetic selection in fishes.

The objective of the present study was to evaluate the effects of different nonrandom mating schemes in reducing inbreeding accumulation over a short term (one generation) in two populations of coho salmon selected by means of an animal model. This evaluation takes into account a series of practical and reproductive limitations relevant to various artificial selection programs in salmonids.

Materials and methods

Study populations

The study was based on data from two coho salmon populations belonging to a genetic improvement center (Centro de mejoramiento genético (CMG)) maintained by the Institute for Fisheries Development and the University of Chile in Coyhaique (XI Region, Chile). The two populations, termed "even" and "odd", were produced in 1992 and 1993, respectively, and are managed in a 2-year productive cycle. Each year class was produced using a hierarchical mating system by means of mating of 30–35 males with approximately 100 females, producing a population of 30–35 families of half-siblings (HS) and 100 families of full siblings (FS). Both populations were submitted to artificial selection: five generations for the even population and four generations for the odd population. Characters selected included the weight at harvest using the BLUP prediction of the breeding value and early spawning by means of phenotypic selection. More details on characters and origins of the populations are given in Martínez et al. (1999) and Winkler et al. (1999). The genealogy has been recorded from the beginning of the program to the present, giving calculated mean rates of inbreeding of 2.37% for the even population and 1.05% for the odd population. The mean inbreeding calculated in the previous year class investigated in this study was $3.16 \pm 2.65\%$ (year class 1999) and $9.4 \pm 2.7\%$ (year class 2000). The inbreeding rate was greater in the even population than in the odd population as a direct consequence of the smaller number of founder individuals in the former population ($N_e = 61$ and 106, respectively).

Mating schemes

The following mating schemes were compared in terms of the level of predicted next-generation inbreeding. (*i*) For random mating of selected individuals (R), crosses between selected males and females were carried out randomly, avoiding crosses between HS and FS. This scheme was routinely used at the CMG until 2001. (*ii*) In compensatory mating (C), a ranking was obtained following the breeding values for harvest weight of all individuals, grouped per spawning day. Based on this ranking, a mating system was simulated in which the male with the highest breeding value was assigned to cross with the female with the lowest breeding value, followed by assignment of the second-ranked male with the next-to-last ranked female and so forth until all individuals had been assigned. If the female was HS or FS with the assigned male, the assignment was replaced with a female that had the next highest breeding value, assigning the next male to this female. (*iii*) For modified compensatory mating (C1), a ranking was arranged of breeding values for harvest weight based on the average of paternal HS. A total of 19 families of half-brothers and 34 families of half-sisters were separately classified. The number of individuals per HS family varied between 1 and 59 for the males and between 3 and 86 for the females. Compensatory matings were carried out in a similar manner to the preceding scheme based on the family average. The male or female breeder with the highest family breeding value was crossed with the female or male with the lowest value for a particular spawning day and so forth. Crosses between HS and FS were avoided. (*iv*) The minimum co-ancestry (MC) scheme took into account the use of all genealogical information to assign the crosses and consisted of selecting a group for crosses of males and females having the minimum average co-ancestry. Co-ancestry between two individuals is the

Table 1. Number of sires (S), dams (D), and crosses (S × D) evaluated per spawning day in two year classes of coho salmon.

2001 year class				2002 year class			
Spawning day	S	D	S × D	Spawning day	S	D	S × D
26 April	8	12	96	27 April	6	12	72
27 April	11	22	242	29 April	5	9	45
30 April	15	28	420	3 May	17	30	510
1 May	17	24	408	7 May	17	29	493
4 May	13	25	325	7 May[a]	14	28	392
8 May	20	40	800	9 May	15	33	495
9 May	24	38	912	9 May[a]	7	13	91
12 May	28	47	1316	11 May	10	18	180
16 May	14	21	294	14 May	16	24	384
22 May	8	12	96	17 May	8	9	72
				20 May	7	8	56
				24 May	5	9	45

