

**A NON-PARAMETRIC DATA ANALYSIS FOR STUDYING GENOTYPE  
× ENVIRONMENT INTERACTION EFFECTS IN MARITIME PINE  
(*PINUS PINASTER* AIT.)**

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**ABSTRACT**

A set of 10 provenances of maritime pine (*Pinus pinaster* Ait.) and their 45 inter-provenance hybrids were compared at two contrasting experimental sites in the French Atlantic and Mediterranean regions. A non-parametric method is adapted to assess genotype × environment interaction effects and interactivity of provenances and inter-provenance hybrids. The method derives from rank comparisons in the two trials. Four traits were studied: height growth at ages 8 and 13 years, stem straightness deviation and coefficient of form. Results showed that GE interaction effects were more important in provenances than in their hybrids for 8-year height but not for 13-year height. Provenances and hybrids interacted strongly with site for the coefficient of form. However, an environmental artifact may influence this trait due to its nature being a squared-ratio of diameters (diameters are strongly affected by environmental factors as competition).

**Keywords:** *Pinus pinaster*, provenances, inter-provenance hybrids, G × E interaction, Relative interactivity index, non parametric analysis.

**INTRODUCTION**

Genotype × environment (GE) interaction is well known by geneticists and breeders but its rigorous evaluation began only when analysis of variance was developed (see review by FREEMAN 1973). It was seen as a departure from the additive model of the two main factors, genotype and environment. The obvious consequence is that the genotype and environment effects cannot be separated from each other without appropriate experimental designs and fitted models. Any genotype has an environmental optimum for expressing itself through a particular phenotype. This optimum can differ among genotypes as it was shown when varieties were compared over a range of environments (WRICKE 1962; FINLAY & WILKINSON 1963; EBERHART & RUSSEL 1966). This can make it difficult to find genotypes with good general performance over all sites, and limits the scope of the breeding program because it is no longer possible to develop a breeding strategy with a single breeding population, unless one consents to lose yield. Genotype × environment interaction results in an upward bias in estimating genetic gains when genotypes are compared only in one location (COMSTOCK & MOLL 1963; LINDGREN 1984).

In forest trees, the problem of GE interaction is acute because the improved populations must often face harsh and fluctuating environments which are not readily manipulated. Therefore, forest tree breeders tends to be more cautious in using any one population over wide areas (WRIGHT 1976; NAMKOONG & KANG 1989). Hence, testing genotypes over a representative sample of environments covering the area of interest is a necessity. The option for a wide or a regional breeding program will be taken following the results from the field tests. With forest species, GE interaction has more frequently been studied at the provenance level (MORGENSTERN & TEICH 1969; MERGEN *et al.* 1974; BROWN *et al.* 1976; PEDERICK 1990; GRIFFIN *et al.* 1982; TEISSIER DU CROS & LÉPOUTRE 1983; MATHESON & RAYMOND 1984; KUNDU *et al.*, 1998) but have been extended afterwards to families (OWINO 1977; OWINO & ZOBEL 1977; JOHNSTONE & SAMUEL 1978; SKRØPPA 1984; GOVINDARAJU & DANCİK 1987; CARSON 1991) and clones (FARMER 1968; SHELBOURNE 1972; HÜHN *et al.* 1987; BENTZER *et al.* 1988; KARLSSON & HÖGBERG 1998). Genotype × environment interaction effects have also been investigated at the species level (GIANNINI *et al.* 1977; ILLINGWORTH 1978; BARNES *et al.* 1984; MULLIN & QUAYLE 1984).

Most available methods (*e.g.*, ecovariance, linear joint regression) have been developed for crops and aim to characterize genotypes rather than environments (WRICKE 1962, FINLAY & WILKINSON 1963; EBERHART & RUSSEL 1966; FREEMAN 1973). BURDON (1977, 1991) developed an alternative method for forest trees, using genetic correlation, which emphasizes the rôle of environments in generating interactions. Indeed, conversely to crops where cultural conditions can be generally readily manipulated, forest trees are growing in nearly natural environments and these need to be better characterized for make safe breeding strategies.

The present work was carried out to study GE interaction for growth and form traits at varying ages in a set of maritime pine (*Pinus pinaster* Ait.) provenances and their crosses. Maritime pine occupies a discontinuous range in the western part of the Mediterranean basin and in the adjacent European Atlantic coast and colonizes diverse ecological conditions, which is associated with a high differentiation of the species (HARFOUCHE *et al.* 1995a, HARFOUCHE & KREMER 2000a). Provenances and/or provenance hybrids are expected to behave differently relative to each other among sites, and the breeding program must take into account GE interaction effects if evident. Our experiment comprises two trials located in contrasting environments (Mediterranean versus Atlantic zones). The low number of sites limits the choice among the available methods and drastically reduce the degrees of freedom for the GE interaction component of variance in ANOVA; moreover the Mediterranean site, which contrasts highly with the Atlantic one, have known problems (pest attack and mortality) and assumptions of normality of error and homogeneity of error variance were violated even when data were transformed. Consequently, a non-parametric method based on the concepts of *concordance – discordance* between two rank distributions (KENDALL 1955) is used for studying GE interaction and stability of genotypes. The method I will develop in this paper is basically different from an existing non-parametric method for studying GE interaction due to HÜHN and NASSAR (NASSAR & HÜHN 1987; HÜHN & NASSAR 1989; HUEHN, 1990a, 1990b), which method is not applicable to an experiment with two sites.

