

1 **Direct and competition additive effects in tree breeding: Bayesian**  
2 **estimation from an individual tree mixed model**

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5 Eduardo P. Cappa<sup>12\*</sup> and Rodolfo J. C. Cantet<sup>13</sup>

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8 <sup>1</sup> Department of Animal Production, University of Buenos Aires,  
9 Avenida San Martín 4453, C1417DSQ Buenos Aires, Argentina.

10 <sup>2</sup> Doctoral fellow, “Fondo para la Investigación Científica y Tecnológica” (FONCyT), Argentina.

11 <sup>3</sup> “Consejo Nacional de Investigaciones Científicas y Técnicas” (CONICET), Argentina.

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13 \* Corresponding author

14 Eduardo Pablo Cappa  
15 Departamento de Producción Animal, Facultad de Agronomía  
16 Universidad de Buenos Aires  
17 Av. San Martín 4453  
18 C1417DSQ Buenos Aires  
19 Argentina

20  
21 ph: +54 11 4524 8000 ext. 8192  
22 fax: +54 11 4514 8735 or 8737  
23 [ecappa@mail.agro.uba.ar](mailto:ecappa@mail.agro.uba.ar)

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27 **Key words:** competition effects, individual tree mixed model, additive and direct competition  
28 effects, estimation of additive (co)variances, Gibbs sampling.

## 29 **Abstract**

30 An individual tree model with additive direct and competition effects is introduced to account for  
31 competitive effects in forest genetics evaluation. The mixed linear model includes fixed effects as  
32 well as direct and competition breeding values plus permanent environmental effects.  
33 Competition effects, either additive or environmental, are identified in the phenotype of a  
34 competitor tree by means of ‘intensity of competition’ elements (IC), which are non-zero  
35 elements of the incidence matrix of the additive competition effects. The ICs are inverse function  
36 of the distance and the number of competing individuals, either row-column wise or diagonally.  
37 The ICs allow standardization of the variance of competition effects in the phenotypic variance of  
38 any individual tree, so that the model accounts for unequal number of neighbors. Expressions are  
39 obtained for the bias in estimating additive variance using the covariance between half-sibs, when  
40 ignoring competition effects for row-plot designs and for single-tree plot designs. A data set of  
41 loblolly pines on growth at breast height is used to estimate the additive variances of direct and  
42 competition effects, the covariance between both effects, and the variance of permanent  
43 environmental effects using a Bayesian method via Gibbs sampling and Restricted Maximum  
44 Likelihood procedures (REML) via the Expectation-Maximization (EM) algorithm. No problem  
45 of convergence was detected with the model and ICs used when compared to what has been  
46 reported in the animal breeding literature for such models. Posterior means (standard error) of the  
47 estimated parameters were  $\hat{\sigma}_{Ad}^2 = 12.553 (1.447)$ ,  $\hat{\sigma}_{Ac}^2 = 1.259 (0.259)$ ,  $\hat{\sigma}_{AdAc} = -3.126 (0.492)$ ,  
48  $\hat{\sigma}_p^2 = 1.186 (0.289)$ , and  $\hat{\sigma}_e^2 = 5.819 (1.07)$ . Leaving permanent environmental competition effects  
49 out of the model may bias the predictions of direct breeding values. Results suggest that selection  
50 for increasing direct growth while keeping a low level of competition is feasible.

## 51 **Introduction**

52           The additive genetic variance is a parameter of uttermost importance in the genetic  
53 improvement of forest trees as it affects the gain and the precision of selection. In order to avoid  
54 bias when estimating additive variance, the statistical model of analysis should include all other  
55 sources of genetic variation as well as all identifiable environmental effects. Tree competition for  
56 resources may bias breeding value estimation from competing individuals (see for example,  
57 Magnussen, 1993; Foster *et al.*, 1998; Radtke *et al.*, 2003) by inducing a negative correlation  
58 between either individual trees or neighbor plots. Competition is defined as the stress suffered by  
59 a plant due to the genotype and the spatial arrangement of neighboring trees (Hinson and Hanson,  
60 1962), and is caused by genetic and environmental sources (Magnussen, 1989). Usually genetics  
61 effects of competition are not accounted for in the model of evaluation in spite of evidence of  
62 their existence (see the references in the discussion of Magnussen, 1993 and Foster *et al.*, 1998).  
63 Cannell (1978) suggested selecting for non-competitive genotypes in order to increase yield per  
64 unit of area in forest trees. This breeding strategy is most effective if direct effects for growth are  
65 negatively correlated to competition effects. In this scenario, plants with a large genetic potential  
66 for growth tend to induce less competition, so that tree density may be increased and, as a result  
67 of both increases, the yield per unit area would be augmented. On the other hand, if the  
68 correlation between direct and competition effects is positive, selection for higher growth will  
69 result in more competitive individuals. As a consequence, total yield per unit area may be  
70 affected as the faster growing individuals would hinder the growth of their neighbors, which in  
71 turn would decrease total production. Inclusion of genetic effects of competition results in an  
72 increased number of additive dispersion parameters in the model of genetic evaluation compared  
73 with those models where competition effects are absent.

74 In a series of papers, Griffing (1967, 1968a, 1968b) described models that include genetic  
75 effects of competition among individuals or groups of individuals, and analyzed the consequences  
76 of using such models for the response to selection. In these models, the phenotype of an  
77 individual is a linear combination of its genetic effects (“*direct genetic effects*”) plus the genetic  
78 contributions from other genotypes (“*indirect genetic effects*”). Whereas direct genetic effects are  
79 expressed in the phenotype of an individual, indirect genetic effects are expressed only in the  
80 phenotype of another individual. A common example of indirect effects is the maternal effect in  
81 mammals (Willham, 1963; Lynch and Walsh, 1998, chapter 23), which is expressed in the  
82 offspring from birth to weaning. When looking at the genetic evaluation of trees, competition is  
83 an indirect genetic effect. Wright (1986) obtained expressions for the covariance between  
84 relatives in the model of Griffing (1967), including additive, dominance and epistasis, for direct  
85 and competition effects. For a single trait individual tree model, 22 genetic (co)variance  
86 components have to be estimated: 3 for additive effects, 3 for dominance effects, and 16 for  
87 epistatic effects. Attempting to fit a model with all 22 parameters to data with the usual family  
88 relationships (full and half-sibs) commonly found in trees seems to be hopeless. Instead, it may  
89 be feasible to fit additive effects, as it requires estimating only three (co)variance components  
90 plus the error term. Muir and Schinckel (2002) described an animal model with direct and  
91 competitive effects. Van Vleck and Cassady (2005) used simulation and a fixed number of  
92 competitors, to determine whether Restricted Maximum Likelihood (REML, Patterson and  
93 Thompson, 1971) with relationships could untangle the covariance structure of direct and  
94 competition genetic variances and the covariance between them, whereas Arango *et al.* (2005)  
95 attempted to estimate the three (co)variance components to a swine population during a growth  
96 test. The results of both studies suggest that the additive relationships among competing  
97 individuals present in the data may be essential in disentangling the information to estimate the

98 (co)variance components. Muir (2005) wrote down the mixed model equations with competition  
99 effects to analyze forest tree data, but he ignored the consequences of a variable number of  
100 competitors (due for example to mortality or thinning) on estimating the additive genetic variance  
101 for competition. All in all, when fitting a model with competition effects it is essential to report a  
102 measure of the variability of the estimates of the dispersion parameters.

103 A shortcoming of REML is that the variability of estimation has to be measured  
104 approximately using large sample theory by means of the inverse of the information matrix from  
105 the marginal or restricted likelihood, as there is no analytic solution for the variance of the  
106 estimating equations: there is no exact sampling distribution for the REML estimators. From a  
107 Bayesian perspective REML can be seen as the mode of the joint posterior distribution of all  
108 (co)variance components after integrating out the fixed effects using a flat prior for the dispersion  
109 parameters (Harville, 1974). Alternatively, a full Bayesian approach by means of the Gibbs  
110 sampler can be attempted for estimating the (co)variance components for additive direct and  
111 indirect effects, by exploiting the similarity with the model of maternal effects (Sorensen and  
112 Gianola, 2002, section 13.3). The basics of the Gibbs sampling is discussed by Casella and  
113 George (1992), whereas Soria *et al.* (1998), Gwaze and Woolliams (2001), Zeng *et al.* (2004) and  
114 Cappa and Cantet (2006) developed some applications of the sampler to the genetic improvement  
115 of forest trees. The goals of this research are: 1) to introduce an additive genetic individual tree  
116 model that includes direct and competition effects, accounting for the number and position of  
117 competitor trees; 2) to estimate the dispersion parameters of the model (additive variances for  
118 direct and competition effects, and the covariance between both effects) using a Bayesian  
119 approach by means of the Gibbs sampler. Developments are illustrated with data on the diameter  
120 at breast height in *Pinus taeda* L. at 13 years of age.

