HYBRIDIZATION AFTER SELF-FERTILIZATION: A NOVEL PERSPECTIVE FOR THE MARITIME PINE BREEDING PROGRAM

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ABSTRACT

Inbreeding depression has been studied in major forest tree species, but heterosis after inbreeding has been much less explored. We report here the results of three half-diallels 6 x 6 between unrelated S_1 parents, assessed in trial at 11-years of age. Inbreeding depression between $S_1 \times S_1$ hybrids and S_2-families ranged from 26% to 65% for vigor traits, but was not significant for straightness. For this last trait only, general combining abilities (GCA) of S_1-parents were strongly correlated with S_2-family means and GCA of S_0-grandparents. Performances of $S_1 \times S_1$ hybrids were compared with standard families: no heterosis was observed for vigor traits, but hybrids were much straighter than standards. These results are shortly discussed in reference to "sublining" breeding strategy.

Key words: *Pinus pinaster*, inbreeding depression, hybridization, heterosis, vigor straightness

INTRODUCTION

Inbreeding depression has been studied in major forest tree species such as *Pinus radiata* D. Don (WILCOX 1983), *Pinus taeda* L. (SNIEZKO & ZOBEL 1988), *Pinus sylvestris* L. (LUNDKVIST *et al.* 1987), *Pseudotsuga menziesii* Mirb. Franco, *Pinus ponderosa* Dougl. Ex. Laws. and *Abies procera* Rehd. (SORENSEN & MILES 1982), *Pinus resinosa* Ait. (FOWLER 1965), *Pinus elliottii* Engelm. (MATHESON *et al.* 1995), *Sequoia sempervirens* Endl. (LIBBY *et al.* 1981), *Eucalyptus regnans* F. Muell. (GRIFFIN & COTHERILL 1988), *Eucalyptus globulus* (HARDNER & POTTS 1995) because of its impact on breeding and selection strategies and on seed orchard production. But heterosis after inbreeding has been much less explored. In the maritime pine (*Pinus pinaster* Ait.) breeding program, inbreeding depression has been first time studied in a diallel design (JOUVE, unpublished data). Then two other mating designs were made to analyze (i) relationships between inbreeding depression and inbreeding coefficient (DUREL *et al.* 1996), and (ii) hybridization after self-fertilization to track heterosis effect. We report here the results of this second design.

MATERIAL AND METHODS

Three half-dialleles 6 × 6 between unrelated S_1-parents (individuals issued from the selfed offsprings of S_0 plus-trees) were realized in the spring of 1978. No selection was made among S_1 trees, except that they were chosen for presence of both female and male strobili. A total of 49 progenies (36 $S_1 \times S_1$ hybrids and 13 S_2-families on the diagonals) were installed in the same test as described in DUREL *et al.* (1996). Mean sizes of the families were 28 trees for $S_1 \times S_1$ hybrids and 14 trees for S_2 families. Several traits were measured in the age of 14: total height (HT), circumference at breast height (CIR), stem straightness assessed by the butt angle of the lean on the first meter (BAL), number of cones per tree (NC) and the bole volume (VOL) assessed by conic equation. Data analyses were: analysis of variance with the diallel model (GARRETSEN & KEULS 1977), computation of correlation coefficients, comparison with standard families. Indeed, progenies from the 3 half-diallels were established in a trial with 51 other families of various levels of F inbreeding coefficient (DUREL *et al.* 1996). Among them, 12 families were non-inbred (F = 0). These families, obtained from traditional crosses (*i.e.*, crosses between non-inbred parents), were used as standard families to be compared with $S_1 \times S_1$ hybrids performance. Since S_1-parents and parents of standard families derived from two different groups of plus-trees, it was necessary to estimate the mean value of the genetic base of each group of plus-trees. A polycross design of all the plus-trees was available for the comparison (same traits assessed in the age of 9).

Table 1: A – Mean values of $S_1 \times S_1$ hybrids and S_2 families with corresponding inbreeding depressions ([H–S_2]/H) for the studied traits (confidence interval at 5%); abbreviations are : HT (total height at the age of 11), CIR (circumference at breast height), VOL (bole volume), BAL (butt angle of lean), NC (number of cones per tree); B – Mean values of standard families with relative differences between hybrids and standard families ([H–St]/St) (confidence interval at 5%); C – Average general combining ability (GCA) of the grand parents (S_0) of the $S_1 \times S_1$ hybrids and of the parents of standard families, with a relative difference. Traits were assessed in a polycross test at the age of 9 years (na – not available).