## MATERIAL AND METHODS

### Material

A set of 31 genetic entries (eight provenances and 23 provenance-hybrid combinations) was the base material for the study. The sample is a part of provenance

selection and inter-provenance hybridization programs in maritime pine in France:

**a. Provenances.** Ten range-wide distributed provenances were sampled and represented by seedlots either produced by controlled pollination in a provenance trial located in the Landes region or collected from natural stands.

**b. Provenance hybrids.** These ten provenances were crossed following a complete diallel mating scheme. The description of the mating scheme is given elsewhere (HARFOUCHE *et al.*, 1995b). Because some crosses failed and/or insufficient seeds were available in amount only eight of the parental provenances and 23 of the 45 possible hybrid combinations were common to the two experimental plantations, *i.e.*, 31 entries as a total.

### Field trials

The experiment is composed of two contrasting sites located in the Mediterranean (site 1) and Atlantic (site 2) parts of the maritime pine range in France. Site 1 is characterized by a severe summer drought, whereas in site 2 no major limiting environmental factors exist. The field design was the same in the two locations, completely randomized incomplete blocks with four-tree row plots and 4 × 1.2 m spacing. The number of replications per entry varied from 3 to 18. At site 2, all the provenances and their 45 crosses were present, whereas only eight provenances and 23 crosses were planted at Site 1. Survival was lower at Site 1 than at Site 2 and an infestation by a coccid pest (*Matsucoccus feytaudi* Duc.) was observed at site 1. The material was outplanted in the fall of 1981 after one year in the nursery.

### Measurements

The measurements reported here were made at the two sites in 1988 and 1993, *i.e.*, at ages 8 and 13 from seed. In 1988, total height (*H8*) and stem straightness deviation from vertical (*SSD*) were measured. In 1993, the total height (*H13*) was measured again in addition to the diameter at breast height ( $d_{1.3}$ ) and at mid-height ( $d_{1/2}$ ) for assessing the coefficient of form (*f*) as  $(d_{1/2} / d_{1.3})^2$ . Damaged trees and those growing abnormally were omitted for the analyses.

### Analysis

The data used in this work were analyzed, separately for each site, in previous studies (HARFOUCHE *et al.* 1995a, 1995b; HARFOUCHE & KREMER 2000a) using analyses of variance to provide estimates for prove-

nance and provenance hybrid performances, general and specific combining abilities. Before final analysis, data were adjusted for the block effects because of the non-orthogonality of the field designs, and *SSD* was transformed using square-root transformation to improve the normality of the distributions and homogenize the variance of the error term.

### Procedure for GE interaction analysis

At the outset, a two-way (genotype and site) analysis of variance was carried out to explore the significance of the main effects and their interaction. The *F*-tests of the interaction (GS) were significant for all the studied characters, but ANOVA assumptions were violated (non-normality of error and non-homogeneity of error variance) and data highly unbalanced; moreover, the degrees of freedom of the interaction component was reduced due to the small number of sites. Hence, only little confidence should be accorded to these results.

As a result, a non-parametric procedure is developed based on the concepts of *concordance-discordance* between two series of ranks (KENDALL 1955), one of them being in descending order of performance; the ordered series was that of site 1 owing to its poor growth relative to site 2. The estimates (provenance and provenance hybrid performances, GCA and SCA) are then ranked for each site. GE interaction effect was tested using the *coefficient of concordance* of KENDALL (KENDALL 1955; SNEDECOR & COCHRAN 1957; KENDALL & PLACKETT 1969; PEARSON & KENDALL 1969; DROESBEKE 1988). To our knowledge, this non-parametric statistical approach has never been used for studying GE interaction. Let  $R_i(x)$  and  $R_i(y)$  be the ranks of the entry  $i$  at site 1 ( $x$ ) and at site 2 ( $y$ ), respectively, and consider the bivariate series  $\{(R_i(x), R_i(y)); i = 1, 2, \dots, n\}$ . The coefficient of concordance of KENDALL is built upon the idea of *concordant* and *discordant* pairs of entries. Let us consider a given pair of entries  $(i, j; i \neq j)$  with ranks  $R_i(x)$  and  $R_j(x)$  for  $i$  and  $R_i(y)$  and  $R_j(y)$  for  $j$ . There is *concordance* ( $c_i$ ) if  $R_i(x) < R_j(x)$  and  $R_i(y) < R_j(y)$  or if  $R_i(x) > R_j(x)$  and  $R_i(y) > R_j(y)$ ; *discordance* ( $d_i$ ) if  $R_i(x) < R_j(x)$  and  $R_i(y) > R_j(y)$  or if  $R_i(x) > R_j(x)$  and  $R_i(y) < R_j(y)$ . Stated in other words, there is *concordance* when  $i$  is better (wonger) than  $j$  in the 2 sites, and *discordance* when  $i$  is better (wonger) in one site and wonger (better) in the other. In the first situation, there is no rank change of  $i$  relatively to  $j$  from a site to another, in the second, such a rank change occurs.