121

122 **The model**

123 ***Breeding values for direct and competition effects.***

124 Consider a trait mostly affected by additive genetic effects, with a direct and a  
125 competition component (Wright, 1986). The dynamics of the joint genetic variability for additive  
126 effects with an indirect component has been developed by Willham (1963) for maternal effects,  
127 and more generally discussed by Wolf (2003) within an evolutionary framework. Let the direct  
128 component of the breeding value for individual  $i$  be  $a_{di}$ , and let the competition breeding value be  
129  $a_{ci}$ . The greater the magnitude of  $a_{ci}$  the higher the competition effects exerted by tree  $i$ . The  
130 phenotypic record of tree  $i$  ( $y_{ij_1..j_m}$ ) is affected by the  $a_{cj}$ 's of neighbor trees  $j$  ( $j = j_1, j_2, \dots, j_m$ ), in a  
131 similar fashion to maternal effects which are expressed in the progeny's phenotype. Thus,  $y_{ij_1..j_m}$   
132 depends on the  $a_{cj}$  of its neighbors but not on its own  $a_{ci}$ . As an individual tree suffers  
133 competition from more than a neighbor, let  $m_i$  be the number of competitors of the  $i^{th}$  tree. For  
134 plantations in a regular grid, the maximum value  $m_i$  can take is 8. The assumption is that any tree  
135 does not compete with other trees than its nearest neighbors (see Figure 1). The notation R-C  
136 indicates that the competitor lies, either in the same row or in the same column, and is represented  
137 with the symbol ' $\leftrightarrow$ ' in Figure 1. In the same way, the letter D refers to competitors that lie  
138 diagonal, and these are represented with the diagonal arrows in Figure 1. To exemplify, in Figure  
139 1 the R-C competitors of tree 5 are plants 2, 4, 6 and 8, whereas individuals 1, 3, 7 and 9 are D  
140 competitors of 5.

141 [Insert **Figure 1** about here]

142 The total additive genetic competition that is exerted over plant  $i$  from trees  $j_1, j_2, \dots, j_{m_i}$  is  
143 equal to

144 
$$f_{i1} \mathbf{a}_{c_1} + f_{i2} \mathbf{a}_{c_2} + \dots + f_{im} \mathbf{a}_{c_m} = \sum_{j=1}^{m_i} f_{ij} \mathbf{a}_{c_j} \quad [1]$$

145 The element  $f_{ij}$  is interpreted as the *intensity of competition* (IC) that  $\mathbf{a}_{c_j}$  ( $j = j_1, j_2, \dots, j_m$ ) exerts  
 146 over the phenotype of the  $i^{th}$  neighbor tree ( $y_{ij^{1..j_m}}$ ). To obtain the IC values, consideration should  
 147 be given to the fact that, in the absence of inbreeding and of genetic relationships among  
 148 competitors and regardless of the number of competitors,

149 
$$\text{Var} \left( \sum_{j=1}^{m_i} f_{ij} \mathbf{a}_{c_j} \right) = \sigma_{Ac}^2 \quad [2]$$

150 where  $\sigma_{Ac}^2$  is the additive variance for competition breeding values. This implies that the  
 151 potential genetic strength for competing with the neighbors, i.e.  $\mathbf{a}_c$ , is split proportionally to  $m_i$ .  
 152 Let  $f_{ijR-C}$  be the IC in [1] for R-C and  $f_{ijD}$  for D competitors to  $i$ . Also, let  $n_{R-C}$  and  $n_D$  be the  
 153 respective numbers of R-C and D competitors, and  $n_{R-C} + n_D = m_i$ . Under all these premises, and  
 154 on using the variance operator in [2], we obtain

155 
$$\text{Var} \left( \sum_{j=1}^{m_i} f_{ij} \mathbf{a}_{c_j} \right) = (n_{R-C} f_{ijR-C}^2 + n_D f_{ijD}^2) \sigma_{Ac}^2 = \left( \sum_{j=1}^{m_i} f_{ijk}^2 \right) \sigma_{Ac}^2 \quad [3]$$

156 where  $k = R-C$  or  $D$ . By equating [2] to [3], the ICs are such that

157 
$$\sum_{j=1}^{m_i} f_{ijk}^2 = n_{R-C} f_{ijR-C}^2 + n_D f_{ijD}^2 = 1 \quad [4]$$

158 Now, it seems reasonable to assume that in trees IC is related to the inverse of the *distance*  
 159 between  $i$  and  $j$  (i.e. Radtke *et al.*, 2003). If  $d$  is the regular spacing of the planting design, for R-  
 160 C competitors the IC is proportional to  $1/d$ . However, the distance of a tree located diagonal to  $i$   
 161 is  $2^{1/2} d$  by the Pythagorean theorem, so that competition is proportional to  $1/(2^{1/2} d)$  for D  
 162 competitors. Now,  $f_{ijR-C} = 1/d$  and  $f_{ijD} = 1/(2^{1/2} d)$ . On solving for  $d$  in both equalities we get  $d = 1/$   
 163  $f_{ijR-C}$  and  $d = 1/f_{ijD} 2^{1/2}$ . Next is to equate the resulting expressions so as to obtain

164 
$$\sqrt{2}f_{ijD} = f_{ijR-C} \quad [5]$$

165 Finally, by replacing with [5] in [4] and solving for  $f_{ijD}$  and  $f_{ijR-C}$  produces

166 
$$n_{R-C} 2f_{ijD}^2 + n_D f_{ijD}^2 = 1 \quad \text{or} \quad (2n_{R-C} + n_D) f_{ijD}^2 = 1$$

167 Thus

168 
$$f_{ijD} = \frac{1}{\sqrt{2n_{R-C} + n_D}} \quad [6]$$

169 A similar argument is used to obtain

170 
$$f_{ijR-C} = \sqrt{\frac{2}{2n_{R-C} + n_D}} \quad [7]$$

171 Notice that  $f_{ij}$  is not necessarily equal to  $f_{ji}$  as  $i$  and  $j$  may have different number of competitors.

172 An interesting feature of expressions [6] and [7] is that the intensity factors end up being

173 independent on the distance  $d$ . The reason is that in row-column arrays there is a relation between

174 the RC-distance and the D-distance based on the theorem of Pythagoras, and the value of  $d$

175 cancels out when obtaining [5]. This approach can be simply extended to planting designs when

176 the distance between rows and columns is not the same, i.e. when  $d_{\text{Row}} \neq d_{\text{Column}}$ .

177 Griffing (1967) and Wright (1986) observed that the covariance between  $\mathbf{a}_{di}$  and  $\mathbf{a}_{ci}$  from

178 the  $i$ -th tree is equal to:

179 
$$\text{cov}(\mathbf{a}_{d_i}, \mathbf{a}_{c_j}) = \mathbf{A}_{ij} \sigma_{AdAc}$$

180 where  $\mathbf{A}_{ij}$  is the additive genetic relationship between tree  $i$  and its  $j$  neighbor, and  $\sigma_{AdAc}$  is the

181 covariance between direct and competition breeding values. Moreover, as the genetic model is

182 exclusively an additive one, we have that

183 
$$\text{Var}(\mathbf{a}_{d_i}) = (1 + F_i) \sigma_{Ad}^2 \quad \text{Var}(\mathbf{a}_{c_j}) = (1 + F_j) \sigma_{Ac}^2$$



184 (Kempthorne, 1969; page 349). In this expression,  $F_i$  and  $F_j$  are the inbreeding coefficients of  $i$   
 185 and  $j$ , respectively;  $\sigma_{Ad}^2$  is the additive variance for direct effect. In terms of the covariance matrix  
 186 of breeding values we have

$$187 \quad \text{Var} \begin{bmatrix} \mathbf{a}_{d_i} \\ \mathbf{a}_{c_j} \end{bmatrix} = \begin{bmatrix} (1+F_i)\sigma_{Ad}^2 & \mathbf{A}_{ij}\sigma_{AdAc} \\ \mathbf{A}_{ij}\sigma_{AdAc} & (1+F_j)\sigma_{Ac}^2 \end{bmatrix}$$

188 ***Additive individual tree mixed model with direct and competition breeding values***

189 On inserting [1] into an additive individual tree model (Borralho, 1995) for the record of  
 190 tree  $i$  competing with neighbors  $j_1, j_2, \dots, j_m$  produces

$$191 \quad y_{ij_1..j_m} = \mathbf{X}_i \boldsymbol{\beta} + \mathbf{a}_{d_i} + \sum_{j=1}^{m_i} f_{ij} (\mathbf{a}_{c_j} + \mathbf{p}_{c_j}) + e_{ij_1..j_m} \quad [8]$$

192 In [8],  $y_{ij_1..j_m}$  is the phenotype of  $i$  ( $i = 1, \dots, n$ ;  $n$  is the total number of trees with data recorded).  
 193 The  $p \times 1$  vector  $\boldsymbol{\beta}$  contains fixed effects such as site or block, and is associated to the data by the  
 194  $i^{\text{th}}$  row of the incidence matrix  $\mathbf{X}$  ( $n \times p$ ). The breeding values  $\mathbf{a}_{d_i}$  and  $\mathbf{a}_{c_j}$  and the  $f_{ij}$  are as defined  
 195 above. Model [8] includes permanent environmental effects through the random variable  $\mathbf{p}_{c_j}$ , so  
 196 that  $\mathbf{a}_{c_j} + \mathbf{p}_{c_j}$  is the phenotypic effect of competitor  $j$  over the phenotype of  $i$  (Muir, 2005).  
 197 Finally,  $e_{ij_1..j_m}$  is the random error term.

