Environmental heterogeneity and competition effects in forest genetics trials

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CONICET

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Outline

Introduction:

- **Introduction to environmental heterogeneity (EH) and competition effects (CE):**
    - Definitions of EH and CE.
    - Consequences of ignoring EH and CE.
    - Spatial models:
        - An introduction to spatial models with autoregressive residuals.
        - An introduction to spatial model with two dimensional B-spline.
    - Competition model:
        - An introduction to mixed model with genetic and environmental competition effects.

Outline

Material & Methods:

1. Diagnosis of EH and CE problems (with examples in *E. globulus*, Western hemlock, Western larch, Loblolly pine, and Douglas-fir tree species):

- Spatial analysis of residuals:
    - Median of residuals - Residual values in two dimensions - Residual against row and column position - Sample variogram - Other ways to identify competition effects.

2. Mixed models to account for EH and CE:

- Matrix expression, and moments:
    - Spatial models with autoregressive residuals.
    - Spatial model with two dimensional B-spline.
    - Competition model.

Outline

Results:

- **Examples of application of the mixed model with a smoothed surface in *E. globulus*, Western hemlock, Loblolly pine, and Douglas-fir.**
- **An example of application of the mixed model with competition effects in Loblolly pine.**

Environmental heterogeneity and competition effects

The "best linear unbiased predictors" (BLUP) of tree breeding values depends on the (co)variance matrices for the assumed model.

Then, the specification of the dispersion parameters should take into account the **positive spatial correlation** due to the **environmental heterogeneity**, and the **negative correlation** caused by **competition among individuals**.

Environmental heterogeneity generates positive auto-correlation between neighbouring plants, and plant interference due to competition generates negative auto-correlation between them.

Environmental heterogeneity and competition effects

Both phenomena, in any given experiment, **are dynamic and coexist simultaneously**.

“Shortly after outplanting (establishment) the spatial correlations will be near zero because the plants have yet to express the quality of their microsites. Gradually the spatial autocorrelation will increase, as neighboring plants respond in similar ways to their shared microsite. Later, after onset of interplant competition, a drop in the correlation must be anticipated as a consequence of competition, which will tend to create "winners" and "losers" at a local scale”.

Magnussen CJFR (1994)

It is clear that there is initially a positive correlation between the sizes of nearby trees, presumably due to microsite similarities. Later, competition overcomes this effect, and the correlation becomes negative. Any competition-induced oscillations in the correlation function, as described by Matérn (1960) and Bachacou and Decourt (1976), would be obscured here by the irregular and nominally rectangular (1.8 × 2.4m) spacing. Figure 5 demonstrates the changes with age in the correlation for the 2m distance.

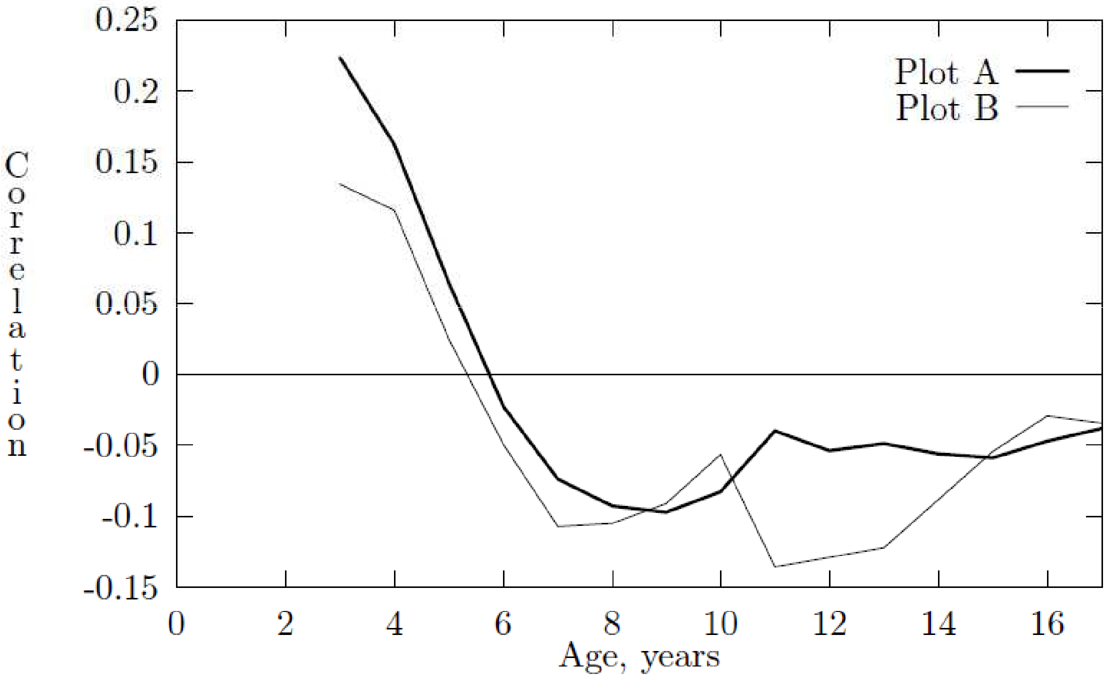

Figure 5: Change in 2m correlations with age

What is a diameter distribution?

Oscar García
Forest Research Institute
Rotorua, New Zealand[*]

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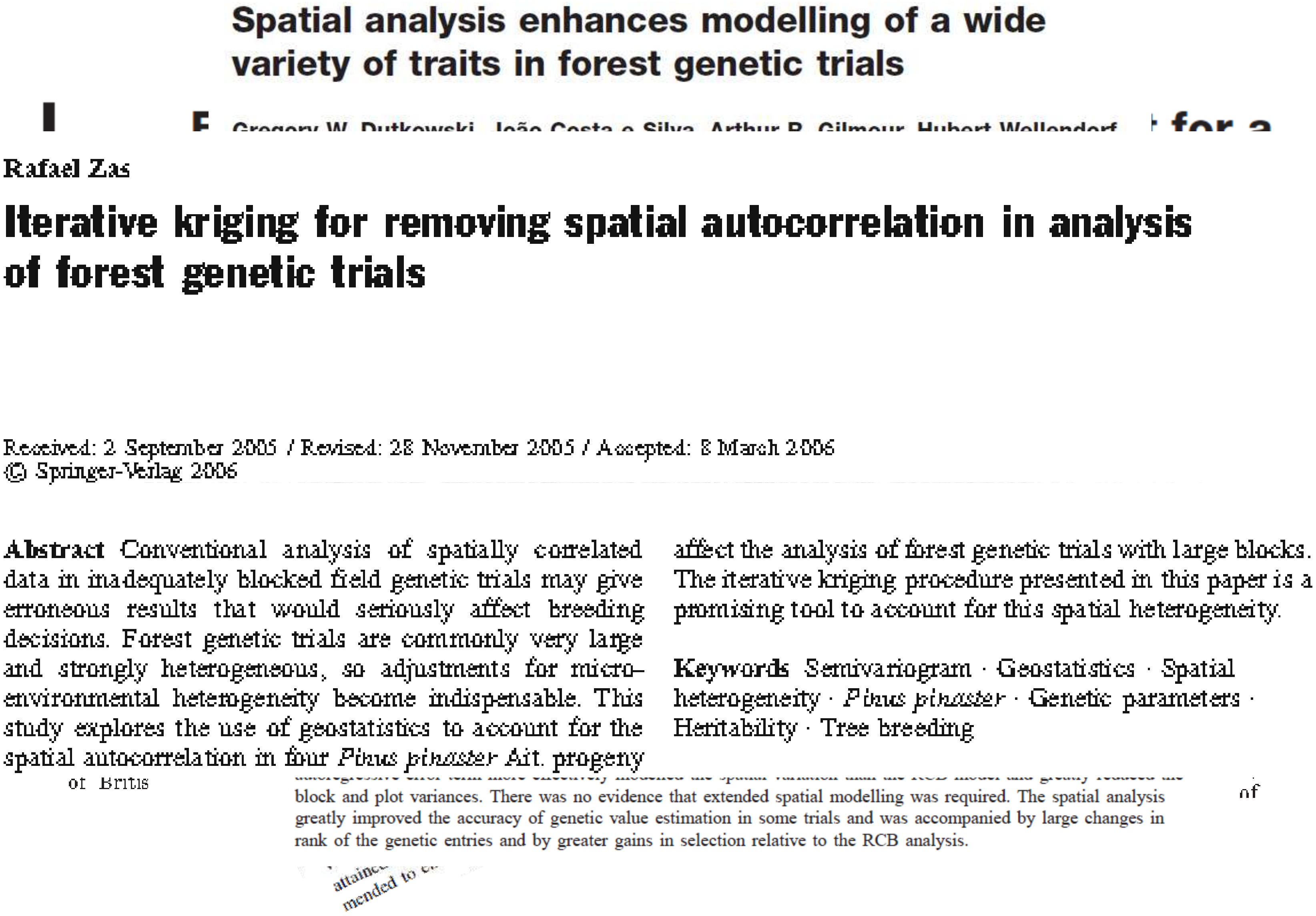
[*] Presented at the IUFRO Symposium on Integrated Forest Management Information Systems, Tsukuba, Japan, October 13–18, 1991

Eduardo Pablo Cappa, June 2015

Introduction

Environmental heterogeneity



Spatial analysis enhances modelling of a wide variety of traits in forest genetic trials

Gregory W. Dutkowski · João Costa e Silva · Arthur R. Gilmour · Hubert Wellendorf

Rafael Zas

Iterative kriging for removing spatial autocorrelation in analysis of forest genetic trials

Received: 2 September 2005 / Revised: 28 November 2005 / Accepted: 8 March 2006

Abstract Conventional analysis of spatially correlated data in inadequately blocked field genetic trials may give erroneous results that would seriously affect breeding decisions. Forest genetic trials are commonly very large and strongly heterogeneous, so adjustments for micro-environmental heterogeneity become indispensable. This study explores the use of geostatistics to account for the spatial autocorrelation in four *Pinus pinaster* Ait. progeny affect the analysis of forest genetic trials with large blocks. The iterative kriging procedure presented in this paper is a promising tool to account for this spatial heterogeneity.

Keywords Semivariogram · Geostatistics · Spatial heterogeneity · *Pinus pinaster* · Genetic parameters · Heritability · Tree breeding

of Britis

block and plot variances. There was no evidence that extended spatial modelling was required. The spatial analysis greatly improved the accuracy of genetic value estimation in some trials and was accompanied by large changes in rank of the genetic entries and by greater gains in selection relative to the RCB analysis.

Spatial analysis

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*"**Spatial analysis should be routinely applied in forest genetic trial analysis** where the spatial arrangement of trees can be determined."*

Dutkowski *et al*. CJFR (2006)

In FGT **ignoring the environmental heterogeneity** can lead to **biases** in the estimation of **genetic parameters** and the prediction of individual additive genetic effects (i.e. **BLUP of BV**).

Ignoring the environmental heterogeneity …

(Terrance Z. Ye & Keith J. S. Jayawickrama 2008 TGG 4: 677-692)

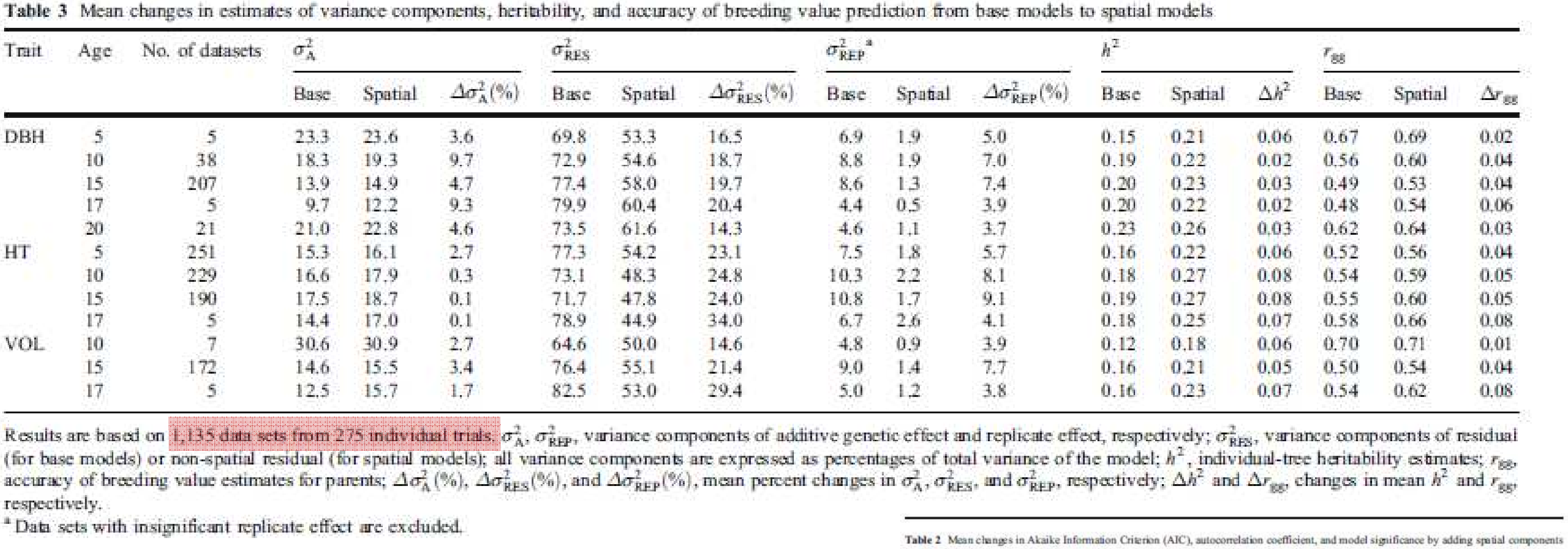


Table 3 Mean changes in estimates of variance components, heritability, and accuracy of breeding value prediction from base models to spatial models

