

GENETIC PARAMETERS AND GAIN EXPECTED FROM DIRECT SELECTION FOR RESISTANCE TO *DIORYCTRIA SYLVESTRELLA* RATZ. (LEPIDOPTERA: PYRALIDAE) IN *PINUS PINASTER* AIT., USING A FULL DIALLEL MATING DESIGN

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ABSTRACT

A complete diallel progeny test of Maritime pine from the Landes provenance was carried out on 14- and 16-year-old trees (1994, 1996) for sensitivity to the stem borer (*Dioryctria sylvestrella*) and tree diameter, using a full diallel mating design. The family effect was significant and the genetic contribution of the parents almost entirely additive for both resistance and diameter. Heritability estimates for resistance in 14- and 16-year-old pine were 0.08 and 0.09 respectively. Strong differences among families for resistance was shown by a high coefficient of variation (2.32 and 1.68 for DS94 and DS96 respectively). Tree susceptibility was positively and genetically correlated with tree diameter. Expected genetic gains for tree resistance and correlative genetic loss for tree diameter growth were estimated. Age and pruning effects on tree sensitivity were included to define proper time for selecting resistant genotypes. The possibility of integrating *D. sylvestrella* resistance in the Maritime pine breeding program is discussed.

Key-words *Pinus pinaster*, *Dioryctria sylvestrella*, diallel, selection, resistance, genetic parameters

INTRODUCTION

Maritime pine, *Pinus pinaster* Ait., is the primary coniferous species in France (MERZEAU 1995) in terms of surface area (1.4 million ha) and harvest yield (5 millions m³ per year). It is also one of the most intensively managed commercial species. JACTEL *et al.* (1994, 1996a) demonstrated that forestry practices which favour tree vigour, such as fertilizing, intensive thinning and low-density planting, or tree wounding, as induced by pruning, may in turn increase the damage by *Dioryctria sylvestrella*, one of the major maritime pine pests (MENASSIEU & LEVIEUX 1990; CARISEY *et al.* 1994). A host-selection model for the stem borer has been proposed: susceptible trees would develop a primary attraction to the stem borer, mediated by some volatile attractants that originate from the constitutive oleoresin exuding from the pruning wounds or bark cracks (JACTEL *et al.* 1996a).

The high cost of intensive management and the potential value of wood yield and quality dictate that stem borer control should be of high priority. Since chemical control is impossible – the insect is hidden under the bark for more than 11 months a year –, the selection of pest-resistant trees would appear to be a promising strategy. Actually, when combined with good forest management, breeding for resistance to insects has proven to be very feasible (ZOBEL & TAL-

BERT 1984). In France, since the 1960s, Maritime pine has been selected for total height ($h^2 \sim 0.4$), stem straightness ($h^2 \sim 0.2$), wood density ($h^2 \sim 0.6$), fineness of the branches ($h^2 \sim 0.2$) and absence of forks ($h^2 \sim 0.1$) in a recurrent breeding program, which has led to the creation of improved varieties (Baradat and Pastuszka 1992). Selection for stem borer resistance has been included occasionally in this program. Only trees that have shown a high level of stem borer attack have been eliminated in mass selection.

This paper aims to examine the possibility of integrating *D. sylvestrella* resistance in the Maritime pine breeding program at the Forestry Research Station of INRA Bordeaux. The genetic parameters of resistance (*i.e.* combining ability, reciprocal effects, additive and dominance variances, heritability, and gain prediction) were estimated, using a diallel mating design, since it provided excellent estimates of combining ability, reciprocal effects and expected gains (FINS *et al.* 1992). This study also investigated the relationships, at the genetic level, between stem borer attack and tree diameter, and assessed the effect on wood production when selecting for the stem borer resistance. All parameters were estimated at two different tree ages in pruned and unpruned trees, in order to assess the effect of age and wounding on the expression of tree susceptibility and consequently to determine the appropriate age for selection.

MATERIALS AND METHODS

Plant material and measurements

Data were obtained from a Maritime pine full diallel cross (including both reciprocal and selfed crosses) between twelve parents. Twenty nine combinations were missing. The 12 parents were "plus trees" phenotypically selected for stem growth and straightness in the local provenance of the Landes de Gascogne and grafted in clonal archives.

The diallel was located in Cestas (Gironde, France) on a semi-humid podzolic soil. It was established in the autumn of 1982, with 2-year-old seedlings. Spacing was 4m between rows and 1.1m between individual trees ie 2272 trees·ha⁻¹.