198 The variance of  $y_{ij_1..j_m}$  in [8] is equal to

$$199 \quad \text{Var} (y_{ij_1..j_m}) = \text{Var} \left( \mathbf{a}_{d_i} + \sum_{j=1}^{m_i} f_{ij} \mathbf{a}_{c_j} \right) + \text{Var} \left( \sum_{j=1}^{m_i} f_{ij} \mathbf{p}_{c_j} \right) + \text{Var} (e_{ij_1..j_m})$$

200 where the first variance is for the additive effects, the second one for the permanent  
 201 environmental effects, and the remaining one for the error. It is shown in the Appendix that total  
 202 additive variance in model [8] is equal to

203 
$$\text{Var}\left(\mathbf{a}_{d_i} + \sum_{j=1}^{m_i} f_{ijk} \mathbf{a}_{c_j}\right) = (1 + F_i) \sigma_{Ad}^2 + \left[ (n_{R-C} f_{iR-C}^2 + n_D f_{iD}^2)(1 + F_j) + 2 \sum_{j \neq j'}^{m_i} f_{ij'k} f_{imk} \mathbf{A}_{jj'} \right] \sigma_{Ac}^2 + 2 \sum_{j=1}^{m_i} f_{ijk} \mathbf{A}_{ij} \sigma_{AdAc}$$

204 [9]

205 When: 1) all individuals are not inbred ( $F_i = F_j = 0$ ), 2) tree  $i$  is unrelated to its competitors ( $A_{ij} =$   
 206 0, for all  $j$ ), and 3) the competitors are unrelated among themselves ( $A_{jj'} = 0$ ), expression [9]  
 207 reduces to  $\sigma_{Ad}^2 + \sigma_{Ac}^2$ .

208 In matrix notation, the individual tree model [8] is

209 
$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_d \mathbf{a}_d + \mathbf{Z}_c \mathbf{a}_c + \mathbf{Z}_p \mathbf{p}_c + \mathbf{e} \quad [10]$$

210 where  $\mathbf{y} = [y_{ij^1..j^m}]$  ( $n \times 1$ ) contains the data;  $\mathbf{X}$  is the  $n \times p$  incidence matrix relating records to the  
 211 vector of fixed effects  $\boldsymbol{\beta}$ ,  $\mathbf{p}_c$  is a vector such that  $\mathbf{p}_c = [p_{cj}]$   $j = 1, \dots, n$ , such that  $\mathbf{p}_c \sim N_n(\mathbf{0}, I_n \sigma_p^2)$ ,  
 212 and  $\mathbf{e}$  ( $n \times 1$ ) is the random vector of i.i.d. errors distributed as  $N_n(\mathbf{0}, I_n \sigma_e^2)$ , being  $\sigma_e^2$  the error  
 213 variance. Direct breeding values are included in the random vector  $\mathbf{a}_d = [a_{di}]$  and competition  
 214 breeding values are in  $\mathbf{a}_c = [a_{ci}]$ . The same  $q$  individuals having direct breeding values in  $\mathbf{a}_d$  are  
 215 also in  $\mathbf{a}_c$ , and in the same order. Direct and competition breeding values are related to  $\mathbf{y}$  by the  $n$   
 216  $\times q$  incidence matrices  $\mathbf{Z}_d$  and  $\mathbf{Z}_c$ , respectively. Every row of  $\mathbf{Z}_d$  has all elements equal to 0 except  
 217 for a 1 in the column belonging to  $a_{di}$ . Similarly, matrix  $\mathbf{Z}_c$  has rows with 0 elements but the  $f_{ij}$  's  
 218 in the columns for the  $a_{ci}$  of the  $m_i$  competitors of tree  $i$ . To exemplify, suppose that in Figure 1  
 219 there is a missing plant in position 3. The row of  $\mathbf{Z}_c$  relating the record of 5 ( $i = 5$ ) to its  
 220 competitors is  $\mathbf{Z}_{c5} = \left[ \frac{1}{\sqrt{11}} \quad \frac{\sqrt{2}}{\sqrt{11}} \quad \frac{\sqrt{2}}{\sqrt{11}} \quad 0 \quad \frac{\sqrt{2}}{\sqrt{11}} \quad \frac{1}{\sqrt{11}} \quad \frac{\sqrt{2}}{\sqrt{11}} \quad \frac{1}{\sqrt{11}} \right]$ , were the columns are related to  
 221 the competition breeding values of trees 1, 2, 4, 5, 6, 7, 8, and 9. As plant 3 is missing, its  
 222 competition breeding value is not included in  $\mathbf{a}_c$ . Also the direct breeding values will not be in  $\mathbf{a}_d$ .  
 223 Using [7] results in  $f_{5jR-C} = [2/(2*4 + 3)]^{1/2} = \frac{\sqrt{2}}{\sqrt{11}}$  for R-C trees 2, 4, 6 and 8, whereas using [6]

224 produces  $f_{5jD} = 1/[2*4 + 3]^{1/2} = 1/\sqrt{11}$  for D trees 1, 7 and 9. The 0 in the fourth column reflects  
 225 that the competition breeding value of 5 is not related to its own record. Matrix  $\mathbf{Z}_p$  is composed of  
 226 the non-zero columns of  $\mathbf{Z}_c$  and has order equal to  $n \times n$ .

227 The covariance matrix of  $\mathbf{a}_d$  is  $\mathbf{A}\sigma_{Ad}^2$ . The  $q \times q$  matrix  $\mathbf{A} = [A_{ij}]$  has diagonal elements  
 228 equal to  $1 + F_i$ , and off-diagonals equal to the additive relationships  $A_{ij}$ . Also,  $\mathbf{a}_c \sim (\mathbf{0}, \mathbf{A}\sigma_{Ac}^2)$  and  
 229  $\text{cov}(\mathbf{a}_d, \mathbf{a}_c) = \mathbf{A}\sigma_{AdAc}$ . Now, we are able to write the total additive covariance matrix in a more  
 230 compact manner as follows

$$231 \quad \text{Var} \begin{bmatrix} \mathbf{a}_d \\ \mathbf{a}_c \end{bmatrix} = \begin{bmatrix} \sigma_{Ad}^2 & \sigma_{AdAc} \\ \sigma_{AdAc} & \sigma_{Ac}^2 \end{bmatrix} \otimes \mathbf{A} = \mathbf{G}_0 \otimes \mathbf{A}$$

232 Taking into account the random effects in model [10], the (co)variance matrix ( $\mathbf{V}$ ) of  $\mathbf{y}$  is  
 233 given by:

$$234 \quad \mathbf{V} = \mathbf{Z}_d \mathbf{A} \mathbf{Z}_d' \sigma_{Ad}^2 + (\mathbf{Z}_d \mathbf{A} \mathbf{Z}_c' + \mathbf{Z}_c \mathbf{A} \mathbf{Z}_d') \sigma_{AdAc} + \mathbf{Z}_c \mathbf{A} \mathbf{Z}_c' \sigma_{Ac}^2 + \mathbf{Z}_p \mathbf{Z}_p' \sigma_p^2 + \mathbf{I}_n \sigma_e^2 \quad [11]$$

### 235 **Bayesian estimation of (co)variance components**

236 As in Soria *et al.* (1998), Gwaze and Woolliams (2001), Zeng *et al.* (2004) and Cappa and  
 237 Cantet (2006), we will estimate the dispersion parameters  $\sigma_{Ad}^2$ ,  $\sigma_{AdAc}$ ,  $\sigma_{Ac}^2$ ,  $\sigma_p^2$  and  $\sigma_e^2$  using a  
 238 Bayesian approach by means of Gibbs sampling (Sorensen and Gianola, 2002). Under normality  
 239 of breeding values and errors, the conditional likelihood of the observed data can be written as  
 240 being proportional to:

$$241 \quad p(\mathbf{y} | \boldsymbol{\beta}, \mathbf{a}_c, \mathbf{a}_d, \mathbf{p}_c, \mathbf{G}_0, \sigma_p^2, \sigma_e^2) \propto (\sigma_e^2)^{-\frac{n}{2}} \exp \left[ -\frac{1}{2\sigma_e^2} (\mathbf{y} - \mathbf{X}\boldsymbol{\beta} - \mathbf{Z}_d \mathbf{a}_d - \mathbf{Z}_c \mathbf{a}_c - \mathbf{Z}_p \mathbf{p}_c)' (\mathbf{y} - \mathbf{X}\boldsymbol{\beta} - \mathbf{Z}_d \mathbf{a}_d - \mathbf{Z}_c \mathbf{a}_c - \mathbf{Z}_p \mathbf{p}_c) \right] \quad [12]$$

242 Conjugate prior densities are chosen for all parameters. In order to reflect a prior state of  
 243 uncertainty for the fixed effects and to obtain a proper posterior distribution (Hobert and Casella,

244 1996), we take  $\boldsymbol{\beta} \sim N_p(\boldsymbol{\theta}, \mathbf{K})$ . Matrix  $\mathbf{K}$  is diagonal with large elements ( $k_{ii} > 10^8$ ). Also, the joint  
 245 prior distribution of the direct and competition breeding values ( $\mathbf{a}_d, \mathbf{a}_c$ ) is

$$246 \quad \begin{bmatrix} \mathbf{a}_d \\ \mathbf{a}_c \end{bmatrix} | \mathbf{A}, \mathbf{G}_0, \sim N\left(\begin{bmatrix} \boldsymbol{\theta} \\ \boldsymbol{\theta} \end{bmatrix}, \mathbf{G}_0 \otimes \mathbf{A}\right)$$

247 On defining  $\mathbf{a} = [\mathbf{a}_d', \mathbf{a}_c']'$ , the corresponding density can be written as

$$248 \quad p(\mathbf{a} | \mathbf{A}, \mathbf{G}_0) \propto |\mathbf{G}_0|^{-\frac{q}{2}} \exp\left\{-\frac{1}{2} \mathbf{a}'(\mathbf{G}_0^{-1} \otimes \mathbf{A}^{-1})\mathbf{a}\right\} \quad [13]$$

249 Let

$$250 \quad \mathbf{S}_g = \begin{bmatrix} \mathbf{a}_d' \mathbf{A}^{-1} \mathbf{a}_d & \mathbf{a}_c' \mathbf{A}^{-1} \mathbf{a}_d \\ \mathbf{a}_d' \mathbf{A}^{-1} \mathbf{a}_c & \mathbf{a}_c' \mathbf{A}^{-1} \mathbf{a}_c \end{bmatrix}$$