Trait	Age	No. of datasets	σ^2_A Base	σ^2_A Spatial	$\Delta\sigma^2_A$(%)	σ^2_{RES} Base	σ^2_{RES} Spatial	$\Delta\sigma^2_{RES}$(%)	σ^2_{REP}[a] Base	σ^2_{REP}[a] Spatial	$\Delta\sigma^2_{REP}$(%)	h^2 Base	h^2 Spatial	Δh^2	r_{gg} Base	r_{gg} Spatial	Δr_{gg}
DBH	5	5	23.3	23.6	3.6	69.8	53.3	16.5	6.9	1.9	5.0	0.15	0.21	0.06	0.67	0.69	0.02
	10	38	18.3	19.3	9.7	72.9	54.6	18.7	8.8	1.9	7.0	0.19	0.22	0.02	0.56	0.60	0.04
	15	207	13.9	14.9	4.7	77.4	58.0	19.7	8.6	1.3	7.4	0.20	0.23	0.03	0.49	0.53	0.04
	17	5	9.7	12.2	9.3	79.9	60.4	20.4	4.4	0.5	3.9	0.20	0.22	0.02	0.48	0.54	0.06
	20	21	21.0	22.8	4.6	73.5	61.6	14.3	4.6	1.1	3.7	0.23	0.26	0.03	0.62	0.64	0.03
HT	5	251	15.3	16.1	2.7	77.3	54.2	23.1	7.5	1.8	5.7	0.16	0.22	0.06	0.52	0.56	0.04
	10	229	16.6	17.9	0.3	73.1	48.3	24.8	10.3	2.2	8.1	0.18	0.27	0.08	0.54	0.59	0.05
	15	190	17.5	18.7	0.1	71.7	47.8	24.0	10.8	1.7	9.1	0.19	0.27	0.08	0.55	0.60	0.05
	17	5	14.4	17.0	0.1	78.9	44.9	34.0	6.7	2.6	4.1	0.18	0.25	0.07	0.58	0.66	0.08
VOL	10	7	30.6	30.9	2.7	64.6	50.0	14.6	4.8	0.9	3.9	0.12	0.18	0.06	0.70	0.71	0.01
	15	172	14.6	15.5	3.4	76.4	55.1	21.4	9.0	1.4	7.7	0.16	0.21	0.05	0.50	0.54	0.04
	17	5	12.5	15.7	1.7	82.5	53.0	29.4	5.0	1.2	3.8	0.16	0.23	0.07	0.54	0.62	0.08

Results are based on 1,135 data sets from 275 individual trials. σ^2_A, σ^2_{REP}, variance components of additive genetic effect and replicate effect, respectively; σ^2_{RES}, variance components of residual (for base models) or non-spatial residual (for spatial models); all variance components are expressed as percentages of total variance of the model; h^2, individual-tree heritability estimates; r_{gg}, accuracy of breeding value estimates for parents; $\Delta\sigma^2_A$(%), $\Delta\sigma^2_{RES}$(%), and $\Delta\sigma^2_{REP}$(%), mean percent changes in σ^2_A, σ^2_{RES}, and σ^2_{REP}, respectively; Δh^2 and Δr_{gg}, changes in mean h^2 and r_{gg}, respectively.

[a] Data sets with insignificant replicate effect are excluded.

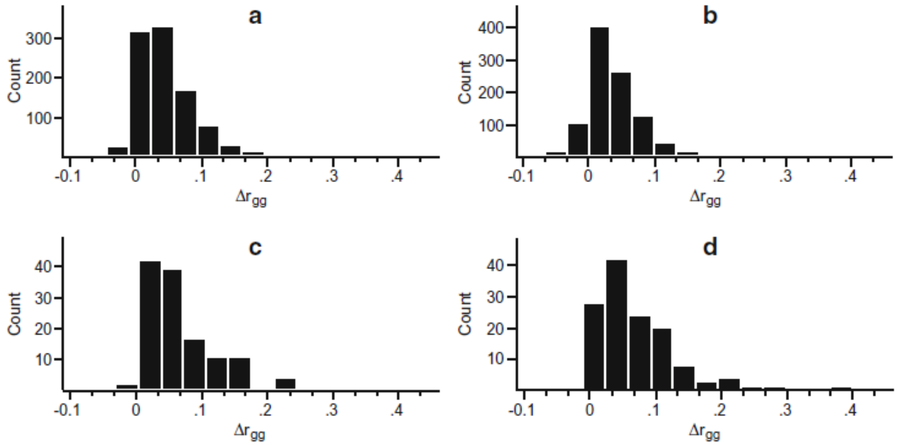


Fig. 2 Changes in accuracy of breeding value prediction (Δr_{gg}) for parents and offspring from base models to spatial models. **a** For parents in reps-in-sets design; **b** for offspring in reps-in-sets design; **c** for parents in sets-in-reps design; and d) for offspring in sets-in-reps design

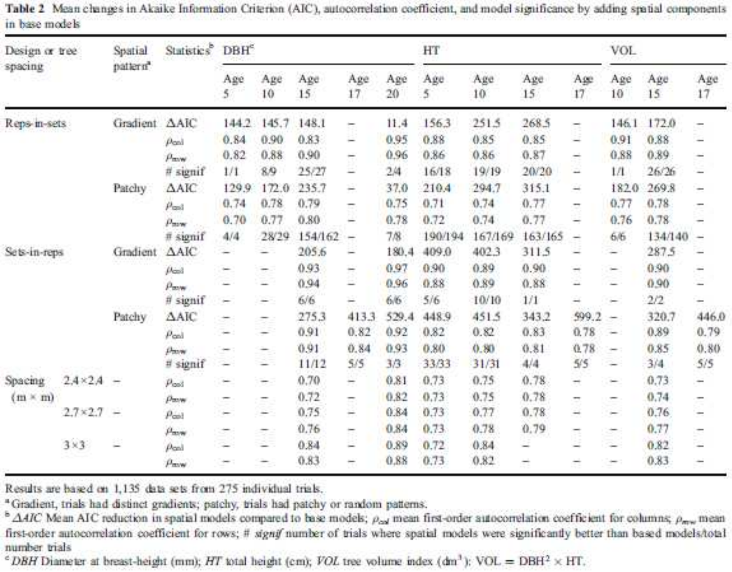


Table 2 Mean changes in Akaike Information Criterion (AIC), autocorrelation coefficient, and model significance by adding spatial components in base models

Design or tree spacing		Spatial pattern[a]	Statistics[b]	DBH[c] Age 5	DBH[c] Age 10	DBH[c] Age 15	DBH[c] Age 17	DBH[c] Age 20	HT Age 5	HT Age 10	HT Age 15	HT Age 17	VOL Age 10	VOL Age 15	VOL Age 17
Reps-in-sets		Gradient	ΔAIC	144.2	145.7	148.1	–	11.4	156.3	251.5	268.5	–	146.1	172.0	–
			ρ_{col}	0.84	0.90	0.83	–	0.95	0.88	0.85	0.85	–	0.91	0.88	–
			ρ_{row}	0.82	0.88	0.90	–	0.96	0.86	0.86	0.87	–	0.88	0.89	–
			# signif	1/1	8/9	25/27	–	2/4	16/18	19/19	20/20	–	1/1	26/26	–
		Patchy	ΔAIC	129.9	172.0	235.7	–	37.0	210.4	294.7	315.1	–	182.0	269.8	–
			ρ_{col}	0.74	0.78	0.79	–	0.75	0.71	0.74	0.77	–	0.77	0.78	–
			ρ_{row}	0.70	0.77	0.80	–	0.78	0.72	0.74	0.77	–	0.76	0.78	–
			# signif	4/4	28/29	154/162	–	7/8	190/194	167/169	163/165	–	6/6	134/140	–
Sets-in-reps		Gradient	ΔAIC	–	–	205.6	–	180.4	409.0	402.3	311.5	–	–	287.5	–
			ρ_{col}	–	–	0.93	–	0.97	0.90	0.89	0.90	–	–	0.90	–
			ρ_{row}	–	–	0.94	–	0.96	0.88	0.89	0.88	–	–	0.90	–
			# signif	–	–	6/6	–	6/6	5/6	10/10	1/1	–	–	2/2	–
		Patchy	ΔAIC	–	–	275.3	413.3	529.4	448.9	451.5	343.2	599.2	–	320.7	446.0
			ρ_{col}	–	–	0.91	0.82	0.92	0.82	0.82	0.83	0.78	–	0.89	0.79
			ρ_{row}	–	–	0.91	0.84	0.93	0.80	0.80	0.81	0.78	–	0.85	0.80
			# signif	–	–	11/12	5/5	3/3	33/33	31/31	4/4	5/5	–	3/4	5/5
Spacing (m × m)	2.4×2.4	–	ρ_{col}	–	–	0.70	–	0.81	0.73	0.75	0.78	–	–	0.73	–
			ρ_{row}	–	–	0.72	–	0.82	0.73	0.75	0.78	–	–	0.74	–
	2.7×2.7	–	ρ_{col}	–	–	0.75	–	0.84	0.73	0.77	0.78	–	–	0.76	–
			ρ_{row}	–	–	0.76	–	0.84	0.73	0.78	0.79	–	–	0.77	–
	3×3	–	ρ_{col}	–	–	0.84	–	0.89	0.72	0.84	–	–	–	0.82	–
			ρ_{row}	–	–	0.83	–	0.88	0.73	0.82	–	–	–	0.83	–

Results are based on 1,135 data sets from 275 individual trials.

[a] Gradient, trials had distinct gradients; patchy, trials had patchy or random patterns.

[b] *ΔAIC* Mean AIC reduction in spatial models compared to base models; ρ_{col} mean first-order autocorrelation coefficient for columns; ρ_{row} mean first-order autocorrelation coefficient for rows; # *signif* number of trials where spatial models were significantly better than based models/total number trials

[c] *DBH* Diameter at breast-height (mm); *HT* total height (cm); *VOL* tree volume index (dm^3): VOL = DBH^2 × HT.

Ignoring the environmental heterogeneity …

(Dutkowsky et al. 2006 CJFR 36:1851-1870)

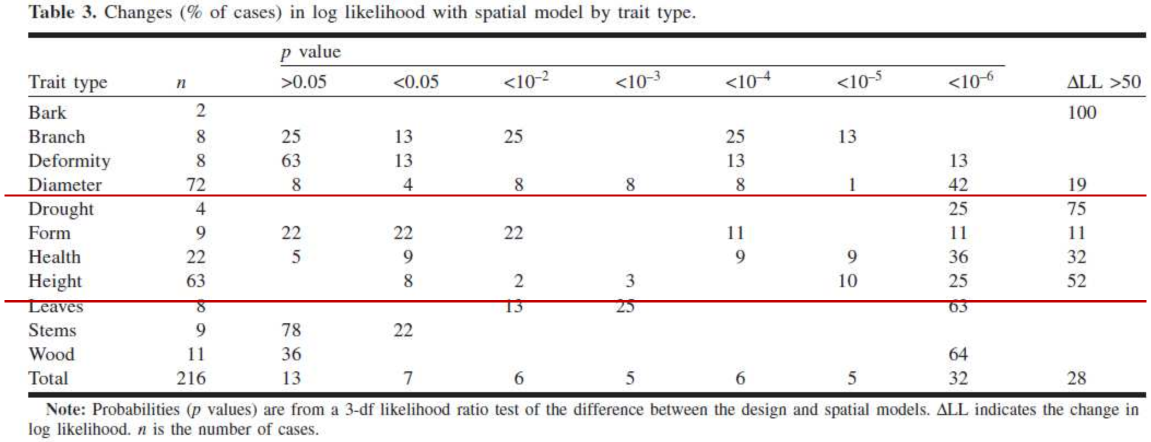


Table 3. Changes (% of cases) in log likelihood with spatial model by trait type.

Trait type	*n*	*p* value >0.05	<0.05	$<10^{-2}$	$<10^{-3}$	$<10^{-4}$	$<10^{-5}$	$<10^{-6}$	ΔLL >50
Bark	2								100
Branch	8	25	13	25		25	13		
Deformity	8	63	13			13		13	
Diameter	72	8	4	8	8	8	1	42	19
Drought	4							25	75
Form	9	22	22	22		11		11	11
Health	22	5	9			9	9	36	32
Height	63		8	2	3		10	25	52
Leaves	8			13	25			63	
Stems	9	78	22						
Wood	11	36						64	
Total	216	13	7	6	5	6	5	32	28

Note: Probabilities (*p* values) are from a 3-df likelihood ratio test of the difference between the design and spatial models. ΔLL indicates the change in log likelihood. *n* is the number of cases.

Fig. 7. Genetic variance (additive or clonal) for design and spatial models by trait type. Note: The variances are expressed as a proportion of the design model error variance. Results from spatial models with nonsignificant model improvement are not shown. Data points mentioned in the text are labelled with the trial code, trait name, and age.

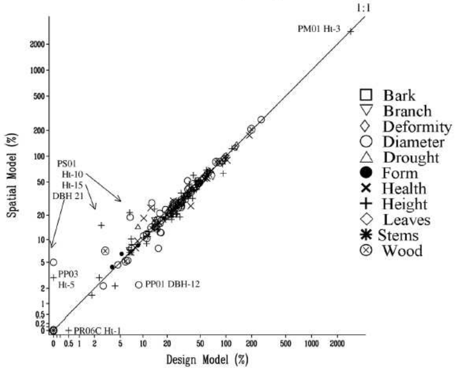


Fig. 8. Change in additive genetic value accuracy from design to spatial models by trait type. Note: Results from spatial models with nonsignificant model improvement are not shown. Data points mentioned in the text are labelled with the trial code, trait name, and age.