If we note  $C(x,y) = \sum c_i$ , the total number of concordant pairs, and  $D(x,y) = \sum d_i$ , the total number of the discordant ones among the  $n(n-1)/2$  pairwise combina-

tions in twos of the  $n$  entries, the *coefficient of concordance* of KENDALL is expressed as:

$$\tau = \frac{C(x,y) - D(x,y)}{n(n-1)/2} \quad [1]$$

For our calculations, a second formulation of  $\tau$  was used and expressed as follows:

$$\tau = 1 - \frac{2D(x,y)}{n(n-1)/2} \quad [2]$$

which is derived from the former expression (Appendix 1).

**Hypothesis** testing GE interaction effects was formalized as below:

$H_0$ : the two rank series are concordant, *i.e.*, no GE interaction, against

$H_1$ : the two rank series are discordant, *i.e.*, GE interaction is significant.

The **rule of decision** (unilateral test) is,  $R$  for rejection and  $\bar{R}$  for acceptance (non-rejection),

$$RH_0 \text{ if } \tau < \tau_{n, 1-\alpha}$$

$$RH_0 \text{ if } \tau \geq \tau_{n, 1}$$

The calculated  $\tau$  is compared to the tabulated KENDALL's coefficient of concordance for  $n$  pairs of observations and at a given probability  $1 - \alpha$  ( $\alpha = 0.05, 0.01$  or  $0.001$ ) (KENDALL 1955; DROESBEKE 1988).

This rule of decision conveys the intuitive reasoning that  $H_0$  is rejected if the calculated  $\tau$  is smaller than the tabulated  $\tau$  at a given level of probability  $p = 1 - \alpha$ .

### Procedure for genotype interactivity assessment

Genotypic interactivity is investigated only if GE interaction effects were significant, *i.e.*, after the rejection of the null hypothesis ( $RH_0$ ). At first, let us develop some new concepts before demonstrating the method of assessment.

(i) *Left-; right- and net discordance*. The *net discordance* arises from the idea of *left- and right-discordances* (the latter corresponding to the discordance of KENDALL (1955)) relatively to a given genotype  $i$ .  $R_i(x)$  and  $R_i(y)$  are arranged in a table with the first series fixed in increasing order (Appendix 2). The *left-discordance* for a given genotype  $i$  is obtained by counting, in the second series  $R_i(y)$ , the observations at the *left* of  $i$  which have an *inferior* rank, *i.e.*, a superior cardinal number (*e.g.*, 5 is an inferior rank compared to 3, and is left-discordant relative to 3 when placed at its left).

The *right-discordance* is obtained by enumerating the observations at the *right* of  $i$  with a *superior* rank, *i.e.*, with an inferior cardinal number (*e.g.*, 2 placed at the right of 3 is right-discordant relative to it). The *left-discordance* is composed of genotypes that have been outperformed by  $i$  at the second site and the *right-discordance* of genotypes that have outperformed  $i$  at the same site. Let  $d_{i(x,y)}^-$ , the *left-discordance* and  $d_{i(x,y)}^+$ , the *right-discordance*, the *net discordance* of  $i$  is defined as

$$\Delta i_{(x,y)} = \left| d_{i(x,y)}^+ - d_{i(x,y)}^- \right| \quad [3]$$

The signs (+) and (-) as exponents have no algebraic meaning; this is only a conventional writing made to distinct the two opposite concepts.

(ii) *Gross, apparent and cryptic discordance.* Each genotype may have left and right discordance; the resultant is the *gross individual discordance*  $\delta i_{(x,y)}$ ,

$$\delta i_{(x,y)} = d_{i(x,y)}^+ + d_{i(x,y)}^- \quad [4]$$

$\delta i_{(x,y)}$  can be partitioned into *two components*, the *individual net (or apparent) discordance*  $\Delta i_{(x,y)}$ , defined above, and the *individual cryptic discordance*  $\partial i_{(x,y)}$ ,

$$\delta i_{(x,y)} = \Delta i_{(x,y)} + \partial i_{(x,y)}$$

Thus,

$$d_{i(x,y)}^+ + d_{i(x,y)}^- = \Delta i_{(x,y)} + \partial i_{(x,y)}$$

and,

$$\partial i_{(x,y)} = d_{i(x,y)}^+ + d_{i(x,y)}^- - \Delta i_{(x,y)} \quad [5]$$

$\partial i_{(x,y)}$  is the portion of  $\delta i_{(x,y)}$  which has no role in  $i$ 's interactivity (Causes no rank changes), whereas  $\Delta i_{(x,y)}$  is the part of  $\delta i_{(x,y)}$  which is  $i$ 's interactivity (Causes rank changes).