251 Then

$$252 \quad \mathbf{a}'(\mathbf{G}_0^{-1} \otimes \mathbf{A}^{-1})\mathbf{a} = [\mathbf{a}_d' \quad \mathbf{a}_c']' \begin{bmatrix} \mathbf{a}_d' \mathbf{A}^{-1} \mathbf{a}_d & \mathbf{a}_c' \mathbf{A}^{-1} \mathbf{a}_d \\ \mathbf{a}_d' \mathbf{A}^{-1} \mathbf{a}_c & \mathbf{a}_c' \mathbf{A}^{-1} \mathbf{a}_c \end{bmatrix} \begin{bmatrix} \mathbf{a}_d \\ \mathbf{a}_c \end{bmatrix} = \text{tr}(\mathbf{G}_0^{-1} \mathbf{S}_g)$$

253 Therefore, [13] can be expressed as

$$254 \quad p(\mathbf{a} | \mathbf{A}, \mathbf{G}_0) \propto |\mathbf{G}_0|^{-\frac{q}{2}} \exp\left\{-\frac{1}{2} \text{tr}(\mathbf{G}_0^{-1} \mathbf{S}_g)\right\} \quad [14]$$

255 *A priori* the permanent environmental effects are distributed as  $\mathbf{p}_c \sim N_n(\boldsymbol{\theta}, \sigma_p^2 \mathbf{I}_n)$ :

$$256 \quad p(\mathbf{p}_c | \sigma_p^2) \propto (\sigma_p^2)^{-\frac{n}{2}} \exp\left\{-\frac{\mathbf{p}_c' \mathbf{p}_c}{2\sigma_p^2}\right\} \quad [15]$$

257 The matrix of the additive (co)variance components  $\mathbf{G}_0$  follows *a priori* an Inverted  
 258 Wishart (IW) density:  $\mathbf{G}_0 \sim \text{IW}(\mathbf{G}_0^*, \nu_g)$  where  $\mathbf{G}_0^*$  is the prior covariance matrix and  $\nu_g$  are the  
 259 degrees of freedom. Thus:

$$260 \quad p(\mathbf{G}_0 | \mathbf{S}_g, \nu_g) \propto |\mathbf{G}_0|^{-\frac{(\nu_g+3)}{2}} \exp\left\{-\frac{1}{2} \text{tr}(\mathbf{G}_0^* \mathbf{G}_0^{-1})\right\} \quad [16]$$

261 *A priori* the permanent environmental variance has as a scaled inverted  $\chi^2$  density so that:

$$262 \quad p(\sigma_p^2 | \nu_p, S_p^2) \propto (\sigma_p^2)^{-\left(\frac{\nu_p}{2} + 1\right)} \exp\left\{-\frac{\nu_p S_p^2}{2\sigma_p^2}\right\} \quad [17]$$

263 with ‘hyperparameters’  $\nu_p$ , the ‘degree of belief’ and  $S_p^2$  the hypervariance. Finally, and

264 following the approach of Jensen *et al.* (1994), the residual variance is assumed to follow *a priori*

265 a scaled inverted  $\chi^2$  with density proportional to:

$$266 \quad p(\sigma_e^2 | \nu_e, S_e^2) \propto (\sigma_e^2)^{-\left(\frac{\nu_e}{2} + 1\right)} \exp\left\{-\frac{\nu_e S_e^2}{2\sigma_e^2}\right\} \quad [18]$$

267 where  $\nu_e$  and  $S_e^2$  are the ‘hyperparameters’.

268 Multiplying [12] with [14], [15], [16], [17], and [18], produces the joint posterior density

269 for all parameters, and this is proportional to

$$270 \quad p(\boldsymbol{\beta}, \mathbf{a}_d, \mathbf{a}_c, \mathbf{p}_c, \mathbf{G}_\theta, \sigma_p^2, \sigma_e^2 | \mathbf{y}) \propto \\ 271 \quad p(\mathbf{y} | \boldsymbol{\beta}, \mathbf{a}_c, \mathbf{a}_d, \mathbf{p}_c, \mathbf{G}_\theta, \sigma_p^2, \sigma_e^2) p(\mathbf{a}_c, \mathbf{a}_d | \mathbf{A}, \mathbf{G}_\theta) p(\mathbf{p}_c | \sigma_p^2) p(\mathbf{G}_\theta | \mathbf{S}_g, \nu_g) p(\sigma_p^2 | \mathbf{S}_p^2, \nu_p) p(\sigma_e^2 | \mathbf{S}_e^2, \nu_e) \quad [19]$$

272 Sorensen and Gianola (2002, page 575) gave the posterior distribution for all parameters

273 of maternal models. On expanding their model to include permanent competition effects, the

274 posterior conditional density for the Gibbs sampling of  $\boldsymbol{\beta}$ ,  $\mathbf{a}_d$ ,  $\mathbf{a}_c$  and  $\mathbf{p}_c$  is equal to

$$275 \quad \begin{bmatrix} \boldsymbol{\beta} \\ \mathbf{a}_d \\ \mathbf{a}_c \\ \mathbf{p}_c \end{bmatrix} | \mathbf{y}, \mathbf{G}_\theta, \sigma_p^2, \sigma_e^2 \sim N \left( \begin{bmatrix} \boldsymbol{\beta} \\ \mathbf{a}_d \\ \mathbf{a}_c \\ \mathbf{p}_c \end{bmatrix}, \begin{bmatrix} \mathbf{X}'\mathbf{X} + \mathbf{K}^{-1} & \mathbf{X}'\mathbf{Z}_d' & \mathbf{X}'\mathbf{Z}_c' & \mathbf{X}'\mathbf{Z}_p' \\ \mathbf{Z}_d'\mathbf{X} & \mathbf{Z}_d'\mathbf{Z}_d + k_{11}\mathbf{A}^{-1} & \mathbf{Z}_d'\mathbf{Z}_c + k_{12}\mathbf{A}^{-1} & \mathbf{Z}_d'\mathbf{Z}_p \\ \mathbf{Z}_c'\mathbf{X} & \mathbf{Z}_c'\mathbf{Z}_d + k_{21}\mathbf{A}^{-1} & \mathbf{Z}_c'\mathbf{Z}_c + k_{22}\mathbf{A}^{-1} & \mathbf{Z}_c'\mathbf{Z}_p \\ \mathbf{Z}_p'\mathbf{X} & \mathbf{Z}_p'\mathbf{Z}_d & \mathbf{Z}_p'\mathbf{Z}_c & \mathbf{Z}_p'\mathbf{Z}_p + \mathbf{I} \left( \frac{\sigma_e^2}{\sigma_p^2} \right) \end{bmatrix}^{-1} \right) \quad [20]$$

276 where  $\begin{bmatrix} k_{11} & k_{12} \\ k_{21} & k_{22} \end{bmatrix} = \mathbf{G}_\theta^{-1} \sigma_e^2$ , and  $\hat{\boldsymbol{\beta}}$ ,  $\hat{\mathbf{a}}_d$ ,  $\hat{\mathbf{a}}_c$  and  $\hat{\mathbf{p}}_c$  are the solutions of the following system of

277 equations

$$278 \begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{X} + \mathbf{K}^{-1} & \mathbf{X}\mathbf{R}^{-1}\mathbf{Z}_d' & \mathbf{X}\mathbf{R}^{-1}\mathbf{Z}_c' & \mathbf{X}\mathbf{R}^{-1}\mathbf{Z}_p' \\ \mathbf{Z}_d'\mathbf{R}^{-1}\mathbf{X} & \mathbf{Z}_d'\mathbf{R}^{-1}\mathbf{Z}_d + k_{11}\mathbf{A}^{-1} & \mathbf{Z}_d'\mathbf{R}^{-1}\mathbf{Z}_c + k_{12}\mathbf{A}^{-1} & \mathbf{Z}_d'\mathbf{R}^{-1}\mathbf{Z}_p \\ \mathbf{Z}_c'\mathbf{R}^{-1}\mathbf{X} & \mathbf{Z}_c'\mathbf{R}^{-1}\mathbf{Z}_d + k_{21}\mathbf{A}^{-1} & \mathbf{Z}_c'\mathbf{R}^{-1}\mathbf{Z}_c + k_{22}\mathbf{A}^{-1} & \mathbf{Z}_c'\mathbf{R}^{-1}\mathbf{Z}_p \\ \mathbf{Z}_p'\mathbf{R}^{-1}\mathbf{X} & \mathbf{Z}_p'\mathbf{R}^{-1}\mathbf{Z}_d & \mathbf{Z}_p'\mathbf{R}^{-1}\mathbf{Z}_c & \mathbf{Z}_p'\mathbf{R}^{-1}\mathbf{Z}_p + \mathbf{I}\left(\frac{\sigma_p^2}{\sigma_e^2}\right) \end{bmatrix} \begin{bmatrix} \boldsymbol{\beta} \\ \mathbf{a}_d \\ \mathbf{a}_c \\ \mathbf{p}_c \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{Z}_d'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{Z}_c'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{Z}_p'\mathbf{R}^{-1}\mathbf{y} \end{bmatrix}$$

279 Expression [20] may suggest that sampling of  $\boldsymbol{\beta}$ ,  $\mathbf{a}_d$ ,  $\mathbf{a}_c$  and  $\mathbf{p}_c$  is in block. However, it is simpler  
 280 to sample the elements of those vectors individually, as discussed by Sorensen and Gianola  
 281 (2002, page 566, expressions (13.11) and (13.12)), which was the way it was done in the current  
 282 research.