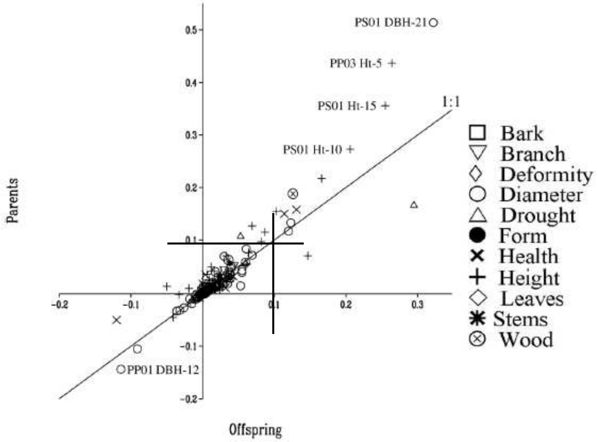
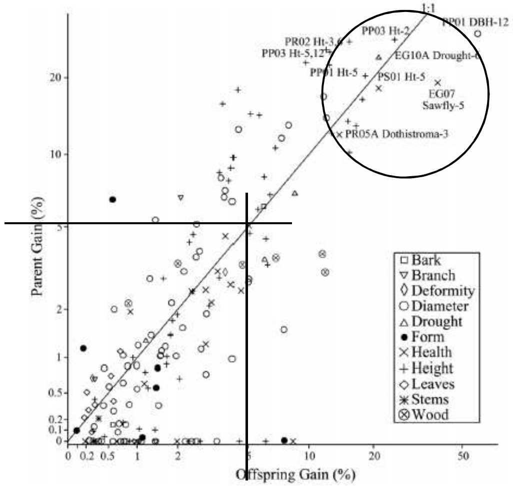


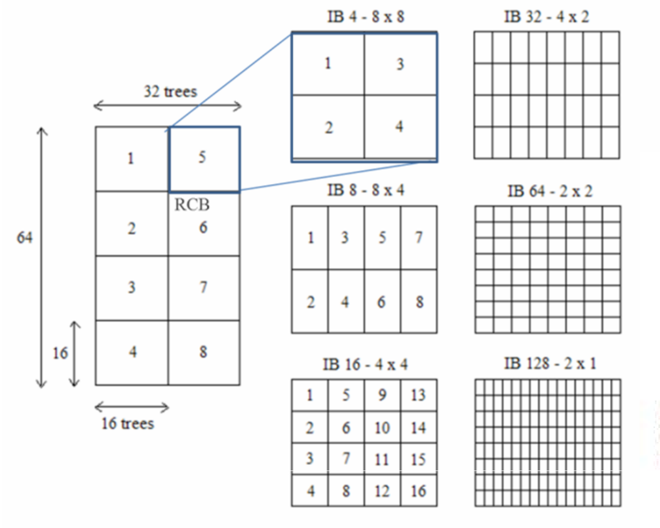
Fig. 10. Gain from selection for spatial models by trait type. Note: Gain is for selection of the best 5% of offspring and 20% of parents. Gain is expressed as the relative value on the scale of genetic values from the spatial model of the trees selected with the spatial model compared with those selected by the design model. Results from spatial models with nonsignificant model improvement are not shown. Data points mentioned in the text are labelled with the trial code, trait name, and age.



Eduardo Pablo Cappa, June 2015

Ignoring the environmental heterogeneity …

(Gezan 2005, PhD thesis University of Florida)



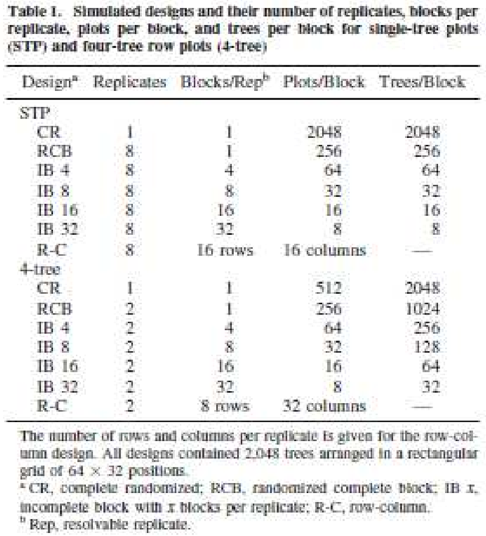


Table 1. Simulated designs and their number of replicates, blocks per replicate, plots per block, and trees per block for single-tree plots (STP) and four-tree row plots (4-tree)

Design[a]	Replicates	Blocks/Rep[b]	Plots/Block	Trees/Block
STP				
CR	1	1	2048	2048
RCB	8	1	256	256
IB 4	8	4	64	64
IB 8	8	8	32	32
IB 16	8	16	16	16
IB 32	8	32	8	8
R-C	8	16 rows	16 columns	—
4-tree				
CR	1	1	512	2048
RCB	2	1	256	1024
IB 4	2	4	64	256
IB 8	2	8	32	128
IB 16	2	16	16	64
IB 32	2	32	8	32
R-C	2	8 rows	32 columns	—

The number of rows and columns per replicate is given for the row-column design. All designs contained 2,048 trees arranged in a rectangular grid of 64 × 32 positions.

[a] CR, complete randomized; RCB, randomized complete block; IB x, incomplete block with x blocks per replicate; R-C, row-column.

[b] Rep, resolvable replicate.

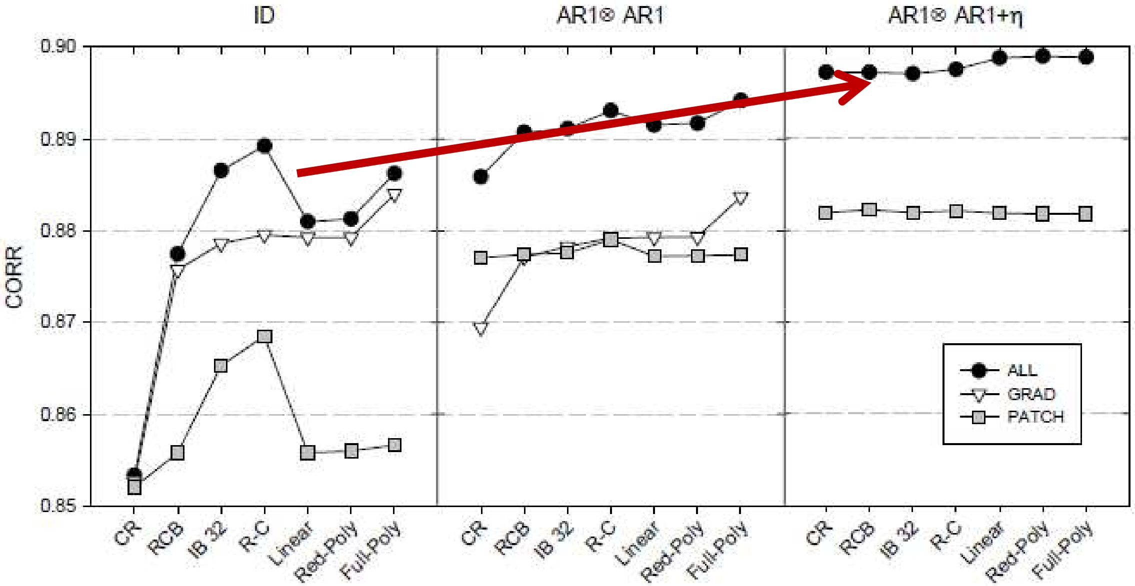


Figure 4-2. Average correlations between true and predicted treatment effects (CORR) in 3 different surface patterns for classical experimental design analyses and polynomial models fitted for the following error structures: independent errors (ID); autoregressive without nugget (AR1⊗AR1); and autoregressive with nugget (AR1⊗AR1+η). Surface GRAD is not shown in the last graph because few simulations converged.

Environmental heterogeneity

Spatial environmental variation within a site is largely of two types: global trend or large-scale variation and/or local trend or small-scale variation.

✓**Global trend**: definida como una variación espacialmente continua que se distribuye por todo el sitio ("gradient").

✓**Local trend**: es la variación espacialmente continua que, a diferencia de la anterior, se manifiesta en un área local ("patches").

Both are well known in forestry field trials **as a result of factors such as variations in soil fertility, moisture, depth, slope or anthropogenic activities** .

Environmental heterogeneity

To account for the environmental heterogeneity, tree breeders use *"a priori" designs: e.i.* randomized complete blocks or incomplete block designs (IBD).

However, setting fixed limits for the blocks makes it difficult to account for continuously varying environmental factors.

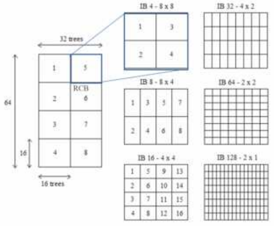
Additionally,

In real progeny trials, the true pattern of environmental variation is never known prior to establishment, which makes choosing an optimum IBD difficult, if not impossible.

Fu et al. CJFR 29: 1871–1878 (1999)

Environmental heterogeneity

(Gezan 2005, PhD thesis University of Florida)



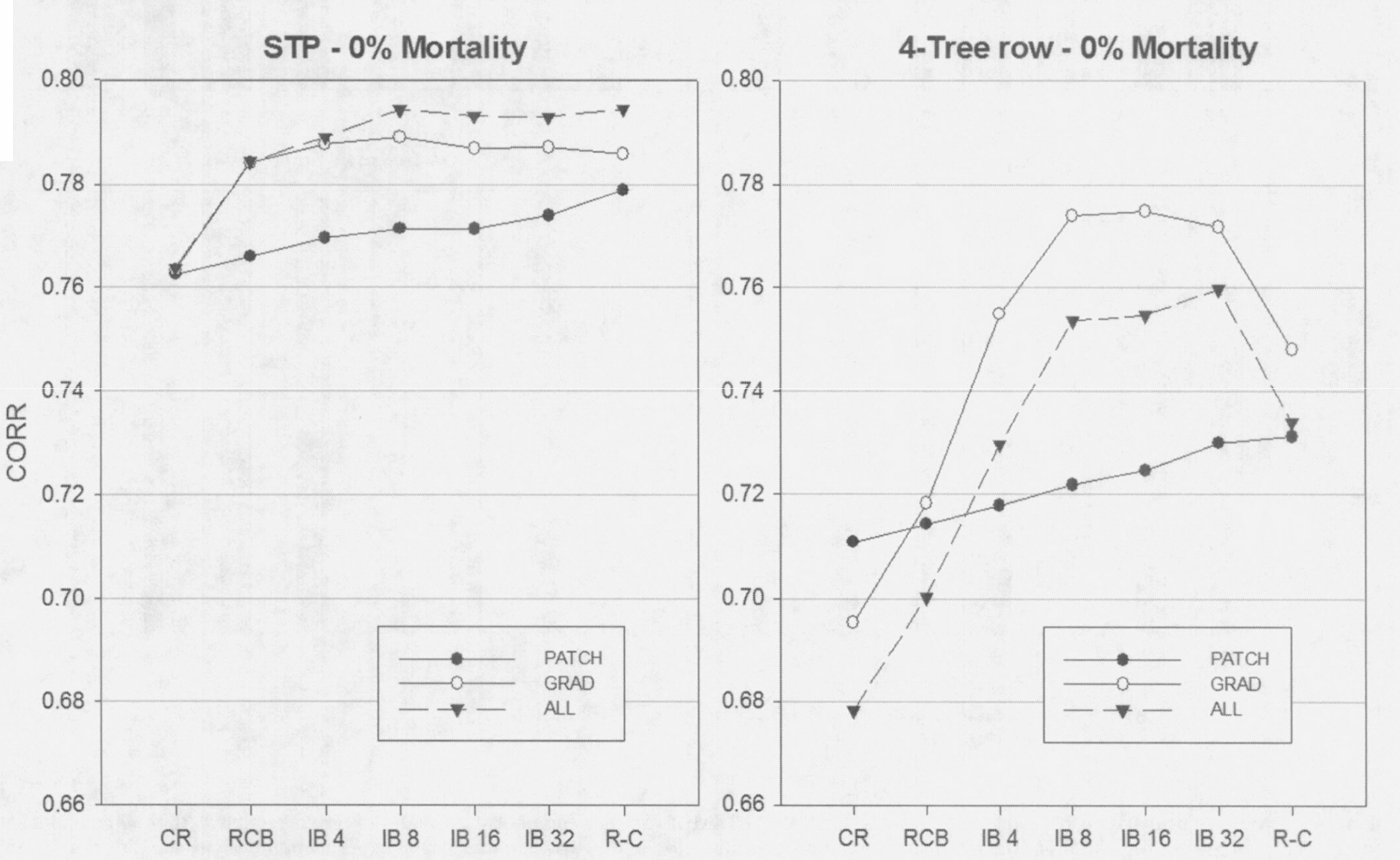


Figure 3. Average estimated correlations between true and predicted clonal values (CORR) obtained from 1,000 simulations for single-tree and four-tree row plots in the 0% mortality case for all surface patterns and designs.

Spatial models

Alternatively, the spatial variation can be accounted for "*a posteriori*" within the model of evaluation.

Spatial models

Several approaches have been developed and applied for **single** forest trials to reduce the effects of the environmental variability.

✓ ***Trend analysis***: El análisis de tendencia es utilizado para describir modelos en donde los efecto fijos de fila y columna se modelan mediante funciones polinómica lineales o cuadráticos o spline suavizadas cúbicas y se asume que los errores son independientes e identicamente distribuidos (*i.i.d*.).

✓"***Nearest-Neihgbor" analysis***: En este caso la variación espacial es modelada incluyendo una estructura de correlación espacial aleatoria (ej. Cullis y Gleeson, 1991; Zimmerman y Harville, 1991).