At the whole level, we compute

$$D_f(x,y) = \sum_{i=1}^n \delta i_{(x,y)} = \sum_{i=1}^n d_{i(x,y)}^+ + \sum_{i=1}^n d_{i(x,y)}^- = 2D(x,y)$$

$$\text{for } \sum_{i=1}^n d_{i(x,y)}^+ = \sum_{i=1}^n d_{i(x,y)}^-$$

where  $D(x,y)$  is the discordance used in the formula of KENDALL.

The *total gross discordance*  $DT(x,y)$  can also be decomposed into two components, the *total apparent discordance*  $DA(x,y)$  and the *total cryptic discordance*  $DC(x,y)$ . Then,

$$DT(x,y) = DA(x,y) + DC(x,y) \quad [6]$$

With

$$DA(x,y) = \sum_{i=1}^n \Delta i_{(x,y)} \quad [7]$$

and

$$DC(x,y) = \sum_{i=1}^n \partial i_{(x,y)} = \sum_{i=1}^n (d_{i(x,y)}^+ + d_{i(x,y)}^- - \Delta i_{(x,y)})$$

(iii) Having defined these concepts, I have developed a method based on testing the significance of the *partial coefficient of concordance*  $\tau(n-i)$ , after removing the net discordance  $\Delta i_{(x,y)}$  due to the genotype  $i$  from the total gross discordance  $DT$

$$\tau(n-1) = 1 - \frac{DT(x,y) - \Delta i_{(x,y)}}{n(n-1)/2} \quad [8]$$

Hypotheses to test for the significance of  $\tau(n-i)$  are, **H0**: the effect of  $i$  is not significant, against **H1**: the effect of  $i$  is significant, the **rule of decision** is,

$$\begin{aligned} \text{RH0} & \quad \text{if } \tau(n-1) > \tau_{n, 1-\alpha} \\ \text{RH1} & \quad \text{if } \tau(n-1) \leq \tau_{n, 1-\alpha} \end{aligned}$$

If the effect of  $i$  was significant, the coefficient of concordance would become more important and statistically significant after removing this effect (*i.e.*, globally no GE interaction without  $i$ ).

The *relative interactivity* of  $i$  ( $RI(i)$ ) may be estimated by

$$RI(i) = \frac{\tau(n-i) - \tau(n)}{\tau(n-i_{total}) - \tau(n)} * 100 = \frac{\Delta i_{(x,y)}}{DA(x,y)} * 100 \quad [9]$$

where,  $\tau(n)$  is the total coefficient of concordance, and  $\tau(n-i_{total})$ , is the *partial coefficient of concordance* after removing the total apparent discordance  $DA(x,y)$ .

This formulation of  $RI(i)$  was found by developing the ratio  $[\tau(n-i) / \tau(n-i_{total})]$ .

Indeed,

$$\tau(n-i) = 1 - \frac{DT(x,y) - \Delta i(x,y)}{n(n-1)/2} = 1 - \left( \frac{DT(x,y)}{n(n-1)/2} - \frac{\Delta i(x,y)}{n(n-1)/2} \right)$$

$$1 - \frac{DT(x,y)}{n(n-1)/2} + \frac{\Delta i(x,y)}{n(n-1)/2} = \tau(n) + \frac{\Delta i(x,y)}{n(n-1)/2}$$

then,

$$\tau(n-i) - \tau(n) = \frac{\Delta i(x,y)}{n(n-1)/2}$$

and, for  $\tau(n-i_{total})$ ,

$$\tau(n-i_{total})$$

$$= 1 - \frac{(DT(x,y) - DA(x,y))}{n(n-1)/2} = 1 - \left( \frac{DT(x,y)}{n(n-1)/2} - \frac{DA(x,y)}{n(n-1)/2} \right)$$

$$= 1 - \frac{DT(x,y)}{n(n-1)/2} + \frac{DA(x,y)}{n(n-1)/2} = \tau(n) + \frac{DA(x,y)}{n(n-1)/2}$$

finally,  $\tau_{(n-total)} - \tau(n) = \frac{DA(x,y)}{n(n-1)/2}$ .

RI(i) has the following properties:

a) RI(i) is statistically significant if  $\tau(n-1)$  is significant, and vice versa;

b) Mathematically, RI(i) accounts for the net discordance explained by a given genetic entry and, theoretically, is:

$$0 \leq RI(i) \leq 100$$

$$\sum RI(i) = 100$$

c) Biologically, this index may be used as a parameter for assessing the genotypic stability.

*Remarks:* An entry with the same ranking at the two sites also contribute to the total gross discordance  $DT(x,y)$ , unless it is ranked first or last. In fact, changes in the second site could be attributed either to  $i$  or to the entries that have moved relatively to it. This is an aspect of cryptic discordance. On the other hand, the values of  $RI(i)$  equal or close to 100 have an inherently low probability of occurrence, because the event  $\Delta i(x,y) = DA(x,y)$  is rare, and when it occurs, the total coefficient of concordance is generally statistically significant, and the GE interaction is non-significant.