283 Collecting the second and third terms in the right of [19], the full conditional posterior  
 284 distribution of  $\mathbf{G}_0$  is equal to

$$285 p(\mathbf{G}_0 | \boldsymbol{\beta}, \mathbf{a}_c, \mathbf{a}_d, \mathbf{p}_c, \sigma_p^2, \sigma_e^2, \mathbf{y}) \propto |\mathbf{G}_0|^{-\frac{(\nu_g + q + 3)}{2}} \exp\left\{-\frac{1}{2} \text{tr} \mathbf{G}_0^{-1} (\mathbf{S}_g + \mathbf{G}_0^*)\right\} \quad [21]$$

286 Expression [21] is the kernel of a  $2 \times 2$  scaled inverted Wishart distribution, with degrees of  
 287 freedom equal to  $(\nu_g + q + 3)$  and scale matrix  $\mathbf{S}_g + \mathbf{G}_0^*$ .

288 For the permanent error variance, the full conditional posterior distribution is

$$289 p(\sigma_p^2 | \boldsymbol{\beta}, \mathbf{a}_d, \mathbf{a}_c, \mathbf{p}_c, \mathbf{G}_0, \sigma_e^2, \mathbf{y}) \propto (\sigma_p^2)^{-\left(\frac{n + \nu_p + 2}{2} + 1\right)} \exp\left\{-\frac{\tilde{\nu}_p \tilde{\delta}_p^2}{2\sigma_p^2}\right\} \quad [22]$$

290 which is a scaled inverted  $\chi^2$  density with  $\tilde{\nu}_p = n + \nu_p$  degrees of freedom and scale parameter

$$291 \tilde{\delta}_p^2 = \frac{(\mathbf{p}_c' \mathbf{p}_c + \nu_p \delta_p^2)}{(\nu_p + n)}.$$

292 Finally, the full conditional posterior density of the residual variance is proportional to

293 
$$p(\sigma_e^2 | \boldsymbol{\beta}, \mathbf{a}_c, \mathbf{a}_d, \mathbf{p}_c, \mathbf{G}_0, \sigma_p^2, \mathbf{y}) \propto (\sigma_e^2)^{-\left(\frac{n+\nu_e+2}{2}+1\right)} \exp\left\{-\frac{\tilde{\nu}_e \tilde{\delta}_e^2}{2\sigma_e^2}\right\} \quad [23]$$

294 which is a scaled inverted  $\chi^2$  density with  $\tilde{\nu}_e = n + \nu_e$  degrees of freedom and scale parameter

295 
$$\tilde{\delta}_e^2 = \frac{(\mathbf{e}'\mathbf{e} + \nu_e \delta_e^2)}{(\nu_e + n)}.$$

296 At each iteration, the Gibbs algorithm proceeds by first sampling  $\boldsymbol{\beta}$ ,  $\mathbf{a}_d$ ,  $\mathbf{a}_c$  and  $\mathbf{p}_c$  from  
 297 [20], then  $\sigma_e^2$  from [23],  $\sigma_p^2$  from [22], and finally  $\sigma_{Ad}^2$ ,  $\sigma_{AdAc}$  and  $\sigma_{Ac}^2$  from [21]. A program  
 298 was written in FORTRAN to perform all these calculations with the data and model described  
 299 below.

300

## 301 **An application to Loblolly pines**

### 302 ***Data***

303 An additive individual tree mixed model with direct and competition breeding values was  
 304 applied to a progeny data set derived from 20 open-pollinated families of Loblolly pine (*Pinus*  
 305 *taeda* L.), originated from Marion (Florida, USA) and belonging to CIEF (Forestry Research and  
 306 Experimentation Centre). Five lots of commercial seeds were used as control populations. The  
 307 trait analyzed was diameter at breast height (1.3 m, DBH) measured at age 13 from 932 trees. The  
 308 trial site was located in Villa Olivari (lat. 27° 36' S long. 56° 55' W), northern Corrientes province  
 309 Argentina, where soils are deep, sandy, yellowish and quartzous. Families were arranged in  
 310 randomized complete blocks, with eight replicates of 5 trees in line per plot, and the spacing was  
 311 3.5 m × 3.5 m. The data available are summarized in Table 1.

312 [Insert *Table 1* about here]

313 ***Model and posterior inference***

314 Besides  $\mathbf{a}_d$ ,  $\mathbf{a}_c$  and  $\mathbf{p}_c$ , the individual tree model included a vector  $\boldsymbol{\beta}$  with 8 block effects.  
 315 The order of  $\mathbf{Z}_d$  and  $\mathbf{Z}_c$  was  $932 \times 957$ , and of  $\mathbf{Z}_p$  was  $932 \times 932$ . Whenever a tree had all 8  
 316 neighbor competitors,  $n_{R-C} = n_D = 4$ . On replacing with these values into [7] and [6] produces the  
 317 non-zero elements of  $\mathbf{Z}_c$ :  $f_{ijR-C} = [2/(2*4 + 4)]^{1/2} = 1/\sqrt{6}$  and  $f_{ijD} = 1/[2*4 + 4]^{1/2} = 1/\sqrt{12}$ .

318 As there no other estimates of  $\sigma_{AdAc}$  and  $\sigma_{Ac}^2$ , several Markov chains with different prior  
 319 values of  $\sigma_{AdAc}$  (+, 0, and -) and of  $\sigma_{Ac}^2$  (high and low relative to  $\sigma_{Ad}^2$ ) were run. Results were  
 320 quite similar so the chain with the best convergence properties was used to estimate the  
 321 (co)variance components. The prior variance for  $\sigma_p^2$  ( $\delta_p^2$ ) was chosen to be equal to the prior  
 322 value for  $\sigma_{Ac}^2$ . A single Gibbs chain of 1 010 000 samples each were drawn as discussed above,  
 323 and the first 10000 iterates were discarded due to *burn-in*. The autocorrelations were calculated  
 324 with “*Bayesian Output Analysis*” (BOA version 1.0.1, Smith 2003) for all lags from 1 to 100. To  
 325 account for the impact of autocorrelations in the chain on measures of variability, posterior  
 326 standard errors of each parameter were corrected for an ‘effective sample size’ (ESS, Neal in  
 327 Kass *et al.*, 1998), which was calculated as:

328 
$$ESS = \frac{1000000}{1 + 2 \sum_{i=1}^{100} \rho(i)}$$

329 where  $\rho(i)$  is the autocorrelation measured at lag  $i$ . The marginal posterior densities for all  
 330 parameters were estimated using the Gaussian kernel method (Silverman, 1986; chapter 2):

331 
$$f(\theta) = \frac{1}{10000 h} \sum_{i=1}^{10000} \frac{1}{\sqrt{2\pi}} \exp\left[-\frac{1}{2} \left(\frac{z - \theta_i}{h}\right)^2\right] \quad [24]$$



332 where  $f(\theta)$  is the estimated posterior density,  $\theta_i$  ( $i=1, \dots, 10\,000$ ) is a sampled value and  $h$  is the  
333 window width estimated by cross-validation. The basic idea of this procedure is to withdraw one  
334 observation at a time and estimate the density. After repeating the procedure  $n$  times the average  
335 of the logs of the estimated densities is maximized with respect to  $h$ . Further details can be  
336 consulted in Silverman (1986, section 3.4.4). The procedure is implemented in the function  
337 *density* within the free-software *R* (<http://www.r-project.org/>). Mean, mode, median, standard  
338 deviation (SD), and 95% high posterior density interval (95% HPD), were obtained with BOA for  
339 all parameters from the individual marginal posteriors, under *R*.

340

## 341 **Results**

342 Posterior statistics for  $\sigma_{Ad}^2$ ,  $\sigma_{Ac}^2$ ,  $r_{AdAc}$ ,  $\sigma_p^2$  and  $\sigma_e^2$  are shown in Table 2. For all parameters  
343 posterior means and medians were quite similar, whereas the modes were somewhat smaller.  
344 Therefore, the marginal posterior distributions were slightly right skewed (Figure 2). The  
345 marginal posterior means and SDs of  $\sigma_{Ad}^2$  and  $\sigma_{Ac}^2$  were respectively equal to 12.553 and 1.259,  
346 and 1.447 and 0.259. The marginal posterior mean of  $r_{AdAc}$  was moderate to large and negative –  
347 0.788 and the SD was 0.056. The posterior means of  $\sigma_p^2$  and  $\sigma_e^2$  were equal to 1.186 and 5.819,  
348 respectively, and their SDs were 0.289 and 1.070. None of the 95% HPD for  $\sigma_{Ad}^2$ ,  $\sigma_{Ac}^2$ ,  $r_{AdAc}$ ,  
349  $\sigma_p^2$ , or  $\sigma_e^2$  included 0, which suggests that these parameters are different from zero.

350 [Insert **Table 2** about here]

351 [Insert **Figure 2** about here]

## 352 Discussion

353 It has been observed that competition among trees may bias the estimated breeding value  
354 of a plant from those of its competitors (Magnussen, 1993; Foster *et al.*, 1998; Radtke *et al.*,  
355 2003, among others). In the current research, we presented an individual tree mixed model that  
356 allows disentangling breeding values for direct and competition effects and estimating their  
357 variances plus the covariance between both effects, as well as the variance of permanent  
358 environmental competition effects. Estimation of the dispersion parameters was accomplished  
359 using a Bayesian method with the Gibbs sampler originally proposed by Jensen *et al.* (1994) for  
360 maternal effects in animals. For direct and competition effects, Van Vleck and Cassady (2005),  
361 Arango *et al.* (2005) and Muir (2005) estimated the (co)variance components by REML. We did  
362 not find problems of convergence and sensitivity to starting values, as reported by Van Vleck and  
363 Cassady (2005) and Arango *et al.* (2005) when estimating the competitive (co)variance  
364 components. It is unlikely that the difference in performance is due to the use of a different  
365 method of estimation, but to different amount of information on competitive effects for forest  
366 trees compared with animals. In trees, each individual may be competing with 8 others at  
367 different intensities (see [6] and [7]), as compared with animal breeding data for individuals  
368 managed in common pens where all ICs are equal. This informativeness of the IC through matrix  
369  $\mathbf{Z}_c$  allowed estimating additive effects of competition and permanent environmental competitive  
370 effects.