Other approaches to account for environmental heterogeneity

The small-scale spatial variability has been modeled using **nearest neighbor techniques** (Magnussen 1990; Anekonda and Libby 1996; Joyce et al. 2002; Kroon et al. 2008), or **kriging** (Hamann et al. 2002; Zas 2006).

Some approaches that account for large-scale continuous spatial variation have been modeled through **post-blocking** (Ericsson 1997; Lopez et al. 2002; Gezan et al. 2006; Kroon et al. 2008), or the inclusion of spatial coordinates expressed as either classification variables such as **polynomials** (Thomson and El-kassaby 1988; Federer 1998; Saenz-romero et al. 2001) or **covariables** or **smoothing splines** (Gilmour et al. 1997; Verbyla et al. 1999).

Spatial model with autoregressive residuals

Dutkowski et al. (2006) have recommended the spatial analysis of single FGT by fitting a separable (Kronecker product) two-dimensional first order autoregressive (AR(1)) error covariance structures for rows and columns (Gilmour et al. 1997).

*“**The autoregressive model is very flexible** in the surface it fits, and while it is **classically used as a local trend model** ....”.*

Dutkowski *et al*. CJFR 2006.

Spatial model with B-splines

Cappa and Cantet (2007) proposed to utilize **tensor products of cubic Basic spline (B-spline) based on a mixed model framework** by treating the B-spline function parameters as random variables in a two-dimensional grid.

B-spline are segmented polynomial functions of low degree (commonly linear, quadratic or cubic) that are locally fitted such that the resulting function is differentiable at the joints of the segments (knots).

Cappa and Cantet (2007) demonstrated that this methodology could account for **large-scale continuous spatial variation** in forest genetic evaluation of individual trials.

Spatial model with B-splines

Cappa et al. (2015, Silvae Genetica *minor revision*) demonstrated the utility of the tensor product of cubic basis functions of B-spline in accommodating **complex patterns of spatial heterogeneity** in several large forest genetics trials of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) with single-tree plots design.

a) small-scale variations,

b) small-scale variations together with large-scale variation in one dimension (i.e., across rows or columns) and,

c) small-scale variations together with large-scale variation in two dimensions (i.e., across rows and columns).

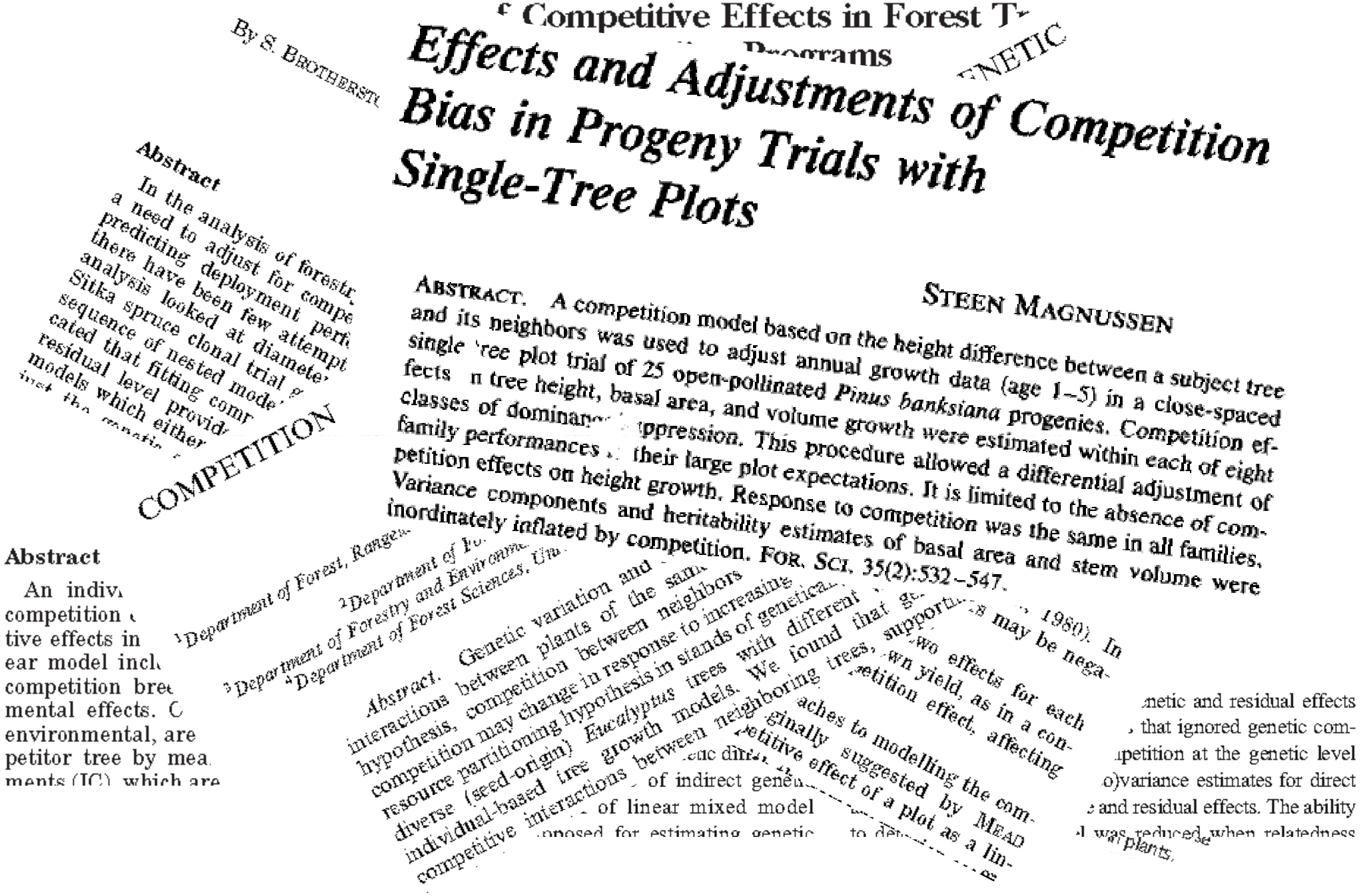
Cappa et al (2011) showed that the tensor product of basis functions of B-spline for rows and columns does provide a useful new alternative to model patterns of spatial variability *a posteriori* **in small forest genetics trials with large multiple-tree contiguous plot configurations**.

Spatial analysis

In general, spatial analysis of single forest genetic trials display a consistent reduction in the error variance and an increase in the heritability. This typically results in a gain in accuracy of breeding values and greater genetic gain when compared with different *a priori* experimental designs.

Introduction

Competition effects



Competitive Effects in Forest T
Programs

By S. BROTHERST

NETIC

Effects and Adjustments of Competition Bias in Progeny Trials with Single-Tree Plots

STEEN MAGNUSSEN

ABSTRACT. A competition model based on the height difference between a subject tree and its neighbors was used to adjust annual growth data (age 1–5) in a close-spaced single tree plot trial of 25 open-pollinated *Pinus banksiana* progenies. Competition effects n tree height, basal area, and volume growth were estimated within each of eight classes of dominan ppression. This procedure allowed a differential adjustment of family performances their large plot expectations. It is limited to the absence of competition effects on height growth. Response to competition was the same in all families. Variance components and heritability estimates of basal area and stem volume were inordinately inflated by competition. FOR. SCI. 35(2):532–547.

Abstract

In the analysis of forestr
a need to adjust for compe
predicting deployment perf
there have been few attempt
analysis looked at diamete
Sitka spruce clonal trial
sequence of nested mode
cated that fitting comp
residual level provid
models which either

COMPETITION

Abstract

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[2] Department of Fo
[3] Department of Forestry and Environme
[4] Department of Forest Sciences, Uni

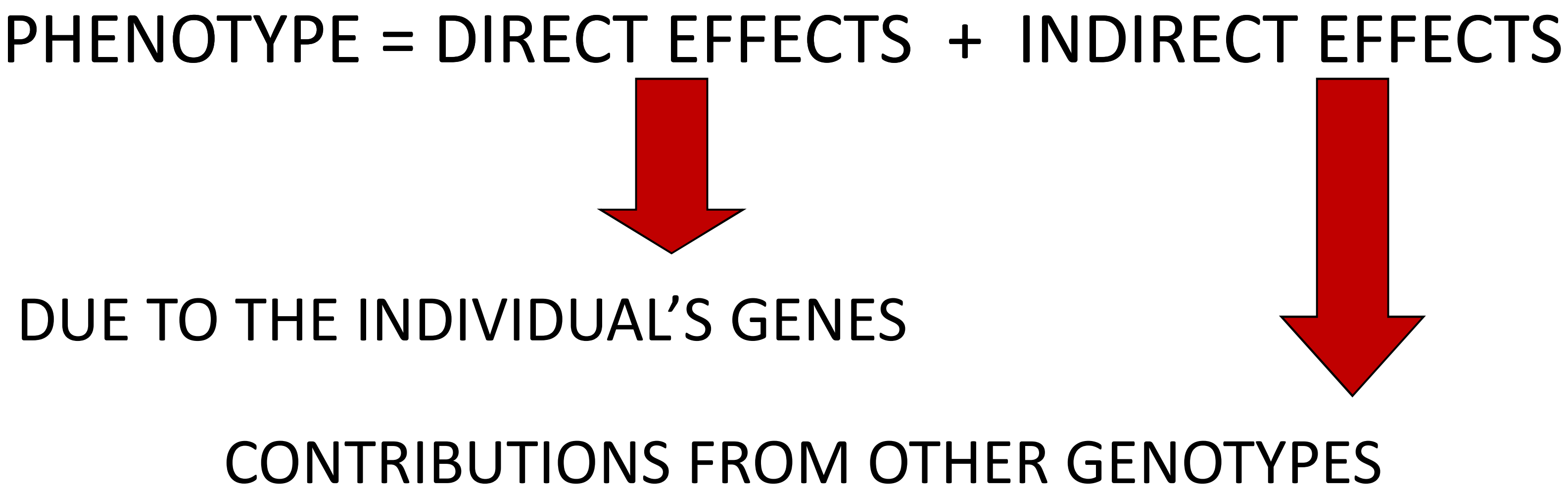
Abstract. Genetic variation and
interactions between plants of the sam
hypothesis, competition between neighbors
competition may change in response to increasing
resource partitioning hypothesis in stands of genetica
diverse (seed-origin) *Eucalyptus* trees with different
individual-based tree growth models. We found that
competitive interactions between neighboring trees, support

1980). In
may be nega-
wo effects for each
wn yield, as in a con-
petition effect, affecting
aches to modelling the com-
ginally suggested by MEAD
petitive effect of a plot as a lin-

of indirect gene
of linear mixed model
posed for estimating genetic

netic and residual effects
that ignored genetic com-
petition at the genetic level
o)variance estimates for direct
e and residual effects. The ability
l was reduced when relatedness
plants.

Competition effects



PHENOTYPE = DIRECT EFFECTS + INDIRECT EFFECTS

DUE TO THE INDIVIDUAL’S GENES

CONTRIBUTIONS FROM OTHER GENOTYPES

Whereas direct genetic effects are expressed on the phenotype of the individual itself, indirect genetic effects are expressed only on the phenotypes of other individuals.

Competition effects

When looking at the genetic evaluation of trees, **COMPETITION** is an indirect genetic effect.

Competition is defined as the stress suffered by a plant due to the **genotype** and the **spatial arrangement of neighboring trees** (Hinson and Hanson, 1962), and is **caused by genetic and environmental sources** (Magnussen, 1989).

Trees may compete at an early stage for water and nutrients, and after canopy closure they compete mainly for light.

Competition effects

Tree **competition** for resources may **bias breeding value** estimation from competing individuals (e.g., Magnussen, 1993; Foster et al., 1998; Radtke et al., 2003; Costa e Silva et al., 2013) by inducing a negative correlation between either individual trees or neighbor plots.