[a]Crosses carried out in the afternoon were considered independent from crosses carried out in the morning.

same as the probability that two alleles for a locus, each one taken from two different individuals, would be equal through descendency (Malecot 1948). This is equivalent to the inbreeding of the hypothetical progeny of these individuals if they are crossed (Falconer and Mackay 1996). Thus, minimization of the co-ancestry of a group of breeders is equivalent to reducing the inbreeding of their progeny. Co-ancestry coefficients were determined using PEDIGREE VIEWER program version 4.9 (B. Kinghorn and S. Kinghorn, University of New England, Armidale, New South Wales, Australia). Determination of which group of crosses minimizes the average co-ancestry has been generally treated as a problem in linear programming (Jansen and Wilton 1985; Sanchez et al. 1999; Weigel and Lin 2000), and this is the strategy used in this study. The following objective function was minimized in the present study:

$$(1) \quad \frac{\sum \sum x_{ij}(f_{ij})}{H}$$

This equation represents the average co-ancestry of the group selected, where x_{ij} is a decision variable that indicates whether the sire and dam are paired ($x_{ij} = 1$) or not ($x_{ij} = 0$), f_{ij} is the coefficient of co-ancestry between the sire i and the dam j, and H is the number of females spawned on a given day (usually between 10 and 40). The objective function must comply with the following conditions:

$$(2) \quad \Sigma\Sigma\, x_{ij} = H$$

$$(3) \quad \Sigma\Sigma\, x_{ij} = 1 \qquad \text{(per each mother)}$$

$$(4) \quad \Sigma\Sigma\, x_{ij} = 1, 2, 3 \quad \text{(per each father)}$$

Equation 2 indicates the number of crosses carried out for a given day, eq. 3 indicates that one dam was crossed with only one sire, and eq. 4 indicates that one sire could cross with one, two, or three females on a particular day. The vector of crosses was obtained using the Hiper Lindo program (Lindo Systems, Inc. 1985).

Practical and reproductive restrictions

The two main limitations in this study were related to the number of crosses that could be evaluated simultaneously. The number of crosses evaluated was limited by the number of breeders successfully spawned each day (Table 1) and not by the entire group of breeders selected for the animal model. This resulted in 58 sires and 279 dams in 2001 (15 660 possible crosses) and 55 sires and 266 dams in 2002 (14 630 possible crosses). Management of the spawning at the CMG was carried out following natural maturation in the fishes, which occurred in periods of 5–6 weeks, following a normal distribution. Gametes were obtained day by day from mature breeders, and after the quantity and quality of the gametes were determined, it was possible to obtain "optimum" crosses using methods cited above for each particular day. In relation to the preceding, a practical limitation was also included as follows. Because of limitations on personnel and space at the CMG, two groups of mature fishes were spawned separately some days, one in the morning and the other in the afternoon. Crosses of each group were optimized separately in 2002.