371 Posterior means of the (co)variance components for a model without permanent  
372 environmental competitive effects were  $\hat{\sigma}_{Ad}^2 = 13.527$ ,  $\hat{\sigma}_{Ac}^2 = 1.488$ ,  $\hat{r}_{AdAc} = -0.659$ , and  $\hat{\sigma}_e^2 =$   
373 5.417. Notice that the estimate of  $\sigma_{Ad}^2$  was larger (13.527 vs. 12.553) and the estimate of  $\sigma_e^2$  was  
374 smaller (5.417 vs. 5.819) than when permanent environmental competitive effects were fitted.

375 This may suggest that leaving those environmental effects out of the model may bias the  
376 predictions of direct breeding values. A possible evidence of this bias is that the predictions of  
377 permanent environmental competition effects of trees having less than 8 competitors (for  
378 example, those plants nearby a site without a tree) were almost a quarter of a standard deviation  
379 larger than the same effects but for trees having all 8 competitors. Thus, the presence of dead  
380 trees promotes a less stressful environment for the surrounding plants that may bias the prediction  
381 of direct breeding values, if permanent environmental effects are not accounted for in the model.

382 As expression [9] shows, ignoring the number of competitors, the additive relationships  
383 between the individual with the competitors, and the relationships among the competitors  
384 themselves results in biased estimates of the dispersion parameters. Arango *et al.* (2005)  
385 accounted for different number of competitors by including the covariable  $1/n$  or  $1/\sqrt{n}$ , whereas  
386 Van Vleck and Cassady (2005) did not account for a variable number of competitors. As progeny  
387 tests in forest trees last several years, mortality or tree stand failure are quite common, and this  
388 results in variable number of competitors. We accounted for unequal number of neighbors ( $m_i <$   
389 8) for either mortality or border location by adjusting  $f_{ijk}$  so that always  
390  $\sum_{j=1}^m f_{ijk}^2 = n_{R-C} f_{ijR-C}^2 + n_D f_{ijD}^2 = 1$ . We also accounted for the additive relationships between any tree  
391 and its competitors and among the competitors themselves. Van Vleck and Cassady (2005) did  
392 not account for additive relationships between individuals in the management unit, which bias the  
393 estimation of  $\sigma_{Ac}^2$ .

394 An individual tree model that includes direct and competition breeding values, taking  
395 into account a variable number of competitors and the relationships among all trees, allows  
396 different selection goals and schemes which capitalizes on (or attenuates) the impact of  
397 competition effects. Compared to a model with direct breeding values, the application of the

398 model discussed here to forest breeding data requires only the positions (row and column) of all  
 399 the trees in the trial. The estimated value of  $\sigma_{Ad}^2$  was almost ten times higher than the magnitude  
 400 of  $\sigma_{Ac}^2$ , whereas the magnitude of the genetic correlation between direct and competitive effects  
 401 was sizable ( $-0.788$ ). Therefore, selecting for high direct effects and low competitive effects to  
 402 increase the yield per unit area is facilitated for a relatively high negative correlation between  
 403 both types of effects.

404 Of further note is the fact that ignoring competitive effects would result in biased  
 405 estimates of the additive variance ( $\sigma_{Ad}^2$ ). To specify the covariance between relatives in the  
 406 additive model two individuals ( $\mathbf{x}$  and  $\mathbf{y}$ ) are required. If indirect effects are involved more  
 407 individuals are needed. For example, the covariance between relatives with maternal effects  
 408 requires four animals ( $\mathbf{x}$ ,  $\mathbf{y}$ , and respective dams  $\mathbf{w}$  and  $\mathbf{z}$ ), and up to 18 individuals have to be  
 409 considered in the additive model with competition effects in [8]:  $\mathbf{x}$  and its competitors  $w_1, \dots, w_8$ ,  
 410 and  $\mathbf{y}$  and its competitors  $z_1, \dots, z_8$ . On applying the covariance operator on the additive effects of  
 411 model [8] results in the following expression for the genetic covariance between the records of  $\mathbf{x}$   
 412 and  $\mathbf{y}$

$$\begin{aligned}
 & \text{cov} \left( \mathbf{a}_{dx} + \sum_{i=1}^8 f_{xw_i} \mathbf{a}_{cw_i}, \mathbf{a}_{dy} + \sum_{j=1}^8 f_{yz_j} \mathbf{a}_{cz_j} \right) \\
 413 \quad & = \text{cov}(\mathbf{a}_{dx}, \mathbf{a}_{dy}) + \text{cov} \left( \sum_{i=1}^8 f_{xw_i} \mathbf{a}_{cw_i}, \mathbf{a}_{dy} \right) + \text{cov} \left( \mathbf{a}_{dx}, \sum_{j=1}^8 f_{yz_j} \mathbf{a}_{cz_j} \right) + \text{cov} \left( \sum_{i=1}^8 f_{xw_i} \mathbf{a}_{cw_i}, \sum_{j=1}^8 f_{yz_j} \mathbf{a}_{cz_j} \right) \quad [25] \\
 & = \mathbf{A}_{xy} \sigma_{Ad}^2 + \left( \sum_{i=1}^8 f_{xw_i} \mathbf{A}_{yw_i} + \sum_{j=1}^8 f_{yz_j} \mathbf{A}_{xz_j} \right) \sigma_{AdAc} + \left( \sum_{j=1}^8 f_{xw_i} f_{yz_j} \mathbf{A}_{w_i z_j} \right) \sigma_{Ac}^2
 \end{aligned}$$

414 Expression [25] is of general form and parameters are associated to additive relationships  
 415 between individuals in the following way:  $\sigma_{Ad}^2$  with  $\mathbf{x}$  and  $\mathbf{y}$ ; the covariance  $\sigma_{AdAc}$  with the  
 416 relationships between the individual  $\mathbf{x}$  ( $\mathbf{y}$ ) and competitors  $w_i$  ( $z_j$ ), and  $\sigma_{Ac}^2$  is associated with the

417 relationships among the members of both groups of competitors. To get further insight into the  
 418 model with competition consider the situation where  $\mathbf{x}$  and  $\mathbf{y}$  are direct competitors.  
 419 Schematically

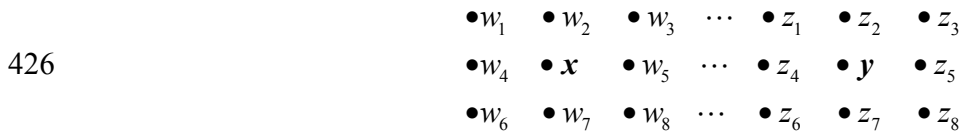


421 Trees  $\mathbf{x}$  and  $\mathbf{y}$  are in the center, surrounded by their respective competitors  $w_1, \dots, w_8, z_1, \dots, z_7,$   
 422 and  $z_8$ . Notice that 6 individuals are common competitors, implying that  $w_2 = z_1, \mathbf{x} = z_4$ , and so on.  
 423 Expression [25] is now equal to

424

$$\begin{aligned} & \text{cov} \left( \mathbf{a}_{d\mathbf{x}} + \sum_{i=1}^8 f_{xw_i} \mathbf{a}_{cw_i}, \mathbf{a}_{d\mathbf{y}} + \sum_{j=1}^8 f_{yz_j} \mathbf{a}_{cz_j} \right) \\ & = \mathbf{A}_{xy} \sigma_{Ad}^2 + \left[ f_{xy} (1 + F_y) + f_{yx} (1 + F_x) + \sum_{i=1}^7 f_{yw_i} \mathbf{A}_{yw_i} + \sum_{j=1}^7 f_{xz_j} \mathbf{A}_{xz_j} \right] \sigma_{Ad\Delta c} + \quad [26] \\ & + \left( \sum_{w_i=z_j} f_{xw_i} f_{yz_j} (1 + F_{w_i}) + \sum_{w_i \neq z_j} f_{xw_i} f_{yz_j} \mathbf{A}_{w_i z_j} \right) \sigma_{\Delta c}^2 \end{aligned}$$

425 Alternatively, if  $\mathbf{x}$  and  $\mathbf{y}$  are distant from each other the scheme is as follows



427 The dots (...) in the scheme stress the fact that trees are separated by at least a column, or they  
 428 may be even positioned in totally different rows, or in any other position within the trial. The  
 429 covariance in [25] reduces to

430

$$\begin{aligned} & \text{cov} \left( \mathbf{a}_{d\mathbf{x}} + \sum_{i=1}^8 f_{xw_i} \mathbf{a}_{cw_i}, \mathbf{a}_{d\mathbf{y}} + \sum_{j=1}^8 f_{yz_j} \mathbf{a}_{cz_j} \right) \\ & = \mathbf{A}_{xy} \sigma_{Ad}^2 + \left[ \sum_{i=1}^8 f_{xw_i} \mathbf{A}_{yw_i} + \sum_{j=1}^8 f_{yz_j} \mathbf{A}_{xz_j} \right] \sigma_{Ad\Delta c} + \left( \sum_{i=1}^8 \sum_{j=1}^8 f_{xw_i} f_{yz_j} \mathbf{A}_{w_i z_j} \right) \sigma_{\Delta c}^2 \quad [27] \end{aligned}$$