A numerical application of the procedure is given in Appendix 2.

## RESULTS

### GE interaction in the mixture of genotypes (provenances and their hybrids combined)

The rankings are made on the provenance and provenance-hybrid performances overall. The values of the coefficient of concordance of KENDALL [2] are given in column (1) of Table 1. These coefficients are significant for 8-year height ( $H8$ ) ( $\tau = 0.377^{**}$ ), 13-year height ( $H13$ ) ( $\tau = 0.612^{**}$ ), and stem straightness deviation to verticality ( $SSD$ ) ( $\tau = 0.505^{**}$ ), suggesting that genotype  $\times$  environment interaction may not be important for these traits when provenances and hybrids are pooled in a single population, *i.e.*, in a population with a composite structure. In contrast, ranks seem to be varying from one site to another for the coefficient of form ( $f$ ) since KENDALL's coefficient of concordance is particularly low for this trait ( $\tau = 0.192^{NS}$ ), suggesting a significant GE interaction.

### GE interaction in provenances

*Provenance performances (per se values).* Results are presented in column (2) of Table 1. There is evidence of GE interaction for total height at 8 ( $H8$ ), and the coefficient of form ( $f$ ) but not for total height at 13 years ( $H13$ ) and stem straightness deviation ( $SSD$ ) as shown by KENDALL's coefficient of concordance values. These values are particularly low for  $H8$  and  $f$  ( $\tau = 0.214^{NS}$  and  $\tau = 0.286^{NS}$ , respectively).

*GCA values.* Concordance among GCA ranks from site to site are high for stem straightness deviation ( $\tau = 0.866^{**}$ ) and 13-year height ( $\tau = 0.555^{**}$ ), whereas they are low for 8-year height ( $\tau = 0.244^{NS}$ ) and coefficient of form ( $\tau = 0.066^{NS}$ ) as shown in Table 1. Therefore, significant changes in ranking occurs for  $H8$  and  $f$  but not for  $SSD$  and  $H13$ .

### GE interaction in hybrids

*Performances.* The provenance hybrid  $\times$  site interaction in terms of changing ranks are unimportant for  $H8$ ,  $H13$  and  $SSD$  as suggested by the significant values of KENDALL's coefficient of concordance ( $\tau = 0.368^{**}$ ,  $0.589^{**}$  and  $0.518^{**}$ , respectively) (Table 1, column (3)). On the other hand, the correlation is not significant for  $f$  ( $\tau = 0.178^{NS}$ ), and there is GE interaction only for this trait.

*SCA values.* According to KENDALL's coefficient of concordance values (Table 1), SCA effects would be particularly sensitive to changing environment for  $f$  ( $\tau = -0.012$ ) and  $SSD$  ( $\tau = 0.170^{NS}$ ). This is not the case for  $H8$  and  $H13$  ( $\tau = 0.256^*$  and  $\tau = 0.320^*$ , respectively).

### Genotypic interactivity

Interactivity assessments using the *relative interactivity index*  $RI(i)$  [9] are made for significant cases of GE interaction evidenced by KENDALL's coefficient of concordance computations.

**Interactivity of provenances.** Provenance values of the index (Table 2) show that Porto-Vecchio (POV), a Mediterranean provenance from South Corsica, and Vivario (VIV), a Mediterranean provenance from North Corsica, both are distinct from the others. Judged by their  $RI(i)$  (27.78% and 22.22%, respectively), these two provenances are the more interactive, although their individual effects are not statistically significant, *i.e.*, the coefficient of concordance remains non-significant even if their respective effects are removed [8]. Conversely, provenances Tamjout (TAM), a North African<sup>2</sup> provenance from Morocco, and Esterel (EST), a Mediterranean provenance from southeastern France, both exhibit high levels of stability between the two sites ( $RI(i) = 0$ ). For the coefficient of form ( $f$ ), Corsican provenances are also unstable ( $RI(i) = 22.22\%$ , statistically significant). On the other hand, Cazorla (CAZ), a Mediterranean provenance from southern Spain and Esterel (EST) are among the most stable ( $RI(i) = 0\%$  and  $5.55\%$ , respectively).

**GCA values.** For H8, as well as for  $f$ , the behaviour of the parental provenances differed from that observed for the *per se* values. Here, the highest values of  $RI(i)$  for H8 are obtained for Navaleno (NAV), an Atlantic<sup>3</sup> provenance from Spain, and Genoa (GEN), a Mediterranean provenance from Italy, whereas Corsican provenances, POV and VIV (the more unstable for *per se* values), record average values. Provenances from Esterel, Leiria (LEI), an Atlantic provenance from Portugal, and above all Tabarka (TAB), a North African provenance from Tunisia, show a good stability in GCA for H8. For  $f$ , the North African provenances (Tabarka and Tamjout) are the more unstable ( $RI(i) = 34.61\%$  and  $26.92\%$ , respectively) in contrast to the provenances Navaleno, Esterel and Leiria, which display low interaction indices ( $RI(i) = 0$ ).