The experimental design consisted of 74 incomplete randomized blocks. Each block comprised 16 plots with 2 to 4 trees. Each family was repeated 4 to 15 times.

In October 1994, 3618 trees were sampled for *D. sylvestrella* infestation and diameter at breast height (1.30m). In May 1996, one tree per plot giving a total of 1006 trees was pruned to increase tree sensitivity. The pruning consisted of the removal of two live whorls. In October 1996, all the 3618 trees were sampled again for *D. sylvestrella* infestation.

Data analysis and estimation of genetic parameters

For each plot (2 to 4 trees), the mean diameter (DBH) and the percentage of attacked trees (DS94 and DS96 in 1994 and 1996, respectively) were calculated. All plot percentage values were transformed by the arc sin square root transformation (DAGNELIE 1973) and the statistical analyses were performed on both percentage and transformed values. Only analyses based on percentage are presented as the conclusions were similar.

Analysis of variance for block and family effects was carried out with the OPEP software (BARADAT 1989; BARADAT & LABBÉ 1995) derived from 'Henderson III' model (SEARLE 1971). Data were adjusted for the block effect, prior to the decomposition of family effect (diallel analysis).

Diallel analysis

Analysis of the diallel (selfed combinations were not considered) was carried out with OPEP using the random model given by GARRETSEN & KEULS (1977). The random model is:

$$y_{ijk} = \mu + \lambda_i + \lambda_j + S_{ij} + \delta_i + \delta_j + r_{ij} + e_{ijk}$$

where $ijk = k^{\text{th}}$ replicate of the cross between the i^{th} female and j^{th} male; $S_{ij} = S_{ji}$, μ = general mean level, λ_i (λ_j) = general combining ability (GCA) of the i^{th} (j^{th}) parent, S_{ij} = specific combining ability (SCA) of the cross between the i^{th} and j^{th} parent, δ_i (δ_j) = general reciprocal effect (GRE) due to the i^{th} female (j^{th} male), r_{ij} = specific reciprocal effect (SRE) due to the cross between the i^{th} female and the j^{th} male, e_{ijk} = error term.

Variance components

Additive and dominance variances are:

$$\sigma_A^2 = 4\sigma_{AGC}^2 \quad \text{and} \quad \sigma_D^2 = 4\sigma_{ASC}^2$$

The phenotypic variance is:

$$\sigma_P^2 = \sigma^2(y_{ijk}) = 2\sigma_{GCA}^2 + \sigma_{SCA}^2 + 2\sigma_{GRE}^2 + \sigma_{SRE}^2 + \sigma_e^2$$

Genetic and environmental correlations

Genetic and environmental correlations were carried out with OPEP using a multicharacter analysis of variance and covariance.

Coefficient of genetic prediction (CGP) and relative genetic gain estimates

The coefficient of genetic prediction (CGP) (BARADAT 1976) was computed as a generalization of the heritability concept (GALLAIS 1973). CGP and relative genetic gain estimates were calculated according to the formulae given by BARADAT and DESPREZ-LOUSTAU (1997). Three different types of selection were simulated: mass selection, selection on progeny test (selection on AGC) which is currently used to create new varieties of Maritime pine and individual-family combined selection which is used to manage the breeding population.

The simulations were carried out using 50 individuals per family. Two selection intensities were used: 5% and 50% corresponding respectively to the rates used in new variety creation and in population management.

RESULTS

In 1994, 10.5% of the trees were infested. Two years later and after pruning, 16.8% of the trees were infested.

Analysis of variances indicated highly significant variation among families for both resistance and diameter (Table 1), which justifies the following genetic analyses. As the block effect was highly significant in all of the traits, data were adjusted in further calculations. Due to sampling methods, age and pruning effects could not be separated.

Table 1. Analysis of variance for the percentage of infested trees in 1994 and 1996 (DS94 and DS96) and the diameter (DBH) in the diallel cross of Maritime pine.

Source	d. f.	Mean square		
		DS94	DS96	DBH
Family (random)	114	0.058	0.081	185.38
		1.86	1.76	4.65
		<10 ⁻³	<10 ⁻³	<10 ⁻³
Block (random)	73	0.055	0.089	139.61
		1.75	1.94	3.50
		0.020	0.001	<10 ⁻³
Error	853	0.031	0.046	398.91

Table 2. Analysis of the genetic effects for the percentage of infested trees in 1994 and 1996 (DS94 and DS96) and the diameter (DBH) in the diallel cross of Maritime pine.