Ignoring competition effects …

(Costa e Silva and Kerr 2013, TGG 9: 1-17; Brotherstone et al. 2011, Silvae Genetica 60: 149-155)

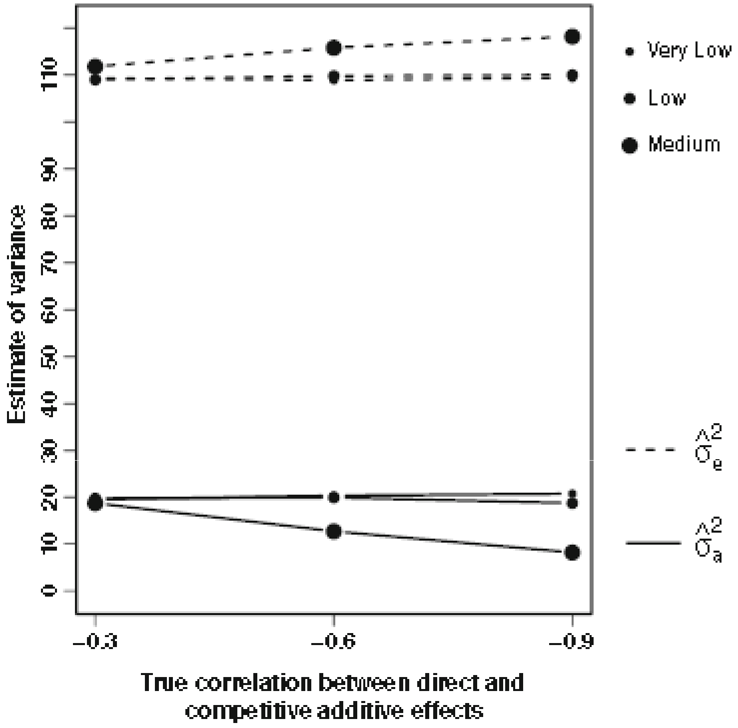


Fig. 3 Estimates of additive ($\hat{\sigma}^2_a$) and residual ($\hat{\sigma}^2_e$) variances from data simulated for a trait representing tree growth and analysed under the B model. The variance estimates are plotted against three simulated values (−0.3, −0.6 and −0.9) of the genetic correlation between direct and competitive additive effects, considering three levels (medium, low and very low) of genetic relatedness within a neighbourhood and 100 % survival. Variances for the underlying true effects in the simulated data were $\sigma^2_d = 20$, $\sigma^2_c = 10$, $\sigma^2_{se} = 80$ and $\sigma^2_{ce} = 20$ for direct additive, competitive additive, independent residual and correlated residual effects, respectively

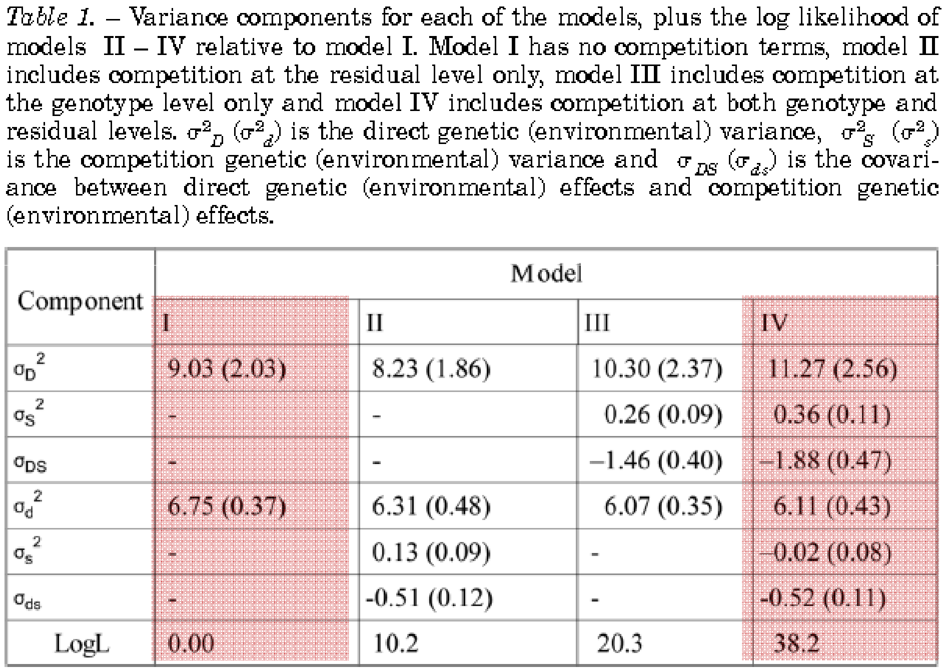


Table 1. – Variance components for each of the models, plus the log likelihood of models II – IV relative to model I. Model I has no competition terms, model II includes competition at the residual level only, model III includes competition at the genotype level only and model IV includes competition at both genotype and residual levels. σ^2_D (σ^2_d) is the direct genetic (environmental) variance, σ^2_S (σ^2_s) is the competition genetic (environmental) variance and σ_{DS} (σ_{ds}) is the covariance between direct genetic (environmental) effects and competition genetic (environmental) effects.

Component	Model			
	I	II	III	IV
σ_D^2	9.03 (2.03)	8.23 (1.86)	10.30 (2.37)	11.27 (2.56)
σ_S^2	-	-	0.26 (0.09)	0.36 (0.11)
σ_{DS}	-	-	−1.46 (0.40)	−1.88 (0.47)
σ_d^2	6.75 (0.37)	6.31 (0.48)	6.07 (0.35)	6.11 (0.43)
σ_s^2	-	0.13 (0.09)	-	−0.02 (0.08)
σ_{ds}	-	-0.51 (0.12)	-	-0.52 (0.11)
LogL	0.00	10.2	20.3	38.2

Ignoring competition effects …

(Cappa and Cantet 2008, Silvae Genetica 57(2): 45-59.)

Loblolly pine data:

Model **without** competition:

$\boldsymbol{\sigma^2_{Ad} = 5.76}$ and $\boldsymbol{\sigma^2_{e} = 12.44}$

Model **with** competition:

$\boldsymbol{\sigma^2_{Ad} = 8.04}$, $\sigma^2_{Ac} = 1.56$, $\sigma_{AdAc} = -3.01$, $\sigma^2_{p} = 1.21$ and $\boldsymbol{\sigma^2_{e} = 8.25}$

Ignoring competition effects ...

Ignoring competitive effects would result in biased estimates of the additive variance.

$$\begin{array}{ccc} w_1 & w_2 & w_3 \\ w_4 & x & w_5 \\ w_6 & w_7 & w_8 \end{array} \qquad\qquad \begin{array}{ccc} z_1 & z_2 & z_3 \\ z_4 & y & z_5 \\ z_6 & z_7 & z_8 \end{array}$$

Single-tree plot design

$$\begin{array}{cccccccc} \bullet w_1 & \bullet\, w_2 & \bullet\, w_3 & \cdots & \bullet\, z_1 & \bullet\, z_2 & \bullet\, z_3 \\ \bullet w_4 & \bullet\, x & \bullet\, w_5 & \cdots & \bullet\, z_4 & \bullet\, y & \bullet\, z_5 \\ \bullet w_6 & \bullet\, w_7 & \bullet\, w_8 & \cdots & \bullet\, z_6 & \bullet\, z_7 & \bullet\, z_8 \end{array}$$

Ignoring competition effects ...

On applying the covariance operator on the additive effects of model

$$y_{ij1..jm.} = \boldsymbol{X}_i \beta + \boldsymbol{a}_{d_i} + \sum_{j=1}^{m_i} f_{ij} \left(\boldsymbol{a}_{c_j} + \boldsymbol{p}_{c_j} \right) + e_{ij1..jm}$$

results in the following expression for the genetic covariance between the records of ***x*** and ***y*** in a single-tree plot design

$$\operatorname{cov}\left(\boldsymbol{a}_{d\,\boldsymbol{x}} + \sum_{i=1}^{8} f_{\boldsymbol{x}w_i} \boldsymbol{a}_{c\,w_i}, \boldsymbol{a}_{d\,\boldsymbol{y}} + \sum_{j=1}^{8} f_{\boldsymbol{y}z_j} \boldsymbol{a}_{c\,z_j} \right)$$

$$= \operatorname{cov}\left(\boldsymbol{a}_{d\,\boldsymbol{x}}, \boldsymbol{a}_{d\,\boldsymbol{y}} \right) + \operatorname{cov}\left(\sum_{i=1}^{8} f_{\boldsymbol{x}w_i} \boldsymbol{a}_{c\,w_i}, \boldsymbol{a}_{d\,\boldsymbol{y}} \right) + \operatorname{cov}\left(\boldsymbol{a}_{d\,\boldsymbol{x}}, \sum_{j=1}^{8} f_{\boldsymbol{y}z_j} \boldsymbol{a}_{c\,z_j} \right) + \operatorname{cov}\left(\sum_{i=1}^{8} f_{\boldsymbol{x}w_i} \boldsymbol{a}_{c\,w_i}, \sum_{j=1}^{8} f_{\boldsymbol{y}z_j} \boldsymbol{a}_{c\,z_j} \right)$$

Ignoring competition effects ...

$$= \boldsymbol{A}_{\boldsymbol{xy}}\sigma^2_{\mathrm{A}d} + \left(\sum_{i=1}^{8} f_{\boldsymbol{x}\mathrm{w}_i} \boldsymbol{A}_{\boldsymbol{y}\mathrm{w}_i} + \sum_{j=1}^{8} f_{\boldsymbol{y}\mathrm{z}_j} \boldsymbol{A}_{\boldsymbol{x}\mathrm{z}_j} \right) \sigma_{\mathrm{A}d\mathrm{A}c} + \left(\sum_{j=1}^{8} f_{\boldsymbol{x}\mathrm{w}_i} f_{\boldsymbol{y}\mathrm{z}_j} \boldsymbol{A}_{\mathrm{w}_i\mathrm{z}_j} \right) \sigma^2_{\mathrm{A}c}$$

The direction and magnitude of the bias will depend on the sign and the magnitude of $\sigma_{\mathrm{A}d\mathrm{A}c}$ as compared with the magnitude of $\sigma^2{}_{\mathrm{A}c}$.

Competition effects

Cappa and Cantet (2008) showed an additive genetic individual tree mixed model for FGE that includes direct and competition effects plus environmental competition effects, accounting for the number and position of competitor trees.

Competition effects

Recently, Costa e Silva et al. (2013; New Phytologist 197: 631–641) applied the Cappa and Cantet (2008) model to fit competition effects in a large progeny trial of *E. globulus*.

Costa e Silva et al. (2013; TGG 9: 1-17) also applied this model to investigate, in simulated data, the relevance of accounting for competitive effects at the genetic and non-genetic levels in terms of the estimation of (co)variance components and selection response. They also studied different experimental designs that resulted in different genetic relatedness levels within a neighbourhood and survival.

Material and Methods

STEP 1:

Diagnosis of environmental heterogeneity and competition effects problems

STEP 1: Diagnosis

To identify spatial patters in the data (global trend, local trend and extraneous variation), Gilmour et al. (1997) suggested examined the spatial distribution of the residuals:

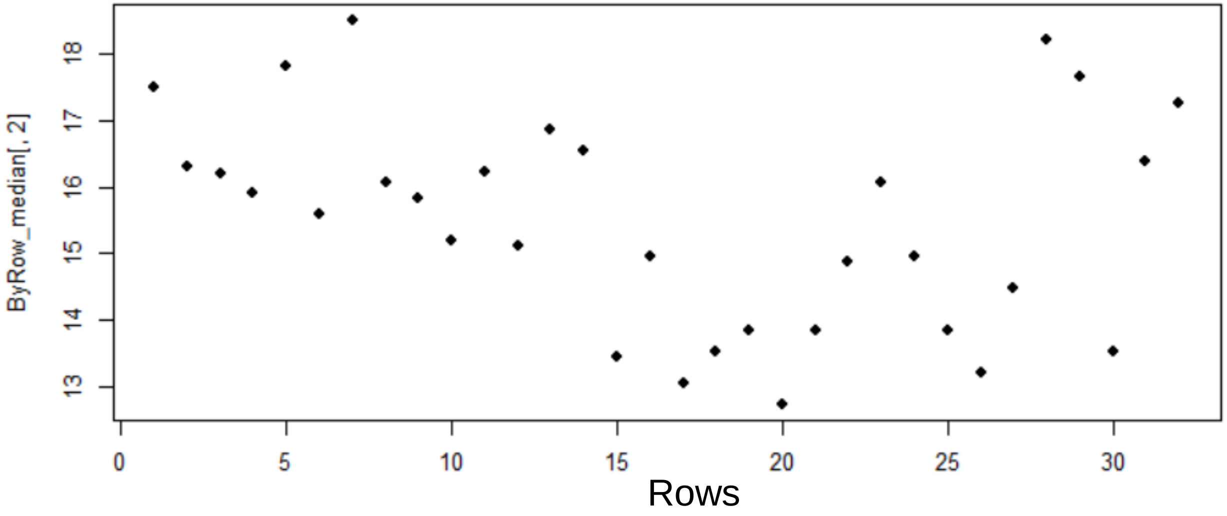
- **Without design effects (replicates, plots, rows, columns, etc.).**
- **Carefully in a family (mother) mixed model with 3/4 of the additive variance.**