	Character				
	HT	CIR	VOL	BAL	NC
A					
$S_1 \times S_1$ hybrids	772	35.7	41.0	7.7	0.72
S_2-family (S_2)	569	22.3	14.3	7.4	0.29
Inbreeding depression	26.4 ± 2.6	37.6 ± 4.7	65.0 ± 10.5	4.4 ± 9.6	59.4 ± 40.0
B					
Standard family (St)	811	37.7	47.1	9.0	0.62
Relative difference	–4.8 ± 1.5	–5.3 ± 2.8	–13.0 ± 5.4	–14.2 ± 6.1	16.1 ± 25.2
C					
Average GCA of hybrid grand-parents	590	32.27	29.2	11.5	na
Average GCA of standard family parents	593	32.32	29.9	11.7	na
Relative difference	–0.6	–0.2	–2.4	–1.5	na

RESULTS

Inbreeding Depression in S_2 by Comparison with $S_1 \times S_1$ Hybrids

Survival rate was rather high for $S_1 \times S_1$ hybrids and S_2-families: 94.6% and 82%, respectively. Phenotypic mean values of $S_1 \times S_1$ hybrids and S_2 families computed for studied traits (Table 1–A) showed that inbreeding depression was rather strong for vigor traits (HT, CIR and VOL), and ranged from 26% to 65%. It was also very important for fertility (NC). On the other hand, no significant inbreeding depression was observed for straightness (BAL, Table 1–A). These results were in a very good agreement with those reported in the previous study (DUREL *et al.* 1996).

Comparison of General Combining Abilities and S_2-family Mean Values

For each half-diallel, general combining abilities (GCA) of the S_1 parents were estimated after analysis of variance. Selfed progenies of the same parents (S_2 families) were also available. Correlation between GCA of S_1 parents and corresponding S_2 family means was very strong for straightness ($r = 0.9$, $P < 0.001$). For HT, CIR and VOL, this correlation had lower insignificant values (about 0.5). Comparisons were also made with GCA of the S_0 grand-parents assessed in the polycross test. Again, a very strong correlation was observed for BAL ($r = 0.88$, $p < 0.001$). Low to medium values of correlation (from 0.20 to 0.56, not significant) were observed for vigor traits.

Performance Comparison between $S_1 \times S_1$ Hybrids and Standard Families

Mean values of $S_1 \times S_1$ hybrids and standard families are presented in the tables 1–A and 1–B for vigor traits. The relative difference between hybrids and standards was approximately –5% for HT and CIR, but was –13% for bole volume (Table 1–B). Thus, $S_1 \times S_1$ hybrids were significantly less vigorous than standard families in this test. The relative difference between the genetic values of the two groups assessed in the polycross test could not explain such difference (Table 1–C).

Conversely, $S_1 \times S_1$ hybrids exhibited a better stem straightness than standard families (Table 1–A and 1–B), whereas a smaller value for BAL expressed a better straightness. The relative difference between the two family groups was about –14% (Table 1–B), whereas the two genetic bases were quite similar (Table 1–C). So, $S_1 \times S_1$ crosses seemed to result in a great improvement of the genetic values of the progenies for stem straightness. This favorable effect could have originated in natural selection at young age against alleles that are lethal or deleterious in the homozygous stage, but influence the root anchorage of the tree in the heterozygous state.

DISCUSSION

Inbreeding Depression in Maritime Pine

In comparison with other conifers, maritime pine seems to be less sensitive to inbreeding for vigor traits (DUREL *et al.* 1996). The values of inbreeding depression reported in this communication confirm previous result and agree with this hypothesis. A lower genetic load in *Pinus pinaster* than in other *Pinus* species could originate from the strong geographic subdivision of this species over its natural range (BARADAT & MARPEAU-BEZARD 1988; BAHRMANN *et al.* 1992, 1994; PETIT *et al.* 1995). The geographic subdivision in South-West of France before domestication, combined with stand disturbances like fires, could have produced an increase of inbreeding in natural stands as reported by BARADAT and MARPEAU-BEZARD (1988). Thus, a significant part of the genetic load could have been removed by natural selection against unfavorable and lethal alleles expressed at a recessive state.

A Novel Perspective for the Maritime Pine Breeding Program

Vigor and straightness are two main selection objectives in the maritime pine breeding program (BARADAT & PASTUSZKA 1992). HT and BAL are generally combined in an index in order to select the best individuals or families. In this test, a large variation was observed among $S_1 \times S_1$ hybrids, and several hybrids showed equivalent vigor and better stem straightness by comparison with the better standard families. Thus, multitrait selection could have resulted in higher individual index in several $S_1 \times S_1$ hybrids than in standard families.

A larger experiment should be necessary to confirm these results. Such favorable effect of inbreeding could be exploited in a sublining strategy as described by WHITE *et al.* (1993) or MCKEAND and BRIDGEWATER (1992) (see also WILLIAMS & SAVOLAINEN 1996). Indeed, specialized sublines could be created with the specific objective of the straightness improvement. Self-fertilization and selection within selfed families could be followed by within-subline hybridization and a new phase of selection. The strong additivity of straightness in the diallels and the very high correlations observed between GCA of S_0-parents, GCA of S_1-parents and S_2-family mean values should be favorable for such strategy.

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