Effect		Traits		
		DS 94	DS 96	DBH
	Mean	10.5 %	16.8 %	12.0 cm
GCA General combining ability	F	5.64	7.20	16.55
	Prob (%)	(0.001)	(<10 ⁻³)	(<10 ⁻³)
	% of phenotypic variance	1.96	2.27	3.36
SCA Specific combining ability	F	0.62	0.58	0.45
	Prob (%)	(93.8)	(96.0)	(99.5)
	% of phenotypic variance	0	0	0
GRE General reciprocal effects	F	0.89	1.11	2.52
	Prob (%)	(55.7)	(38.2)	(2.26)
	% of phenotypic variance	0	0.11	1.52
SRE Specific reciprocal effects	F	1.85	1.65	2.10
	Prob (%)	(0.28)	(1.30)	(0.04)
	% of phenotypic variance	43.41	37.26	50.29

Genetic parameters of Maritime pine resistance to *D. sylvestrella*: relationship with diameter

The study showed a complete lack of significance of specific combining ability effects (SCA) for both tree diameter and resistance to *D. sylvestrella* (DS94 and DS96) coupled with consistent highly significant general combining ability effects (GCA) (Table 2) indicating strict additive effects for both characters. The general reciprocal effects (GRE) were only significant for DBH. The specific reciprocal effects were significant for all characters: DBH, DS94 and DS96 (Table 2). GCA and SCA variance component accounted for

less than 4% of the total phenotypic variance whilst the reciprocal components (GRE+SRE) accounted for 37.4% (DS96) and 51.8% (DBH) respectively. Reciprocal effects were included in the phenotypic variance, as components of the environmental variance, before the calculation of heritabilities and coefficient of genetic prediction.

The heritability estimate for DBH was moderate ($h^2_{st} = 0.13$) and estimates for Maritime pine resistance to *D. sylvestrella* were slightly lower: 0.08 and 0.09 for DS94 and DS96 respectively (Table 3). The CGP estimates between DBH and tree sensitivity were positive and quite low, 0.06 and 0.08 for CGP (DBH,

Table 3. Coefficients of genetic prediction *sensu stricto*. Values in the diagonal represent the heritability.

	DS94	DS96	DBH
DS94	0.08		
DS96	0.08	0.09	
DBH	0.06	0.08	0.13

Table 4. Additive (upper half) and total (lower half) genetic correlations between diameter and susceptibility to *D. sylvestrella* in the diallel cross of Maritime pine.

	DS94	DS96	DBH
DS94	1	0.95	0.55
DS96	0.95	1	0.74
DBH	0.55	0.74	1

Table 5. Environmental (upper half) and phenotypic (lower half) correlations between diameter and susceptibility to *D. sylvestrella* in the diallel cross of Maritime pine.

	DS94	DS96	DBH
DS94	1	0.85	0.31
DS96	0.86	1	0.35
DBH	0.33	0.39	1

DS94) and CGP (DBH, DS96) respectively. The values of the phenotypic coefficient of variation were respectively 2.32 and 1.68 in DS94 and DS96.

Tree sensitivity exhibits an important and positive genetic correlation with DBH (Table 4), increasing with tree age (0.55 and 0.74 for DS94 and DS96 respectively). The environmental correlations between tree resistance and DBH were moderate but positive (Table 5).

Determination of genetic gains estimates in resistance to *D. sylvestrella*. Consequences for tree diameter

Important relative genetic gains can be obtained for Maritime pine resistance to *D. sylvestrella* (Fig.1). When using a selection on progeny test (value of the progeny to select the parents) with a selection rate of 5%, which is the case in producing new varieties, the expected gains could reach 95% based on DS94 criteria. Gains would be slightly lower with DS96. However the associated loss on DBH would be close to 10%.

Using a scenario of breeding population management (individual-family combined selection with a rate of 50%), the gains in tree resistance would reach 31% or 25% based on DS94 or DS96 respectively. The genetic loss on DBH would then be close to 5%.

Because tree infestation by *D. sylvestrella* was recorded twice, the risk of selecting genotypes in families not attacked in 1994 but attacked in 1996 could be assessed. To simulate a selection strategy, families were arranged first in increasing order of infestation level in 1994 and secondly in decreasing order of mean diameter (Fig. 2). According to the new level of infestation in 1996, the number of families outside the selection interval was calculated. The risk of choosing unattacked genotypes that subsequently reveal their susceptibility is high when selecting resistant trees in 1994: respectively 22.4% and 60% of selected families would be misclassified using selection rates of 5% and 50%.