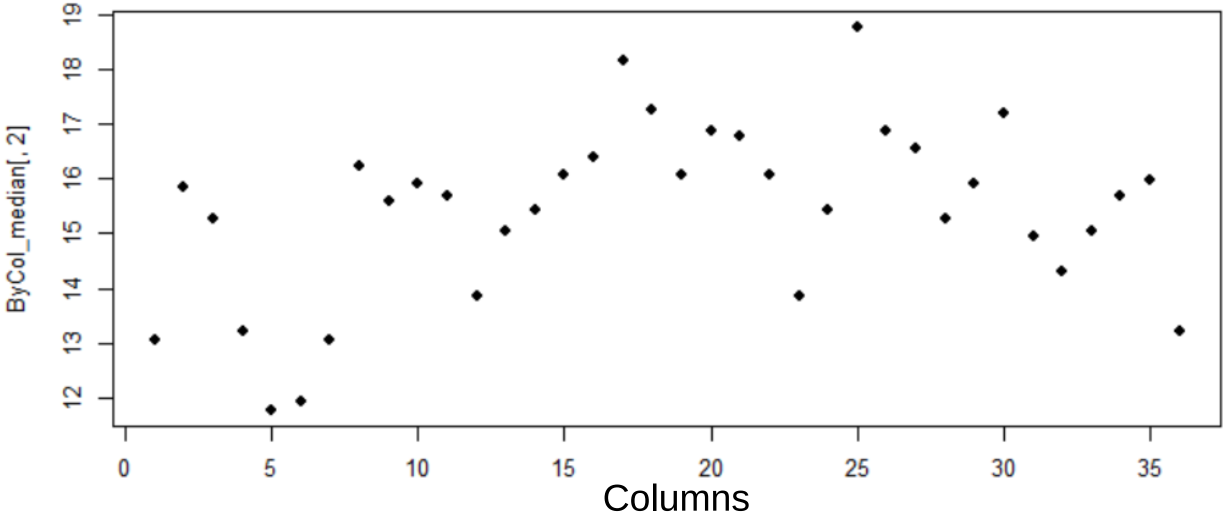
$$y = \xcancel{X\beta} + Z\,a + e$$

Diagnosis: Spatial analysis of residuals

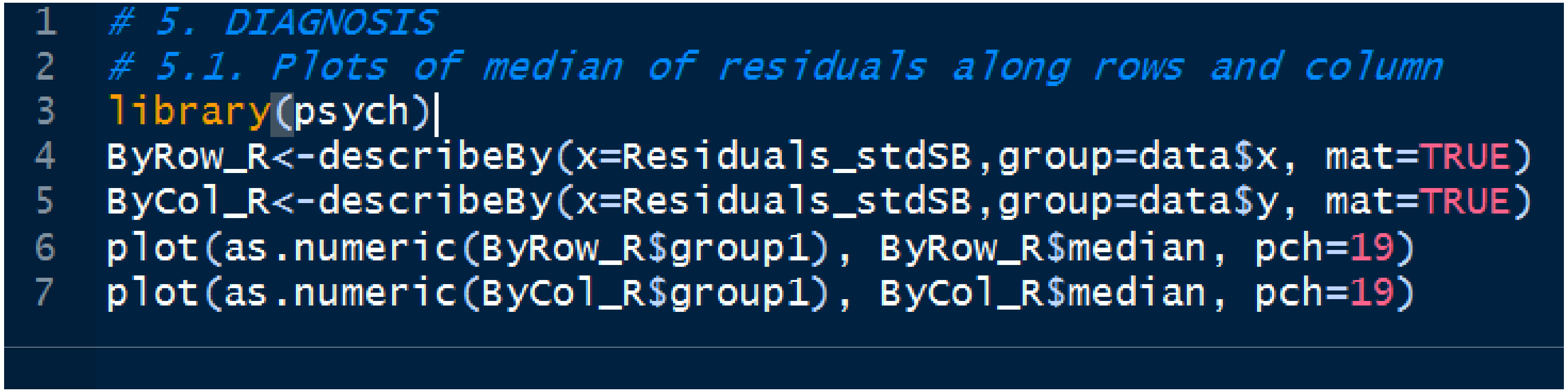
1) Calculate the mean o median (robust to different number of observation within row or columns) of residuals along rows and columns.
2) **Plot the distribution of the residual values in two dimension (rows and columns), where the color intensity represents the magnitude of the residuals.**
3) Plot the residual against row and column position, to detect dissimilar patterns in any row (across columns), or in any column (across rows).
4) The sample variogram.

1. Median of residuals along rows and columns: Environmental heterogeneity in E. globulus



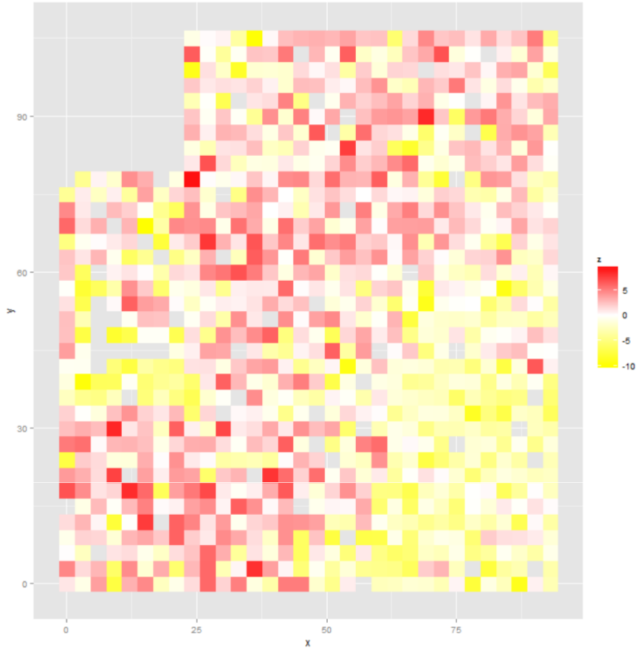


1. Median of residuals along rows and columns: Environmental heterogeneity in E. globulus

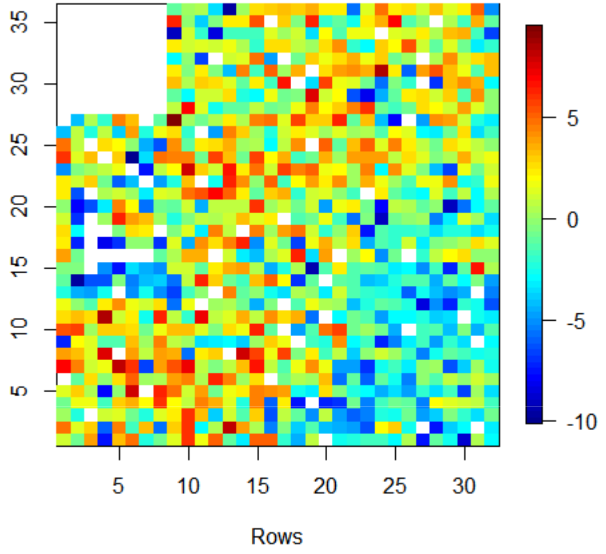


```r
# 5. DIAGNOSIS
# 5.1. Plots of median of residuals along rows and column
library(psych)
ByRow_R<-describeBy(x=Residuals_stdSB,group=data$x, mat=TRUE)
ByCol_R<-describeBy(x=Residuals_stdSB,group=data$y, mat=TRUE)
plot(as.numeric(ByRow_R$group1), ByRow_R$median, pch=19)
plot(as.numeric(ByCol_R$group1), ByCol_R$median, pch=19)
```

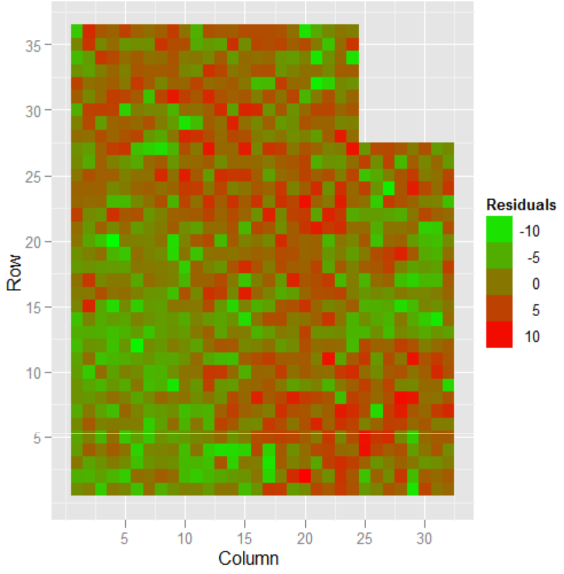
2. Residual values in two dimension: Environmental heterogeneity in E. globulus



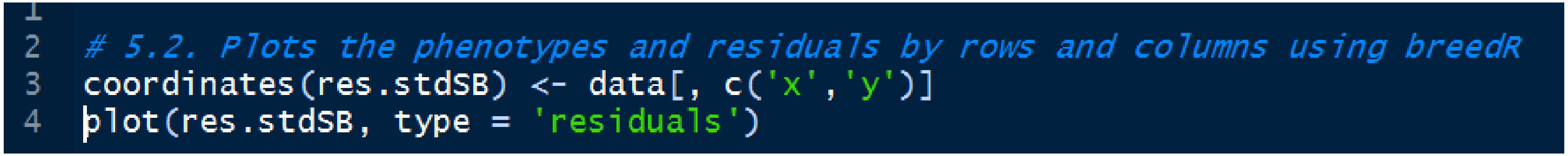
plot, R-breedR



mage.plot, R-Fields



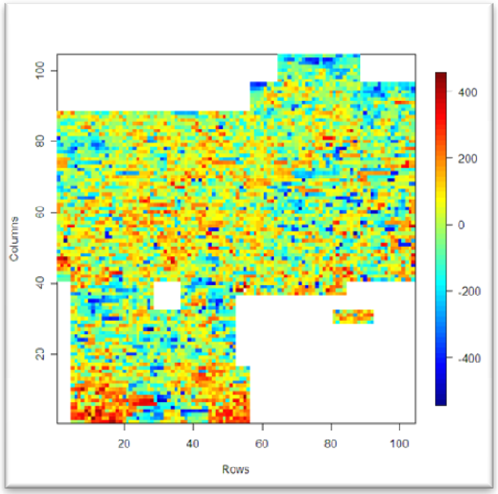
qplot, R-ggplot2



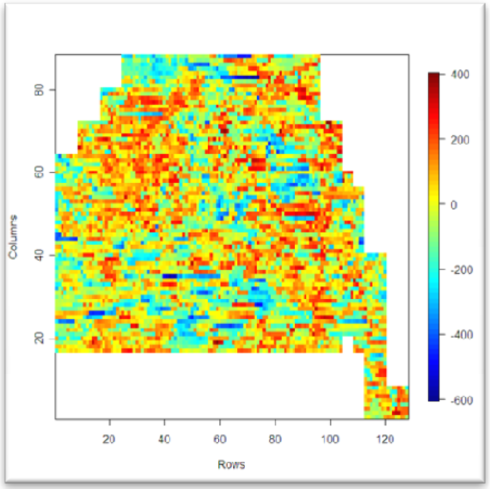
```
# 5.2. Plots the phenotypes and residuals by rows and columns using breedR
coordinates(res.stdSB) <- data[, c('x','y')]
plot(res.stdSB, type = 'residuals')
```