431 Formula [26] may be applied to row-plot designs where related individuals are planted nearby, an  
432 example of which is the structure in the data set analyzed in the current research. On the other  
433 hand, expression [27] is associated with single-tree plot designs where individuals of the same  
434 family are positioned distant to each other. Consider the estimation of heritability in a single-tree  
435 plot design using half-sib families. The additive variance will be estimated as 4 times the  
436 covariance between half-sibs, i.e. the variance between mothers. Trees  $\mathbf{x}$  and  $\mathbf{y}$  have a relationship  
437 equal to  $A_{\mathbf{xy}} = 1/4$  and are distant to each other, and this defines the first term in [27]. In order for  
438 the covariance between half-sibs to be an unbiased estimator of the additive variance, all terms  
439 related with  $\sigma_{AdAc}$  and  $\sigma_{Ac}^2$  should be equal to zero. The second term will be null as long as  
440 competitors of any individual ( $\mathbf{x}$ , say) are unrelated with a distant half-sib ( $\mathbf{y}$ ). However, it is  
441 unlikely that all competitors of any plant  $\mathbf{x}$  are unrelated to the competitors of all possible  $\mathbf{y}$ , and  
442 this will introduce bias in the estimation of additive variance. All sources of variation and  
443 covariation that are not accounted for the covariance between half-sibs will fall into the error  
444 term. Of particular interest is the covariance between any two unrelated and distant individuals  $\mathbf{x}$   
445 and  $\mathbf{y}$ . It is most likely that the second and third terms in [27] are not zero as some  $\mathbf{x}$ 's are related  
446 to any of the  $z$ -competitors, or some  $\mathbf{y}$ 's are related to any of the  $w$ -competitors, or some  $w$ -  
447 competitors are related to any of the  $z$ -competitors. Any of these covariances will go into the error  
448 and will bias the error variance upwards. Therefore, even if the bias on the additive variance is  
449 small, the estimate of heritability will be affected as the error variance is most likely biased.  
450 However, the direction and magnitude of the bias will depend on the sign and the magnitude of  
451  $\sigma_{AdAc}$  as compared with the magnitude of  $\sigma_{Ac}^2$ . In comparison, in data structures where related  
452 individuals are next to each other and competing such as in the row-plot field design, the  
453 covariance between half-sibs will be more affected than in the case of the single-tree plot. This is

454 due to the fact that the third term in [26] will not be null as the competitors of  $\mathbf{x}$  are related to the  
 455 competitors of  $\mathbf{y}$ , being many times the same individuals ( $\mathbf{x} = z_4, \mathbf{y} = w_5$ ). Also the second term in  
 456 [26] will not be zero as when looking at the covariance between  $\mathbf{x}$  and the competitors of  $\mathbf{y}$  (or  $\mathbf{y}$   
 457 and the competitors of  $\mathbf{x}$ ),  $\mathbf{x}$  is also a competitor of  $\mathbf{y}$  and  $\mathbf{y}$  a competitor of  $\mathbf{x}$ . Hence,  $f_{xy}$  and  $f_{yx}$  are  
 458 not zero. For the error variance we will look at the covariance between unrelated individuals ( $A_{xy}$   
 459 = 0) that are either competing or distant. As in the case of single-tree plot, in the row-plot design  
 460 the error variance will also be affected, as the second and third terms in [26] will not be zero: any  
 461 pair of unrelated  $\mathbf{x}$  and  $\mathbf{y}$  will have relatives competing to the other individual in the pair, i.e. there  
 462 will be  $z$ -competitors related to  $\mathbf{x}$ ,  $w$ -competitors related to  $\mathbf{y}$ , and  $z$ -competitors related to  $w$ -  
 463 competitors. The size of the bias when estimating the additive and error variances will depend on  
 464 the sign and the magnitude of  $\sigma_{AdAc}$  as compared with the magnitude of  $\sigma_{Ac}^2$ . When looking into  
 465 the data analysis, estimates of the dispersion parameters in the model with competition effects  
 466 were  $\hat{\sigma}_{Ad}^2 = 12.553$ ,  $\hat{\sigma}_{AdAc} = -3.126$ ,  $\hat{\sigma}_{Ac}^2 = 1.259$ ,  $\hat{\sigma}_p^2 = 1.186$ , and  $\hat{\sigma}_e^2 = 5.819$ . On the other hand,  
 467 the estimated variances in the model with direct effects only (no competition) were  $\hat{\sigma}_{Ad}^2 = 10.644$ ,  
 468 and  $\hat{\sigma}_e^2 = 9.257$ . The difference between the estimates of  $\sigma_{Ad}^2$  can be explained by the negative  
 469 sign and the absolute value (3.126) of  $\sigma_{AdAc}$  relative to the small value of  $\hat{\sigma}_{Ac}^2$ , which gives more  
 470 weight to the 2<sup>nd</sup> than the 3<sup>rd</sup> term in [26]. As a consequence,  $\hat{\sigma}_{Ad}^2$  in the model with competition  
 471 was higher than in the model excluding competitive effects. The value of  $\hat{\sigma}_e^2$  in the model were  
 472 competition effects were absent was larger than in the model with competition. This is probably  
 473 due to the larger number of covariances related to 3<sup>rd</sup> as compared to 2<sup>nd</sup> term in [26]. A quick  
 474 look at this formula shows that, whereas a maximum of 16 elements are related to  $\sigma_{AdAc}$ , up to 64  
 475 elements are associated with  $\sigma_{Ac}^2$ . Therefore, even tough  $\hat{\sigma}_{AdAc}$  was negative and larger in absolute

476 value than  $\hat{\sigma}_{Ac}^2$ , the higher number of elements in the third term gave more weight to  $\sigma_{Ac}^2$  than  
477 to  $\sigma_{AdAc}$ .

478 In the current research, a Bayesian procedure coupled with a Markov Chain Monte Carlo  
479 technique (Gibbs sampling), has been used to estimate the (co)variance components. An  
480 alternative approach for estimating dispersion parameters is the use of REML. Comparison of  
481 frequentist and Bayesian estimators is difficult due to the fact that central issues related to the  
482 comparison of frequentist estimators (such as repeated sampling or bias) do not have the same  
483 meaning in the Bayesian school (Gelman *et al.*, 1995, page 108). When comparing REML vs  
484 Bayes Gibbs sampling for estimating (co)variance components in mixed models by stochastic  
485 simulation, both methods were seemingly unbiased (Van Tassell *et al.*, 1995; Duangjinda *et al.*,  
486 2001). Models compared included different genetic or environmental effects, and different data  
487 based selection policies were performed. For the sake of completeness, we obtained REML  
488 estimates of the dispersion parameters using the EM algorithm (Dempster *et al.*, 1977), using  
489 formulae described in Appendix B. The estimated (co)variance components were  $\hat{\sigma}_{Ad}^2 = 13.889$ ,  
490  $\hat{\sigma}_{AdAc} = -3.335$ ,  $\hat{\sigma}_{Ac}^2 = 1.521$ ,  $\hat{\sigma}_p^2 = 1.150$ , and  $\hat{\sigma}_e^2 = 3.997$ . On the other hand, the estimated  
491 REML-EM variances in the model with direct effects only (no competition effects) were  $\hat{\sigma}_{Ad}^2 =$   
492  $7.572$ , and  $\hat{\sigma}_e^2 = 12.496$ . Although there were some differences, both sets of estimates of the  
493 (co)variance components for the model with competition effects obtained were similar. For the  
494 model without competition effects, the REML-EM estimate of the additive variance was smaller  
495 and the estimated error variance was larger than corresponding Bayesian estimates. An analytical  
496 comparison can be established for the prediction of breeding values using either REML+BLUP or  
497 Bayesian posterior means. Arora and Lahiri (1997, theorem 1, page 1056) showed that BLUP



498 prediction of random effects from a general mixed model with estimated variance components  
499 (for example, those resulting from the use of REML) have the same expected value as the  
500 Bayesian posterior means from the same model. However, the mean square error of the Bayesian  
501 posterior mean is always smaller than the one obtained from the REML+BLUP predictions. Thus,  
502 one may expect the predictions to be similar on average, but the mean square of the Bayes  
503 posterior means will be smaller than their BLUP counterparts. The exclusion of competition  
504 effects introduces bias in the prediction of breeding values for direct effects, either in an  
505 individual tree model or in a parental or family model. If the individual tree model with  
506 competition effects is difficult to fit, the same predictions of breeding values can be calculated by  
507 means of an equivalent model (Henderson, 1977) that has a reduced number of equations: the  
508 number of fixed effects plus the number of parent trees. This is the topic of a future publication.

509 Another subject for research in the future is the search for optimal experimental designs to  
510 estimate direct and competition (co)variance components, as for example the use of single-tree  
511 plot *vs* lineal or squared plots. In all cases the additive relationships between competing  
512 individuals should be of major concern.