### Interactivity of provenance hybrids (Table 3)

**Hybrid performances.** Hybrids showed important GE interaction only for the coefficient of form ( $f$ ) as it was reported previously. A set of five hybrids (out of a total of 23) caused the most part of the effect and four of them had Tamjout (TAM) or Tabarka (TAB) as one parent. On the other hand, hybrids with Landes (LAN), an Atlantic provenance from southwestern France, or Navaleno (NAV) as one parent are on average among the more stable.

**SCA values.** For SSD,  $GEN \times LAN$  is the most unstable with  $RI(i) = 11.80\%$  (statistically non signifi-

cant). For  $f$ ,  $LEI \times LAN$  seems to be unstable ( $RI(i) = 10.30\%$ , statistically non significant) and seven hybrids explained more than 55 % of the total apparent discordance [7], six of them having Tamjout (TAM) or Leiria (LEI) as one parent. In contrast, Navaleno (NAV) is frequently involved in stable combinations.

## DISCUSSION

### Limitations of the study and their consequences

As reported in the INTRODUCTION, the Mediterranean site (Site 1) has known problems (Pest attack) resulting in high level of mortality for certain (3 or 4) genotypes (Provenances and provenance-hybrid combinations); as a result, mean estimates for these genotypes were not as precise as for the others. In addition, assumptions of normality and variance homogeneity of within-genotype error were frequently infringed, even with variable transformation. Hence, results from a two-way model (Genotype, environment) of analysis of variance were regarded with caution. Though, it is now largely admitted that  $F$  statistics is robust against such violations (Non-normality and heteroscedasticity) and calculation programs exist for dealing with data more or less problematic, one may consider cautiously issues from such data. Moreover, in analysis of variance, interactions are global and comprises both scalar (constant coefficients of variation) and non-scalar (inconstant coefficients of variation) variance differences as well as ranking changes (BURDON 1977; BURDON *et al.* 1992; KREMER 1986); and if non-scalar effects or outliers exist  $F$  statistics would be biased even if data are transformed. On the other hand, a few methods of analysing GE interaction are available to deal with such experiments with only two sites (Too small number of degrees of freedom). Hence, the analysis of variance approach is completed with this non parametric method in order to overcome or minimize those problems. This method which is based on ranks is considered to address well our needs as breeders. As the two sites are not a random sample of the all possible sites in the maritime pine range, the results presented here are valid for the two concerned regions. The sample of provenances and provenance hybrids in this study is not well-balanced because the test was intended to estimate combining abilities and heterosis as well as combinations of economic attributes in provenance hybrids. For strict comparison of concordance coefficient values, the numbers of pairs must be constant. In this study, these numbers were eight (8) for pure provenance performances, ten (10) for GCA values and 23 for provenance-hybrid performances. On the other hand, estimates (*Per se* values, GCAs and

SCAs) are not performed with the same level of precision. In particular, SCA estimates are based on a smaller number of observations than GCA estimates; so, SCAs may not be as precise as GCAs. Therefore, comparisons of KENDALL's coefficients of concordance between the different types of populations and estimates may or not be highly meaningful.

### GE interaction and population structure

The present study dealt with two different population structures: within-provenance crosses or pure provenances based on within-provenance crosses and wide crosses, *i.e.*, interprovenance crosses. We first considered the two populations combined, and then separately. This approach might relate to alternative or complementary strategies in breeding and reforestation: first, a strategy using provenances and hybrids simultaneously, second, a strategy based on provenance selection, third, a strategy based on interprovenance crosses.

KENDALL's coefficient of concordance calculations on genotype performances, *i.e.*, on provenance mean values and on provenance hybrid performances, have shown the two types of population expressed relatively different responses for height growth. Indeed, the latter category displays no interaction for height either at age 8 or age 13 whereas the former exhibited such effects at age 8 only. Thus, in maritime pine, provenances or local crosses may be more sensitive to GE interaction effects in height growth than provenance hybrids or wide crosses. Pure provenances are expected to be populations more homogenous (Though they are not pure lines) than their hybrid combinations, because variance is expected to be amplified and genotypes more numerous when provenances are intercrossed. NAMKOONG & KANG (1990) have already shown the intensity of GE interaction depends on the population structure. Genetically homogenous populations, pure lines or F1 hybrids for instance, composed by a single genotype, would be more sensitive to changes in environments than heterogenous varieties, composed by several homo- or heterozygote genotypes. ALLARD & BRADSHAW (1964), related the differential buffering capacity of the crops to their genetic diversity deriving either from heterozygosity (Different alleles in individuals) or from heterogeneity (Mixture of different genotypes in populations).