DISCUSSION

Heritability estimates

The estimate of the Maritime pine diameter heritability given in the present paper is generally consistent with those reported in *P. pinaster* at the same age by DUREL (1990) ($h^2 \approx 0.1$) and COSTA & DUREL (1996) ($h^2 \approx 0.2$), in *Pinus radiata*, by DEAN *et al.* (1983) ($h^2 \approx 0.23$), BURDON *et al.* (1983) ($h^2 \approx 0.14$) and MATHESON & RAYMOND (1984) ($h^2 \approx 0.18$), and in *Pinus elliotii*

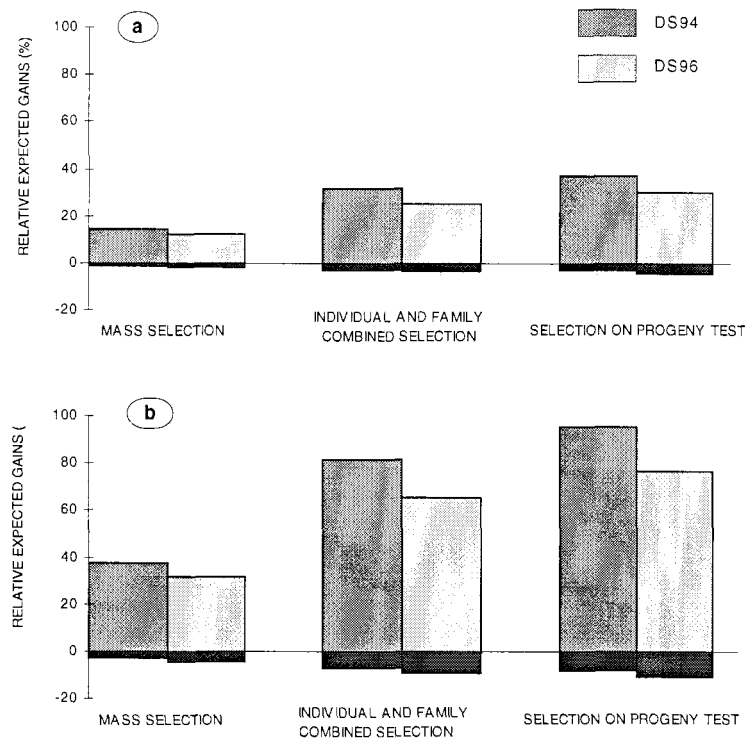


Figure 1. Genetic gain estimates (relative %) expected in Maritime pine resistance to *D. sylvestrella* and associated genetic loss in tree diameter according to the type and the date of selection using a selection rate of (a) 50% and (b) 5%.

Engelm. by DIETERS (1996) ($h^2 \approx 0.2$). The low heritability of diameter may be due to environmental effects, competition effects and location of resources (LEMOINE 1980; VON EULER *et al.* 1992). For Maritime pine resistance to *D. sylvestrella*, heritabilities were slightly lower than for diameter ($h^2 \approx 0.09$). In a previous study based on a Maritime pine progeny test (factorial design) of 11- and 12-year-old trees, heritability estimates of the resistance ranged from 0.07 to 0.09 (SUERON 1982). BARADAT & DESPREZ-LOUSTAU (1997) found a heritability estimate of 0.06 for 3-year-old Maritime pine resistance to twisting rust (*Melampsora pinitorqua*) on the same diallel mating design than studied here. The heritability estimates of tree resistance to insects or pathogens are usually low to moderate. Individual-tree heritability for Sitka spruce resistance to the white pine weevil was ~ 0.40 (KING *et al.* 1997) and CILAS *et al.* (1995) estimated the heritability of *Theobroma cacao* L. resistance to *Phytophthora sp.* to be 0.13 in a diallel mating design.

In our study, diameter at breast height and Maritime pine resistance to *D. sylvestrella* at the 14- and 16-year-old stage presented highly significant GCA effects associated with an absence of SCA effects, indicating that the genetic variance for these characters is almost entirely additive. The low value of heritability estimates

for the resistance could be partly explained by the presence of reciprocal effects which contributed up to 37.4% of the phenotypic variance. General reciprocal effects were low with significance only for diameter indicating the absence of maternal effects in the transmission of Maritime pine resistance to *D. sylvestrella*. Specific reciprocal effects for the three characters were highly significant. Their presence should be solved before the integration of the resistance to *D. sylvestrella* in the Maritime pine breeding programme. No obvious explanation of such effects was readily apparent. They might result from environmental effects although no method of adjustment allowed for the elimination of these effects. SAMUEL (1991) found the same genetic effects for diameter of 15-year-old Sitka spruce (*Picea sitchensis* [Bong.] Carr.) in a diallel cross: presence of GCA effects, absence of SCA effects, presence of reciprocal effects but these last effects accounted for a smaller proportion of the total variance.