513

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603

604

## Appendix A

605

### *Derivation of the additive genetic variance with additive competition effects*

606

607

The additive genetic variance for direct and competition breeding values in (6) is:

608

$$\text{Var}(a_{d_i}) + \text{Var}\left(\sum_{j=1}^{m_i} f_{ijk} a_{c_j}\right) + 2 \text{Cov}\left(a_{d_i}, \sum_{j=1}^{m_i} f_{ijk} a_{c_j}\right) \quad [\text{A.1}]$$

609 Using the variance operator in the first term produces

$$610 \quad \text{Var}(a_{d_i}) = (1 + F_i) \sigma_{Ad}^2 \quad [\text{A.2}]$$

611 For the second term in [A.1] we have

$$\begin{aligned} \text{Var}\left(\sum_{j=1}^{m_i} f_{ijk} a_{c_j}\right) &= \text{Var}(f_{i1D} a_{c_1} + f_{i2R-C} a_{c_2} + \dots + f_{imk} a_{c_m}) \\ 612 \quad &= \text{Var}(f_{i1D} a_{c_1}) + \text{Var}(f_{i2R-C} a_{c_2}) + \dots + \text{Var}(f_{imk} a_{c_m}) + 2 \left[ \text{Cov}(f_{i1D} a_{c_1}, f_{i2R-C} a_{c_2}) + \dots + \text{Cov}(f_{ij'k} a_{c_{j'}}, f_{imk} a_{c_m}) \right] \\ &= f_{i1D}^2 \text{Var}(a_{c_1}) + \dots + f_{imk}^2 \text{Var}(a_{c_m}) + 2 \left[ f_{i1D} f_{i2R-C} \text{Cov}(a_{c_1}, a_{c_2}) + \dots + f_{ij'k} f_{imk} \text{Cov}(a_{c_{j'}}, a_{c_m}) \right] \\ 613 \quad &= \sum_{j=1}^{m_i} f_{ijk}^2 \text{Var}(a_{c_j}) + 2 \sum_{j \neq j'}^{m_i} f_{ij'k} f_{imk} \text{Cov}(a_{c_{j'}}, a_{c_m}) \\ 614 \quad &= \sum_{j=1}^{m_i} f_{ijk}^2 (1 + F_j) \sigma_{Ac}^2 + 2 \sum_{j \neq j'}^{m_i} f_{ij'k} f_{imk} A_{jj'} \sigma_{Ac}^2 \end{aligned}$$

615 where  $A_{jj'}$  indicates the relationship between competitors  $j$  and  $j'$ . Therefore

$$616 \quad \text{Var}\left(\sum_{j=1}^{m_i} f_{ijk} a_{c_j}\right) = \left[ (n_{R-C} f_{iR-C}^2 + n_D f_{iD}^2) (1 + F_j) + 2 \sum_{j \neq j'}^{m_i} f_{ij'k} f_{imk} A_{jj'} \right] \sigma_{Ac}^2 \quad [\text{A.3}]$$

617 For the third term in [A.1] we use the covariance operator so that

$$\begin{aligned} \text{Cov}\left(a_{d_i}, \sum_{j=1}^{m_i} f_{ijk} a_{c_j}\right) &= \text{Cov}(a_{d_i}, f_{i1D} a_{c_1} + f_{i2R-C} a_{c_2} + \dots + f_{imk} a_{c_m}) \\ 618 \quad &= \text{Cov}(a_{d_i}, f_{i1D} a_{c_1}) + \text{Cov}(a_{d_i}, f_{i2R-C} a_{c_2}) + \dots + \text{Cov}(a_{d_i}, f_{imk} a_{c_m}) \\ &= f_{i1D} \text{Cov}(a_{d_i}, a_{c_1}) + f_{i2R-C} \text{Cov}(a_{d_i}, a_{c_2}) + \dots + f_{imk} \text{Cov}(a_{d_i}, a_{c_m}) \\ &= \sum_{j=1}^{m_i} f_{ijk} A_{ij} \sigma_{AdAc} \end{aligned} \quad [\text{A.4}]$$

619 Now, by replacing in [A.1] with [A.2], [A.3] and [A.4] gives the additive variance terms for the

620 variance of  $y_{ij^1..j^m}$  in [9] as

$$621 \quad \text{Var}\left(a_{d_i} + \sum_{j=1}^{m_i} f_{ijk} a_{c_j}\right) = (1 + F_i) \sigma_{Ad}^2 + \left[ (n_{R-C} f_{iR-C}^2 + n_D f_{iD}^2) (1 + F_j) + 2 \sum_{j \neq j'}^{m_i} f_{ij'k} f_{imk} A_{jj'} \right] \sigma_{Ac}^2 + 2 \sum_{j=1}^{m_i} f_{ijk} A_{ij} \sigma_{AdAc}$$

622

623

## Appendix B

624 *REML-EM equations for the (co)variance components in a model with additive direct, additive*  
 625 *competition breeding values and permanent environmental competition effects.*

626

627 In order to obtain REML-EM of dispersion parameters in model [10], we take a similar  
 628 approach to Cantet *et al.* (1993). Let the mixed model equations for the mixed model [10] be:

$$629 \begin{bmatrix} X'R^{-1}X & X'R^{-1}Z_d' & X'R^{-1}Z_c' & X'R^{-1}Z_p' \\ Z_d'R^{-1}X & Z_d'R^{-1}Z_d + k_{11}A^{-1} & Z_d'R^{-1}Z_c + k_{12}A^{-1} & Z_d'R^{-1}Z_p \\ Z_c'R^{-1}X & Z_c'R^{-1}Z_d + k_{21}A^{-1} & Z_c'R^{-1}Z_c + k_{22}A^{-1} & Z_c'R^{-1}Z_p \\ Z_p'R^{-1}X & Z_p'R^{-1}Z_d & Z_p'R^{-1}Z_c & Z_p'R^{-1}Z_p + I\left(\frac{\sigma_p^2}{\sigma_e^2}\right) \end{bmatrix} \begin{bmatrix} \hat{\beta} \\ \hat{a}_d \\ \hat{a}_c \\ \hat{p}_c \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z_d'R^{-1}y \\ Z_c'R^{-1}y \\ Z_p'R^{-1}y \end{bmatrix} \quad [B.1]$$

630 The inverse of the coefficient matrix in [B.1] is

$$631 \begin{bmatrix} X'R^{-1}X & X'R^{-1}Z_d' & X'R^{-1}Z_c' & X'R^{-1}Z_p' \\ Z_d'R^{-1}X & Z_d'R^{-1}Z_d + k_{11}A^{-1} & Z_d'R^{-1}Z_c + k_{12}A^{-1} & Z_d'R^{-1}Z_p \\ Z_c'R^{-1}X & Z_c'R^{-1}Z_d + k_{21}A^{-1} & Z_c'R^{-1}Z_c + k_{22}A^{-1} & Z_c'R^{-1}Z_p \\ Z_p'R^{-1}X & Z_p'R^{-1}Z_d & Z_p'R^{-1}Z_c & Z_p'R^{-1}Z_p + I\left(\frac{\sigma_p^2}{\sigma_e^2}\right) \end{bmatrix}^{-1} = \begin{bmatrix} C^{\beta\beta} & C^{\beta a_d} & C^{\beta a_c} & C^{\beta p_c} \\ C^{a_d\beta} & C^{a_d a_d} & C^{a_d a_c} & C^{a_d p_c} \\ C^{a_c\beta} & C^{a_c a_d} & C^{a_c a_c} & C^{a_c p_c} \\ C^{p_c\beta} & C^{p_c a_d} & C^{p_c a_c} & C^{p_c p_c} \end{bmatrix}$$

632 Then, the REML-EM estimating equations of the dispersion parameters in the  $k^{\text{th}}$  iteration are

$$633 \hat{\sigma}_{Ad}^2 [k] = \frac{[\hat{a}_d' A^{-1} \hat{a}_d]^{[k]} + \text{tr}(A^{-1} C^{a_d a_d}) \hat{\sigma}_e^{2[k-1]}}{q}$$

$$634 \hat{\sigma}_{Ac}^2 [k] = \frac{[\hat{a}_c' A^{-1} \hat{a}_c]^{[k]} + \text{tr}(A^{-1} C^{a_c a_c}) \hat{\sigma}_e^{2[k-1]}}{q}$$

$$635 \hat{\sigma}_{AcAd} [k] = \frac{[\hat{a}_d' A^{-1} \hat{a}_c]^{[k]} + \text{tr}(A^{-1} C^{a_c a_d}) \hat{\sigma}_e^{2[k-1]}}{q}$$

$$636 \hat{\sigma}_p^2 [k] = \frac{[\hat{p}_c' \hat{p}_c]^{[k]} + \text{tr}(C^{p_c p_c}) \hat{\sigma}_e^{2[k-1]}}{n}$$

$$637 \hat{\sigma}_e^2 [k] = \frac{[\hat{e}' \hat{e}]^{[k]} + (p + 2q - f^{[k]} \hat{\sigma}_e^{2[k-1]}) \hat{\sigma}_e^{2[k-1]}}{n}$$

638 where  $\hat{\mathbf{e}}^{[k]} = \mathbf{y} - \mathbf{X}\hat{\boldsymbol{\beta}}^{[k]} - \mathbf{Z}_d\hat{\mathbf{a}}_d^{[k]} - \mathbf{Z}_c\hat{\mathbf{a}}_c^{[k]} - \mathbf{Z}_p\hat{\mathbf{p}}_c^{[k]}$ , and

639 
$$f^{[k]} = \left[ \text{tr}(\mathbf{A}^{-1}\mathbf{C}^{dd})\mathbf{g}^{dd} + 2\text{tr}(\mathbf{A}^{-1}\mathbf{C}^{dc})\mathbf{g}^{dc} + \text{tr}(\mathbf{A}^{-1}\mathbf{C}^{cc})\mathbf{g}^{cc} + \text{tr}(\mathbf{C}^{p_c p_c})\hat{\boldsymbol{\sigma}}_p^{-2} \right]$$

640 with  $\mathbf{G}_0^{-1} = \begin{bmatrix} \mathbf{g}^{dd} & \mathbf{g}^{dc} \\ \mathbf{g}^{cd} & \mathbf{g}^{cc} \end{bmatrix}$ .