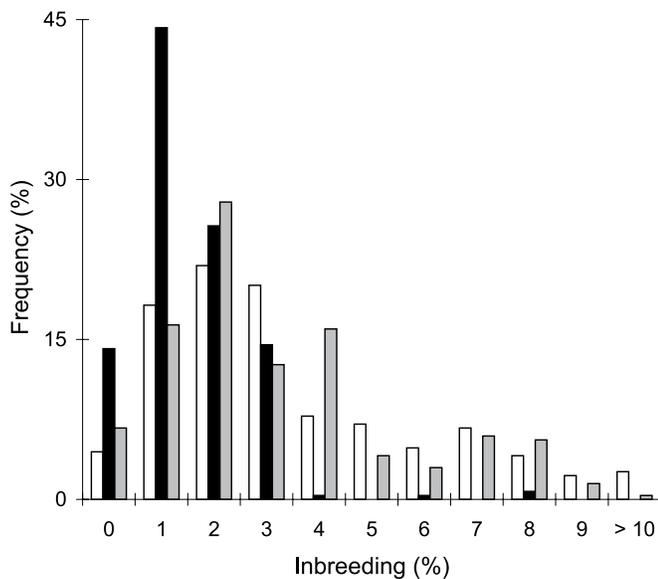**Evaluation of the mating schemes**

Evaluation of the different mating schemes was carried out in two steps, each one involving the year class of each population (2001–2002). Only the reproductive limitation was applied to year class 2001. Here, the efficiency in reducing inbreeding in the next generation was compared between two nonrandom mating schemes, including the C mating and MC mating versus the R mating schemes of selected individuals carried out in this year. In year class 2002, the CMG placed into practice the C1 mating scheme instead of the R mating schemes used until this time. In this stage, both reproductive and practical restrictions were taken into account. The efficiency of the C1 scheme was compared with that of the MC scheme, which had been found to be the better scheme from the previous stage. Following the system of hierarchical crosses used in this program, and with the objective that the comparisons between the different schemes should be carried out under the same expected genetic response level, each breeder was utilized the same number of times in

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Table 2. Mean inbreeding (F) and inbreeding ratios between random mating of selected individuals (R), minimum co-ancestry (MC), and compensatory (C) mating of the coho salmon 2001 year class by spawning day.

Spawning day	Mean F			Inbreeding ratio					
	R	MC	C	MC/R	P	MC/C	P	C/R	P
26 April	4.77	1.92	5.16	0.40	*	0.37	*	1.08	ns
27 April	3.04	1.81	3.07	0.60	**	0.59	ns	1.01	ns
30 April	3.48	1.76	3.47	0.51	**	0.51	**	1.00	ns
1 May	4.57	1.99	3.33	0.44	**	0.60	**	0.73	ns
4 May	3.67	1.91	2.95	0.52	*	0.65	**	0.80	ns
8 May	4.21	1.91	3.47	0.45	**	0.55	**	0.82	ns
9 May	3.86	1.94	3.19	0.50	**	0.61	**	0.83	ns
12 May	4.13	1.82	4.17	0.44	**	0.44	**	1.01	ns
16 May	4.15	2.61	4.20	0.63	*	0.62	**	1.01	ns
22 May	4.57	3.65	5.91	0.80	ns	0.62	ns	1.29	ns
Mean	3.99	2.01	3.70	0.50	***	0.54	***	0.93	ns

Note: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, nonsignificant.

Fig. 1. Frequency distribution of inbreeding in hypothetical progeny of the coho salmon 2001 year class for random mating of selected individuals (open bars), compensatory mating (shaded bars), and minimum co-ancestry mating (solid bars) ($N = 269$ families).

each mating scheme (identical genetic contribution of each parent between mating schemes).

Statistical analyses

In both year classes, the efficacy of each scheme in reducing the inbreeding rate was evaluated by day and by spawning season, at the population level. The total number of crosses evaluated per spawning day was between 96 and 1316 for the 2001 year class and between 45 and 510 for the 2002 year class (Table 1). To compare mean inbreeding per spawning day among schemes, a nonparametric Mann–Whitney test was used, whereas the variances of inbreeding were compared using an F test (Zar 1996). A Kolmogorov–Smirnov analysis (Zar 1996) was used at the population level to compare the distribution of frequencies of inbreeding arising from all of the crosses selected in each year class by the mating schemes.