The heritability of resistance increased slightly with the age of trees. According to the model of tree infestation given by JACTEL *et al.* (1996a), pine attractiveness could be enhanced by factors which increase the resin flow. In our study, tree pruning (JACTEL *et al.* 1994) and two years growth – which involves bark cracking- (JACTEL *et al.* 1996a) may have resulted in a higher

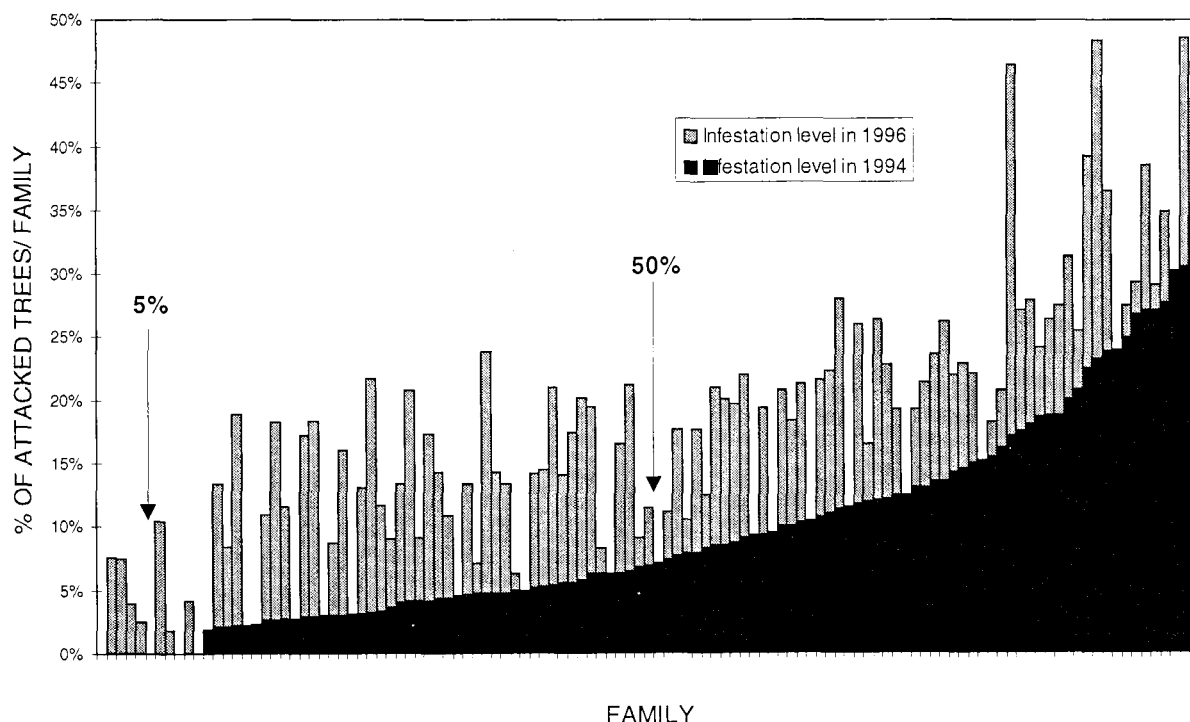


Figure 2. Comparison of the infestation level by *Dioryctria sylvestrella* in 115 Maritime pine families at two different tree ages (14- and 16-year-old trees). Families were arranged in increasing order of infestation at 14 years and in decreasing order of mean diameter. 5% and 50% correspond to the two selection levels used to simulate a selection strategy. DS94: Percent of attacked trees at 14 years; DS96: Percent of attacked trees at 16 years.

expression of the tree sensitivity.

Relationships between tree diameter and sensitivity to *D. sylvestrella*

The genetic correlations between tree diameter and sensitivity to *D. sylvestrella*, were large and positive indicating that faster growing families have a lower level of genetic resistance. The correlation level increased with the age of the tree, indicating that the role of diameter in host selection increases with age. A genetic correlation may have three causes: pleiotropy, linkage (that a genetic mapping is about to assess), and statistical association without genetic significance. Pleiotropy would be consistent with the host selection model proposed by JACTEL *et al.* (1994): radial growth and consequently bark cracking and tree attractiveness would depend on the same group of genes. This case (and to a lesser extent linkage) is unfavorable for breeding, as the selection for global tree resistance to *D. sylvestrella* would systematically and negatively affect wood production. Statistical association could also be the cause of the genetic correlation, in a population originating from twelve plus tree parents only: genes controlling tree sensitivity and radial growth may have been associated at random in those parents.