Among conifers, results varied for height. In loblolly pine, wide crosses and local crosses did not differ significantly in stability performance (OWINO 1977). In jack pine, provenance hybrids exhibited intermediate stability when compared to control provenances (MAGNUSSEN & YEATMAN 1988). This was also the case in Norway spruce for height and survival (NILSSON 1984; EKBERG *et al.* 1982). The specific response of a population is likely dependent on its genetic structure and

diversity.

### GE interaction and components of genotypic effects

Our results have shown that GCA and SCA were also sensitive to environment changes for H8 but not for H13. For stem straightness, interactions with environment are significant in SCA but not in GCA whereas this effect is important in both for coefficient of form. Still, comparisons may be biased owing to differing numbers of observations for GCA and SCA (10 and 23, respectively) and/or for SCAs are estimated with less accuracy than GCAs. To my knowledge, studies on this topic are rare in forest trees. In Norway spruce, interactions were significant for GCA in stem volume (ERIKSSON & ILSTEDT 1986). However, data are too fragmentary for drawing conclusions about a hypothetical general trend in comparing GCA and SCA  $\times$  environment interaction.

### GE interaction and traits

Some traits exhibit less GE interaction than others (NAMKOONG & KANG 1990). In our case and according to KENDALL's coefficient of concordance calculations, GE interaction is more important in coefficient of form and height at age 8. Stem straightness shows an intermediate behaviour. In loblolly pine, growth traits displayed greater GE interaction effects than stem form traits (VAN BUIJTENEN 1978). In *Pinus radiata*, results from a study in Australia, have shown that diameter growth was more sensitive to varying environments than stem straightness and branch habit traits (PEDERICK 1990), whereas a study from New Zealand has revealed stem straightness and branch habit to be relatively less interactive than growth diameter (CARSON 1991). In Norway spruce, G  $\times$  E interaction in height growth and stem quality traits were the same relative magnitudes (ERIKSSON & ILSTEDT 1986; ILSTEDT & ERIKSSON 1986).

### GE interaction and age

GE interaction has been shown to decline with age (NAMKOONG & KANG 1990). The present study reveals a similar trend for height growth. In Norway spruce, GE interaction at age 1 was greater than at age 5 (BENTZER *et al.* 1988). It is not easy to make hypotheses on such a phenomenon although one might think that, after an intense action of natural selection factors, only the more hardy individuals survived, and populations composed by such individuals would subsequently display higher homeostasis and stability. Also, one may evoke differential changes with age in gene expression and/or gene regulation resulting in poor age-age genetic

correlations among sites and populations. In this respect, BURDON (personal communication) suggests that transient interactions at very early ages in *Pinus radiata* (BURDON *et al.* 1992) might be regarded as “incomplete age-age genetic correlations if age is reckoned in terms of height attained rather than chronology”.

## CONCLUSION

It may be justified to use such a non-parametric approach to complement a classical parametric method as ANOVA when data are more or less problematic (severe unbalance, aberrant data and outliers, error variance differences due to non-scalar effects, etc.) and for experiments with only two sites (could it be generalized to more than two sites?). Its main features is the simplicity and ease to compute; also, it develops a well-understanding meaning of GE interaction in relation to the concepts of *concordance-discordance* between two rank distributions. With this approach, owing to the own properties of the coefficient of concordance of KENDALL, a fresh look can be taken at the concept of GE interaction as a *probability of similarity or dissimilarity* between two sites with regard to the relative phenotypic expression of genotypes.

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**APPENDIX 1: Obtaining expression (2) from expression (1) of KENDALL's coefficient.**

$$\tau = \frac{C(x,y) - D(x,y)}{N(N-1)/2} = \frac{C(x,y)}{N(N-1)/2} - \frac{D(x,y)}{N(N-1)/2} = \pi(C) - \pi(D) = (1 - \pi(D)) - \pi(D) = 1 - 2\pi(D)$$

and,

$$1 - 2\pi(D) = 1 - \frac{2D(x,y)}{N(n-1)/2} = 1 - \frac{DT(x,y)}{N(n-1)/2}$$

where,  $\pi(C)$  and  $\pi(D)$  are the probabilities of concordance and discordance, respectively.

**APPENDIX 2: GE interaction and genotypic stability analyses. Numerical application.**

Provenance <i>i</i>	POV	LAN	VIV	EST	LEI	NAV	CAZ	TAM	Total	
Rankings in site 1:	1	2	3	4	5	6	7	8		
Ri(1)										
Rankings in site 2:										
Ri(2)	6	1	7	4	2	3	5	8		
ci(1,2)	2	6	1	3	2	3	2	1	0	C = 17
di(1,2) = di+(1,2)	5	0	4	2	0	0	0	0	0	D* = 11
di-(1,2)	0	1	0	2	3	3	2	0	0	D- = 11
δi(1,2)	5	1	4	4	3	3	2	0	0	DT = 22
∂i(1,2)	0	0	0	4	0	0	0	0	0	DC = 4
Δi(1,2)	5	1	4	0	3	3	2	0	0	DA = 18
RI(i) (%)	27.78	5.55	22.22	0.00	16.67	16.67	11.11	0	100.00	

**Computation of concordance (ci(1,2))**

For each provenance observation,  $c_i(1,2)$  is obtained by counting, in  $Ri(1)$  series, the number of observations at its right that have a inferior rank (i.e., a superior cardinal rank). For the first observation (6, POV), we count 2 (observations 7 and 8), for the second (1, LAN), we count 6 (observations 7, 4, 2, 3, 5 and 8) and so on up to the observation 8 for that we count zero. So,  $ci(1,2) = \{2, 6, 1, 2, 3, 2, 1, 0\}$ , and  $\Sigma ci(1,2) = C = 17$ .