Environmental heterogeneity in Western hemlock

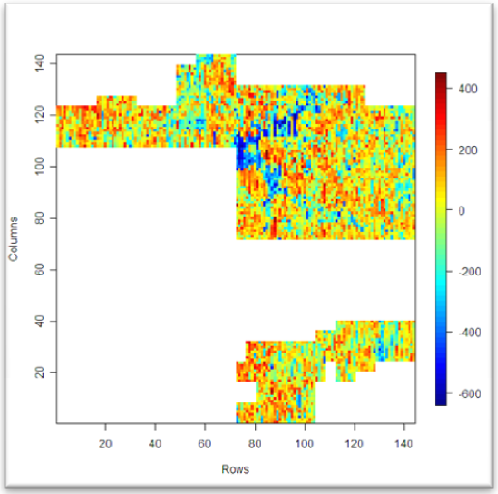
Jordan 2



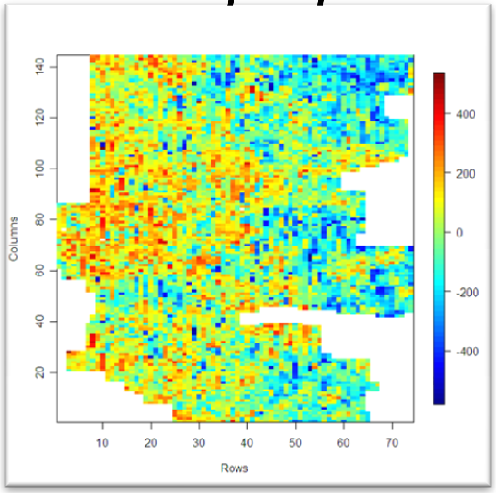
Kiyu



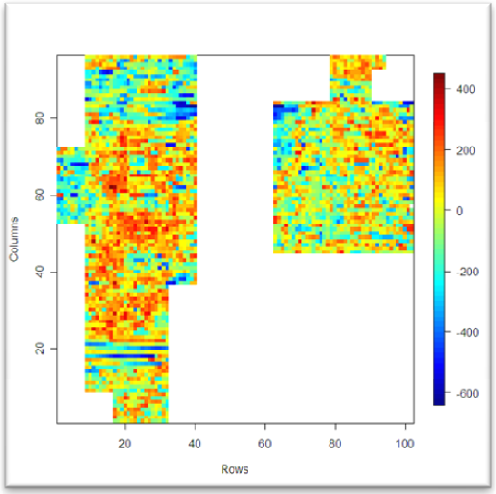
Rupert 1



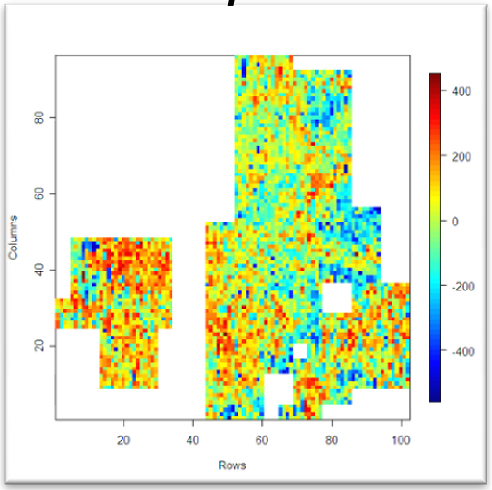
Humptulips



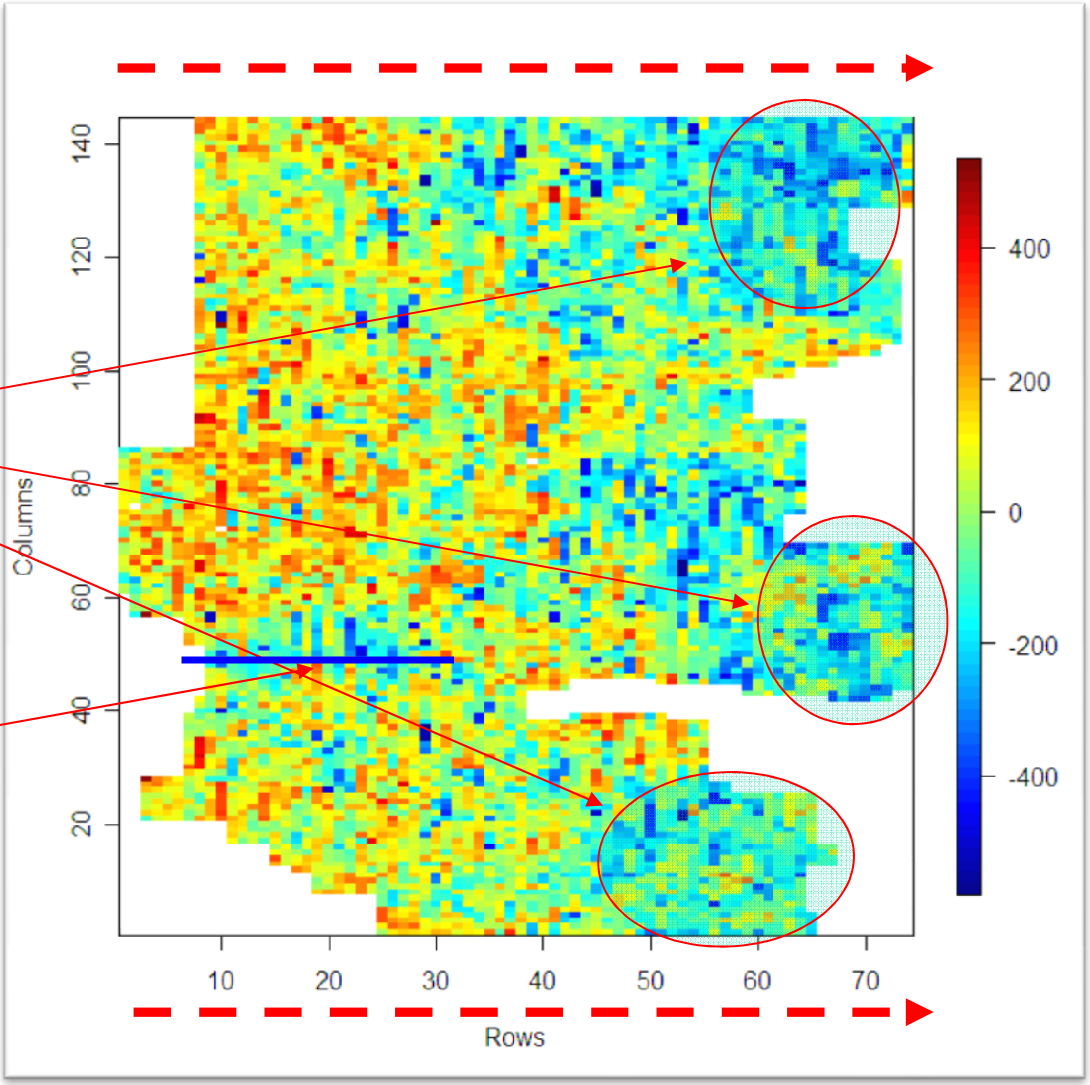
Klanawa



Tlupana



Humptulips



Top of ridge, well drained

Poorly draned soil

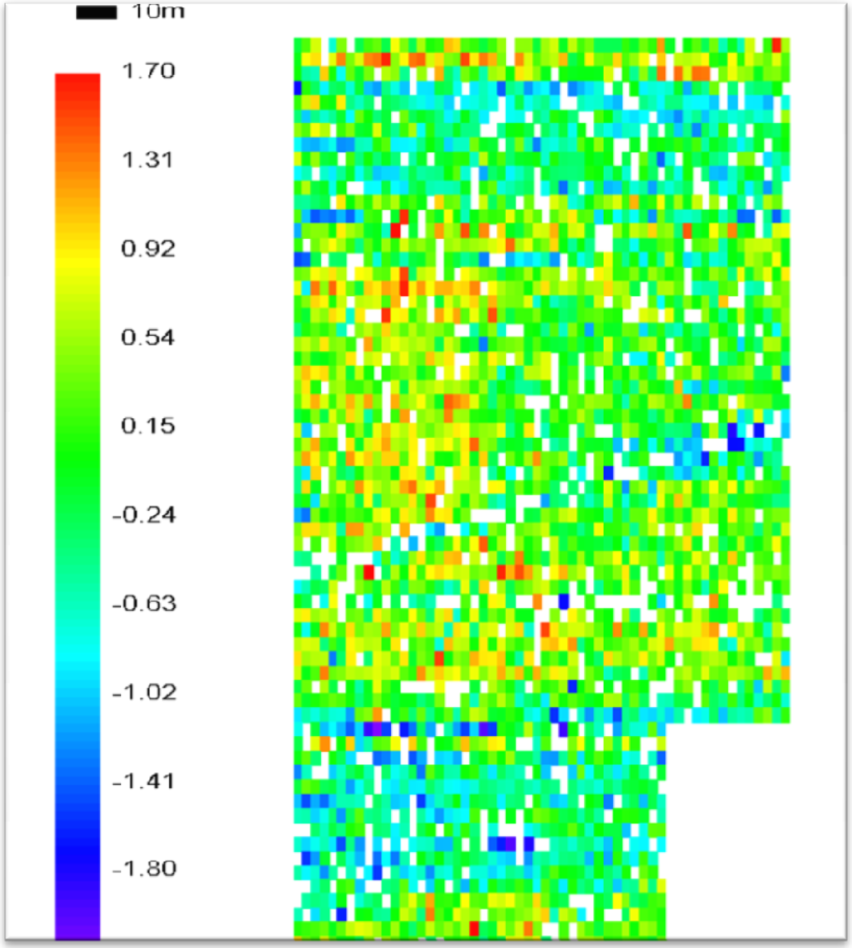
Old road

Top of ridge

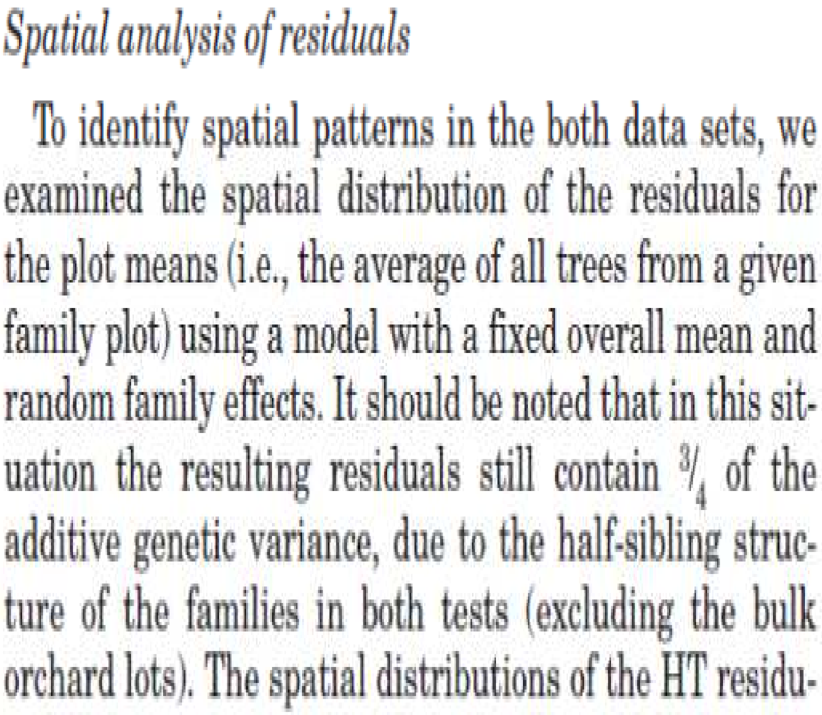
Flatter water receiving

Bottom of ridge, water receiving

Environmental heterogeneity in Loblolly pine

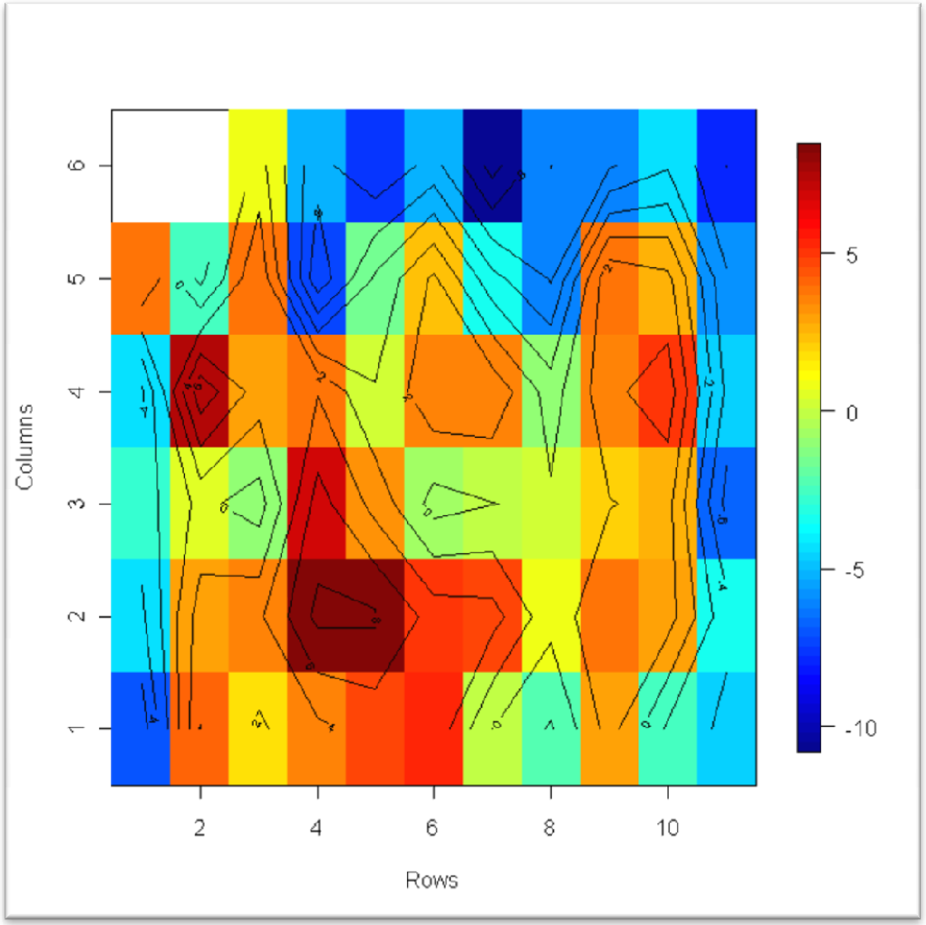


Environmental heterogeneity in Western larch (33 x 18 mts)



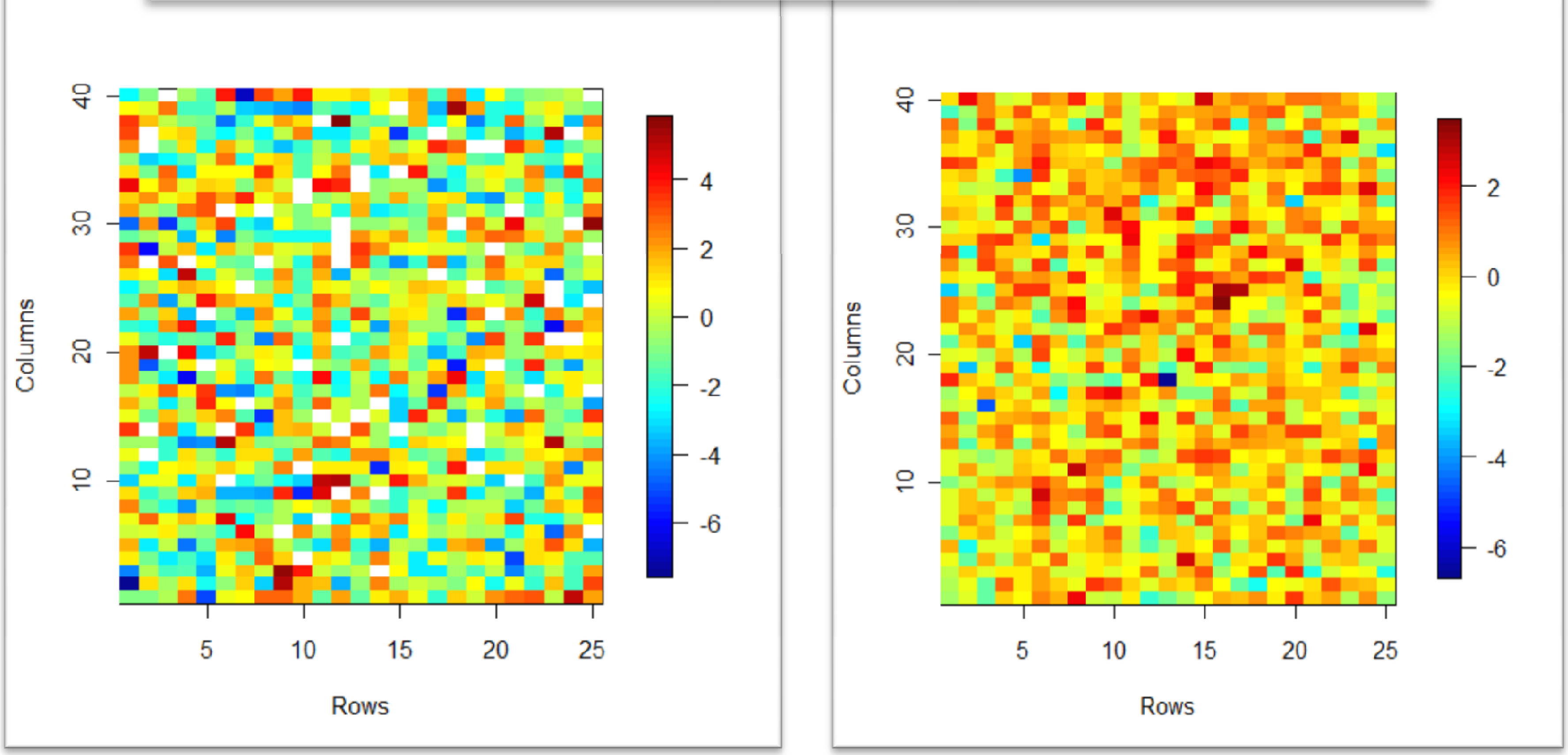
Spatial analysis of residuals

To identify spatial patterns in the both data sets, we examined the spatial distribution of the residuals for the plot means (i.e., the average of all trees from a given family plot) using a model with a fixed overall mean and random family effects. It should be noted that in this situation the resulting residuals still contain $^3/_4$ of the additive genetic variance, due to the half-sibling structure of the families in both tests (excluding the bulk orchard lots). The spatial distributions of the HT residu-