However, plus trees are not related, and were initially selected on stem form and volume, excluding severely attacked trees (ILLY 1966). Thus a random association between low resistance and good growth was not favoured.

Environmental correlations between tree susceptibility to *D. sylvestrella* and tree diameter were positive and moderate, suggesting that environmental effects on the expression of the genes controlling these traits were similar. Environmental conditions are considered to largely affect the diameter growth. According to the host selection model given by JACTEL *et al.* (1994), tree vigor favors tree susceptibility to *D. sylvestrella*. Then, environmental conditions which affect tree vigor, might indirectly affect tree susceptibility in the same direction.

Expected gains

In spite of low heritabilities, high relative expected genetic gains could be obtained when selecting for resistance to *D. sylvestrella*, due to large phenotypic coefficients of variation. High gains were also found by BARADAT & DESPREZ-LOUSTAU (1997) for Maritime pine resistance to twisting rust on the same diallel progeny test. The mean expected gain was equal to 36%

for a varietal creation (selection on progeny test at a 5% rate) and to 12% for breeding population management (combined selection at a 50% rate). Associated genetic loss in tree height at 5 years was estimated between 4% to 11%, but was inconsistent with other results (positive genetic correlation between juvenile height and twisting rust resistance). Furthermore, juvenile height has a weak predictive value for adult volume. Thus, BARADAT & DESPREZ-LOUSTAU (1997) suggested including the resistance to twisting rust in the management of the Maritime pine breeding population without any increase in the program cost. In our study, a direct selection for resistance would induce an associated loss in tree diameter up to 10%, which represents a 20% decrease in volume at constant height, at an age where volume is a good predictor of adult growth (KREMER 1992). If such a direct selection of a resistant-specific variety can not realistically be integrated into the Maritime pine breeding program, it indicates the necessity to take into account this criteria in the usual selection, to avoid an increased tree sensitivity to *D. sylvestrella* in breeding population or varieties selected for stem volume. *D. sylvestrella* resistance could then be integrated into the usual selection index, with the coefficient fixed so as to obtain an optimum compromise between genetic gains on all characters.

Time of selection

The expected gain on tree resistance is better for DS94 than for DS96, in spite of a slightly higher heritability estimate for DS96. This difference is due to a lower phenotypic coefficient of variation of DS96, resulting from the effect of age and pruning on tree attractiveness, which increases the mean and decreases the standard deviation of the percent of attacked trees. But the error rate made in selection if genotypes were chosen in the families with the higher diameter and the lower infestation level in 1994 instead of their infestation level in 1996 would have been very high (22 to 60% for selection rates of 50 and 5% respectively). It would therefore appear advantageous to delay the date of selection, in order to wait for a more optimal expression of tree susceptibility to *D. sylvestrella* or to prune the tree in order to accelerate this process.

CONCLUSIONS

The expected genetic gain for Maritime pine resistance to *D. sylvestrella* indicate that quite marked improvements can be made for this trait. Some further experiments are required to refine the estimation of the resistance heritability and its coefficient of genetic prediction with the diameter. According to the lack of

SCA (*i.e.* entirely additive genetic contribution of the parents), the acquisition of new results would appear to be easy to obtain in the progeny test. The main limit of a direct selection would be the negative effects on volume and the time of selection. Because the expression of tree susceptibility depends on the natural infestation and increase with age, breeders would have to delay selection after 15 years to decrease the error made in genotype choice. Pruning trees may represent an effective way to speed up this process. Because tree resistance to *D. sylvestrella* and radial growth are negatively correlated, indirect selection using traits unrelated to stem volume should be investigated. JACTEL *et al.* (1996b) related Maritime pine sensitivity to *D. sylvestrella* to the proportion of some monoterpenes in the wood resin. Since the oleoresin composition was stable in time and space within the same tree and variable between pine trees (JACTEL *et al.* 1996b), these compounds may yield suitable markers in an indirect selection program for *D. sylvestrella* resistance in Maritime pine, provided that the heritability of the terpene profile in the wood resin can be demonstrated. It would present the advantage to decrease notably the age of selection from 15 years to 7 or 8 years since terpene composition in the oleoresin is stable at this age.

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