Results

Evaluation of mating schemes for the 2001 year class

The MC scheme was more efficient in reducing the average inbreeding and the variance of the inbreeding in the next generation in comparison with the other mating schemes evaluated. The MC scheme reduced the inbreeding ($P < 0.001$) 50% compared with the R mating schemes of selected individuals and 46% compared with the C mating scheme (Table 2). In relation to spawning day, this reduction in average inbreeding ranged between 20% and 60%. In comparison, the C scheme was only slightly more effective (7%) at reducing inbreeding in comparison with the R scheme, although none of the daily differences in the tests was significant (Table 2). Also, the MC scheme significantly reduced ($P < 0.001$) the variance in the inbreeding by 59% compared with the R scheme and 54% compared with the C scheme (Fig. 1). Conversely, the C scheme reduced ($P < 0.05$) the variance of the inbreeding only 12% when compared with the R scheme (Fig. 1). Consequently, the frequency distribution of inbreeding was significantly different between MC and R (Kolmogorov–Smirnov test, $D = 0.42$, $P < 0.001$) and between MC and C (Kolmogorov–Smirnov test, $D = 0.37$, $P < 0.001$) but not between C and R (Kolmogorov–Smirnov test, $D = 0.081$, P not significant).

Evaluation of mating schemes for the 2002 year class

The MC scheme was more efficient in reducing the inbreeding in all of the parameters evaluated in comparison with the C1 scheme. The MC scheme reduced the inbreeding by an average of 14% in comparison with C1 (Table 3), whereas on a per spawning day basis, this reduction ranged between 5% and 17%. As with year class 2001, the MC scheme also significantly reduced ($P < 0.001$) the variance of the inbreeding, with an average reduction of 39% (Table 3). Consequently, the frequency distribution of the inbreeding was significantly different (Kolmogorov–Smirnov test, $D = 0.33$, $P < 0.001$) between the two nonrandom mating schemes (data not shown).

The practical and reproductive restrictions evaluated in this year class limited the efficiency of the MC scheme over the C1 scheme in inbreeding reduction when less than

Table 3. Mean inbreeding (*F*) and standard deviation of the inbreeding and the inbreeding ratio between minimum co-ascendancy (MC) and modified compensatory (C1) mating in the coho salmon 2002 year class per number of crosses evaluated (*N*).

| | Mean *F* | | | | Standard deviation | | | |
| | | | Inbreeding ratio | | | | Inbreeding ratio | |
N	C1	MC	MC/C1	*P*	C1	MC	MC/C1	*P*
45	10.6	10.0	0.95	ns	1.5	0.9	0.60	ns
45	10.8	10.0	0.93	ns	1.5	1.9	1.27	ns
56	11.3	10.1	0.89	ns	1.2	1.1	0.92	ns
72	11.0	9.6	0.87	ns	2.0	1.0	0.50	*
72	10.6	9.9	0.94	ns	2.0	0.9	0.45	*
91	11.0	9.9	0.90	ns	2.2	1.3	0.59	*
180	12.0	9.9	0.83	*	2.9	1.8	0.62	*
384	11.3	9.6	0.85	**	1.9	1.4	0.74	ns
392	11.3	9.7	0.86	**	2.0	1.1	0.55	**
493	11.1	9.2	0.83	***	2.0	0.7	0.35	***
495	11.2	9.4	0.84	***	2.0	1.2	0.60	**
510	11.1	9.7	0.88	*	2.5	1.4	0.56	**
Total	11.2	9.7	0.86	***	2.1	1.3	0.61	***

Note: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, nonsignificant.

100 crosses were evaluated simultaneously (Table 3). The reduction in inbreeding was not significant when the number of crosses dropped from 91 to 45; however, when 180–510 crosses were evaluated simultaneously, the reduction in inbreeding was highest and significant.

Discussion

This study showed that the MC scheme was the most efficient in reducing mean inbreeding of the next generation when compared with the other mating schemes applied to coho salmon at the CMG. Other authors have obtained similar results on the efficiency of the MC method for reducing inbreeding both over short (Weigel and Lin 2000) and medium (Sanchez et al. 1999) terms. Also, in agreement with various theoretical predictions (Grundy et al. 1994; Caballero et al. 1996; Sonesson and Meuwissen 2000), the random mating schemes of selected individuals were less efficient in reducing inbreeding even when avoiding mating FS and HS individuals in each generation. In spite of this evidence, previously described random mating schemes are still commonly used in selective breeding programs (Pante et al. 2001*a*; Argue et al. 2002; Bolivar and Newkirk 2002).