**Computation of discordance (di(1,2))**

For each provenance observation,  $di^+(1,2)$  is obtained by counting in  $Ri(2)$  series the number of observations at its right that have an inferior rank. For the first observation 6 (POV), we count 5 (viz, observations 1, 4, 2, 3 and 5); for the second observation 1 (LAN), we count 0 (no observation at its right with rank inferior to 1); for the third observation 7 (VIV), we count 4 (viz;

observations 4, 2, 3 and 5) and so on up to the last observation. So,  $di(1,2) = \{5, 0, 4, 2, 0, 0, 0, 0\}$ , and  $\Sigma di(1,2) = D = 11$ . Right discordance  $di^+(1,2) = di(1,2)$ ; left discordance  $di^-(1,2)$  is obtained by counting the number of observations at the left of  $i$  with higher rank. The individual net discordance  $\Delta i(1,2) = |di^+(1,2) - di^-(1,2)|$ , and the total apparent discordance  $DA = \Sigma \Delta i(1,2)$ . In addition,  $\delta i(1,2) = \Delta i(1,2) + \partial i(1,2) = di^+(1,2) + di^-(1,2)$ .

The method for counting  $ci(1,2)$ ,  $di^+(1,2)$  and  $di^-(1,2)$  is indicated for  $i = EST$  which ranks 4 .in Site 1 ( $Ri(1)$ ) and 4 in Site 2 ( $Ri(2)$ ). The upper right way (1) counts  $ci(1,2)$  for EST; each descending arrow points to a concordant observation relative to EST; we count 2 arrows pointing to the ranks of CAZ (5) and TAM (8). These two provenances have been outperformed by EST in the 2 sites. Then,  $ci(1,2) = 2$  for EST. The lower right path (2) counts  $di^+(1,2)$  for the same provenance EST; each ascending arrow points to a right discordant observation relative to  $i = EST$ ; we have 2 such arrows

(One pointing to 2 and other to 3, the respective ranks of LEI and NAV in Site 2). Provenance EST is better than these two provenances in Site 1 but not in Site 2. So,  $di^+(1,2) = 2$  for EST. The lower left path (3) counts  $di^-(1,2)$  for EST; each upward arrow indicates a left discordant observation relative to EST; we count 2 arrows (one pointing to 7 and other to 6, the respective ranks of VIV and POV in Site 2). Provenance EST is better than these two provenances in Site 2 but not in Site 1. Then,  $di^-(1,2) = 2$  for EST.

To sum up, all we have to do to obtain  $C(1,2)$  is to count, in  $RI(2)$  series, the number of observations, at the right of a given entry  $i$ , with an inferior rank (*i.e.*, with a superior cardinal number) and add for the  $n$  entries. To obtain  $D^+(1,2)$ , we have to count, in the same series, the number of observations, at the right of  $i$ , with a superior rank (*i.e.*, with an inferior cardinal number) and add for  $n$ ;  $D^-(1,2)$  is obtained by counting, at the left of  $i$ , the number of observations with an inferior rank (*i.e.*, with a superior cardinal number) and then add for the  $n$  entries.

Finally, we have the elements (1) to test GE interaction with the help of the coefficient of concordance of KENDALL and (2) to assess the relative interactivity of the provenances with the help the *Relative Interactivity index*  $RI(i)$ .

**Genotype × environment interaction**

$$\tau = \frac{17 - 11}{8(7/2)} = 1 - \frac{2(11)}{8(7/2)} = 0.214$$

The tabulated value (KENDALL , DROESBEKE 1988) at a probability  $1 - \alpha = 0.95$  and  $N = 8$  is 0.410. So  $H_0$  is rejected in favour of  $H_1$ : the two rank series are discordant; *i.e.*, GE interaction effects in  $H8$  are significant at the probability of  $1 - \alpha = 0.95$  for the set of provenances.

We can now investigate how much each provenance participates to GE interaction by estimating its relative interactivity.

**Interactivity of the provenances**

The application of the formula

$$RI(i) = \frac{\tau(N - i) - \tau(N)}{\tau(N - i_{total}) - \tau(N)} * 100 = \frac{\Delta i(1,2)}{D_A(1,2)} * 100$$

(POV), South Corsica, for instance, a value

$$RI(i) = \frac{5}{18} * 100 = 27.78\%$$

This provenance has higher relative instability index than the other provenances, which is an indication of the interactivity of this provenance with changing environments for total height at age 8.