The MC scheme reduced the variance of inbreeding between 40% and 60% in relation to the other schemes studied, producing families that were more homogeneous among themselves with regard to inbreeding. Similar results were obtained by Sanchez et al. (1999), who found that the variance of inbreeding was reduced by one to seven times in comparison with random mating of selected individuals. This is a desirable situation in the sense that families having high levels of inbreeding within each generation will not be produced, reducing the probability of inbreeding depression being expressed (Gjerde et al. 1983; Su et al. 1996; Pante et al. 2001*b*).

In the present study, the evaluations were carried out under the conditions of two restrictions that limited the number of crosses tested simultaneously. The reproductive restriction limited the number of breeders evaluated simultaneously to those successfully spawned on a given day, and the practical restrictions in the handling of the fishes prevented a large number of them from being spawned and evaluated simultaneously. Limited by these two restrictions, only between 45 (5 males and 9 females) and 510 (17 males and 30 females) crosses could be evaluated in 2002. This was lower than the number of crosses potentially carried out at CMG on any given day (30 males and 150 females, 4500 possible crosses) and much lower than the total of theoretically possible crosses if all of the available fishes could have been spawned simultaneously (14 630 possible crosses). At least two alternative forms of spawning management could be adopted to avoid the limitations on the number of breeders simultaneously evaluated and to increase the efficiency of the minimal co-ancestry scheme. These include a reduction of the spawning period to a few days by the use of hormonal induction and the preservation of semen from early-spawning males to be used later in the fertilization process. Both techniques, especially the first one, have been incorporated in Chilean culture farms and may be efficiently utilized in the short term in genetic selection programs applied to salmonids.

Practical application of MC scheme was more time consuming than the two mating schemes previously utilized at the CMG. The MC method requires in situ (each day of spawning) construction of matrices of co-ancestry among all of the possible crosses of the breeders selected, as well as matrices necessary to adapt the selection of optimal crosses for each spawning day to a linear programming context (optimization by Hiper Lindo program, Lindo Systems Inc. 1985). In the first step, PEDIGREE VIEWER program version 4.9 (B. Kinghorn and S. Kinghorn, University of New England, Armidale, New South Wales, Australia) was used to calculate the co-ancestry of all possible crosses, but the second step was made manually. In fact, this procedure delayed the fertilization of green eggs by 2 or 3 h in comparison with R or C1 schemes. In the last step, however, the use

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of a computer program to adapt the selection of optimal crosses could reduce the time consumed in this period.

In this study, the comparisons among mating schemes were made after selection had been carried out and on the same level of expected genetic response; therefore, the selection and mating decisions were made independently. Under these conditions, the MC mating scheme can delay the inbreeding accumulation in the short term but does not reduce it permanently because the genetic contribution of each parent remains constant between mating schemes and the effective population size is not modified. Thus, in the long term, two populations with similar effective population size but different mating scheme should reach the same inbreeding level. Nevertheless, the MC scheme can be improved (e.g., reducing inbreeding permanently) if selection and mating decisions are simultaneously made. In the context of linear programming, an objective function should be constructed to maximize the genetic response, with a restricted inbreeding rate (Sanchez et al. 1999). However, in this case, it is expected that a compromise between the genetic response and the inbreeding rate exists where looking for a low rate of inbreeding will produce a smaller genetic response (Villanueva et al. 1996).

The MC scheme, shown to be a useful tool in delaying the accumulation of inbreeding in the short term, also reduced the variance of the inbreeding, thus limiting the early expression of inbreeding depression. These results were obtained even when the tests were carried out on very small groups of possible crosses (45–1316) because of reproductive and practical limitations. Although the MC scheme was more time consuming than the two mating schemes previously used at the CMG (R mating of selected individuals and C1 mating), we recommend this scheme to carry out crosses in each generation.

Acknowledgements

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