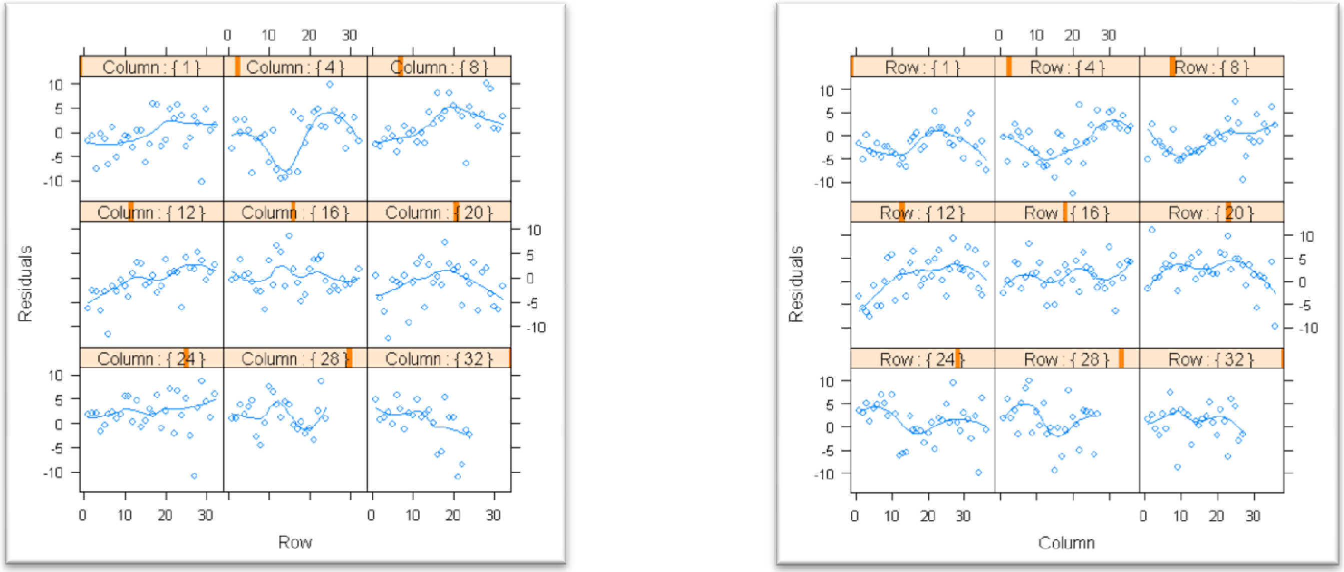


Residual values in two dimension: Competition effects and Environment heterogeneity in Loblolly pine

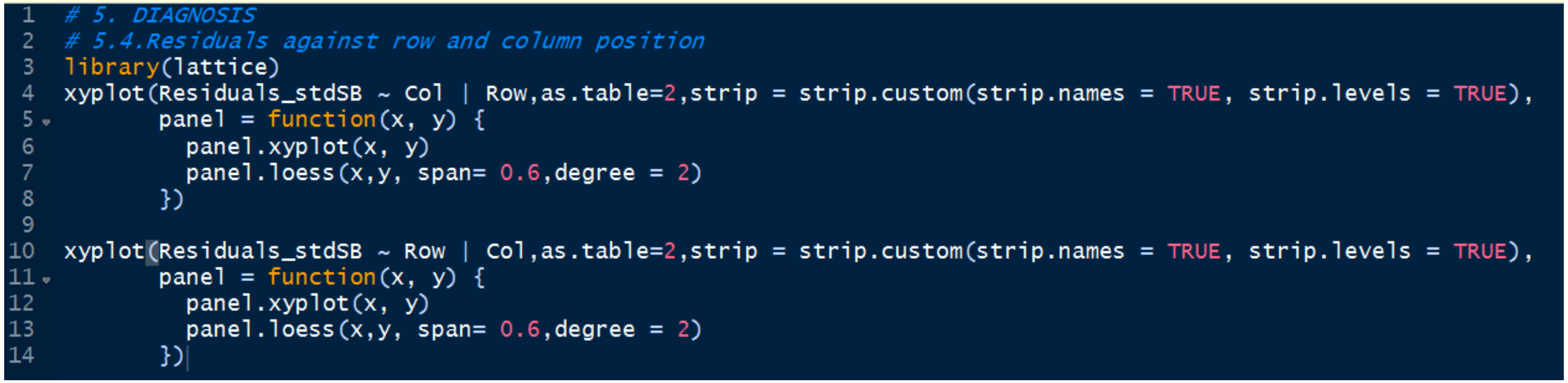
Figura 1. Patrón espacial de residuales para el carácter diámetro a la altura del pecho (**DAP; izquierda**) y altura total (**AT; derecha**) en la base de datos de *Pinus taeda* L. El color de los cuadrados representan la magnitud de los residuales.



3. *Residual against row and column position: Environmental heterogeneity in E. globulus*



xyplot, R-Latice.



```
# 5. DIAGNOSIS
# 5.4.Residuals against row and column position
library(lattice)
xyplot(Residuals_stdSB ~ Col | Row,as.table=2,strip = strip.custom(strip.names = TRUE, strip.levels = TRUE),
       panel = function(x, y) {
         panel.xyplot(x, y)
         panel.loess(x,y, span= 0.6,degree = 2)
       })

xyplot(Residuals_stdSB ~ Row | Col,as.table=2,strip = strip.custom(strip.names = TRUE, strip.levels = TRUE),
       panel = function(x, y) {
         panel.xyplot(x, y)
         panel.loess(x,y, span= 0.6,degree = 2)
       })
```

4. *Sample Variogram*

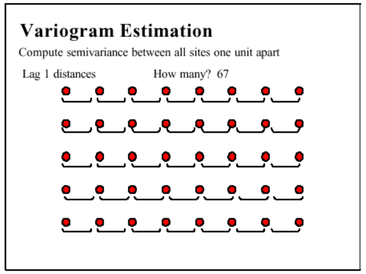
El estimador de momentos de la semivarianza es:

$$\hat{\gamma}_{d_{fil}d_{col}} = \frac{1}{2n_{d_{fil}d_{col}}}\sum_{i=1}^{n_{fila}}\sum_{j=1}^{n_{col}}[e_{ij} - e_{i+d_{fil},\,j+d_{col}}]^2$$

Media para las diferencias al cuadrado de los residuales para un determinado *lag* en la dirección de las filas y columnas para *n* pares de residuales.

donde,

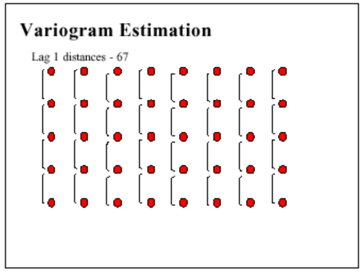
γ es la media de la semivarainza para *n* pares de residuales a una dada separación de distancia (llamada *lag*) en la dirección de las filas o columnas**.** Por ejemplo para el *lag* = 1, 3 and 7



Variogram Estimation

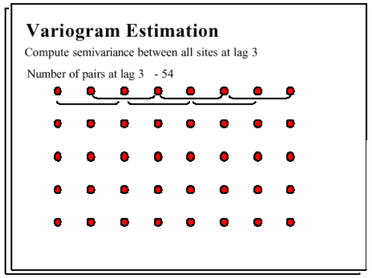
Compute semivariance between all sites one unit apart

Lag 1 distances How many? 67



Variogram Estimation

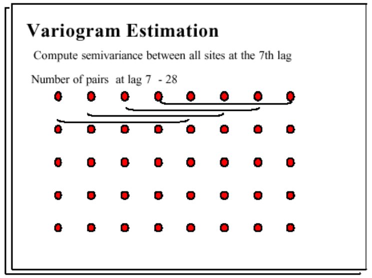
Lag 1 distances - 67



Variogram Estimation

Compute semivariance between all sites at lag 3

Number of pairs at lag 3 - 54



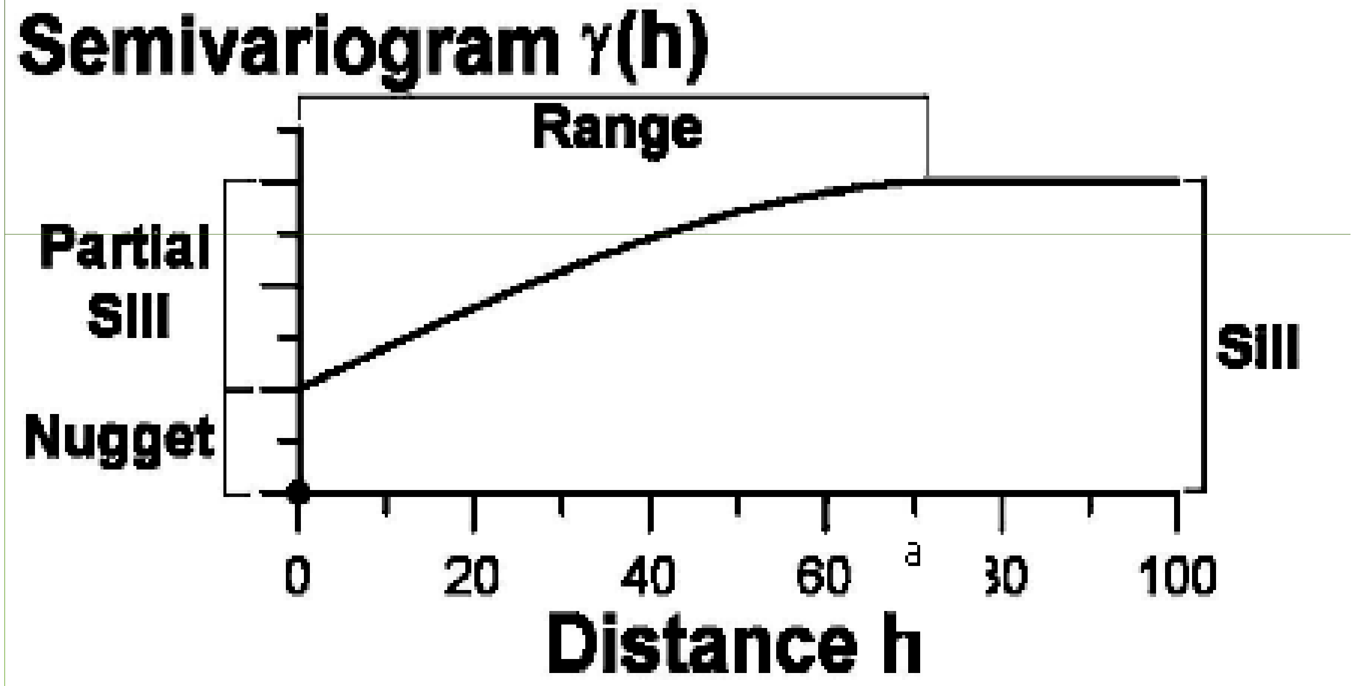
Variogram Estimation

Compute semivariance between all sites at the 7th lag

Number of pairs at lag 7 - 28

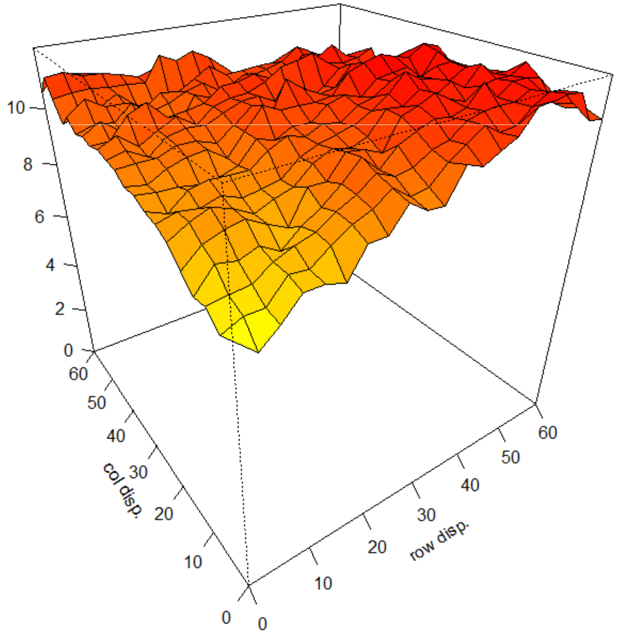
Sample Variogram

El variograma muestra la semivarianza como una función de la distancia entre unidades.

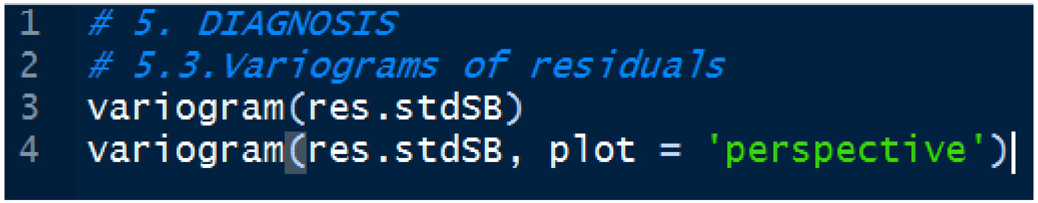


Sample Variogram in E. globulus: Environmental heterogeneity

En el caso de dos dimensiones: Existe un consistente incremento de la semivarianza a medida que aumentamos la distancia en la dirección de las filas y columnas.



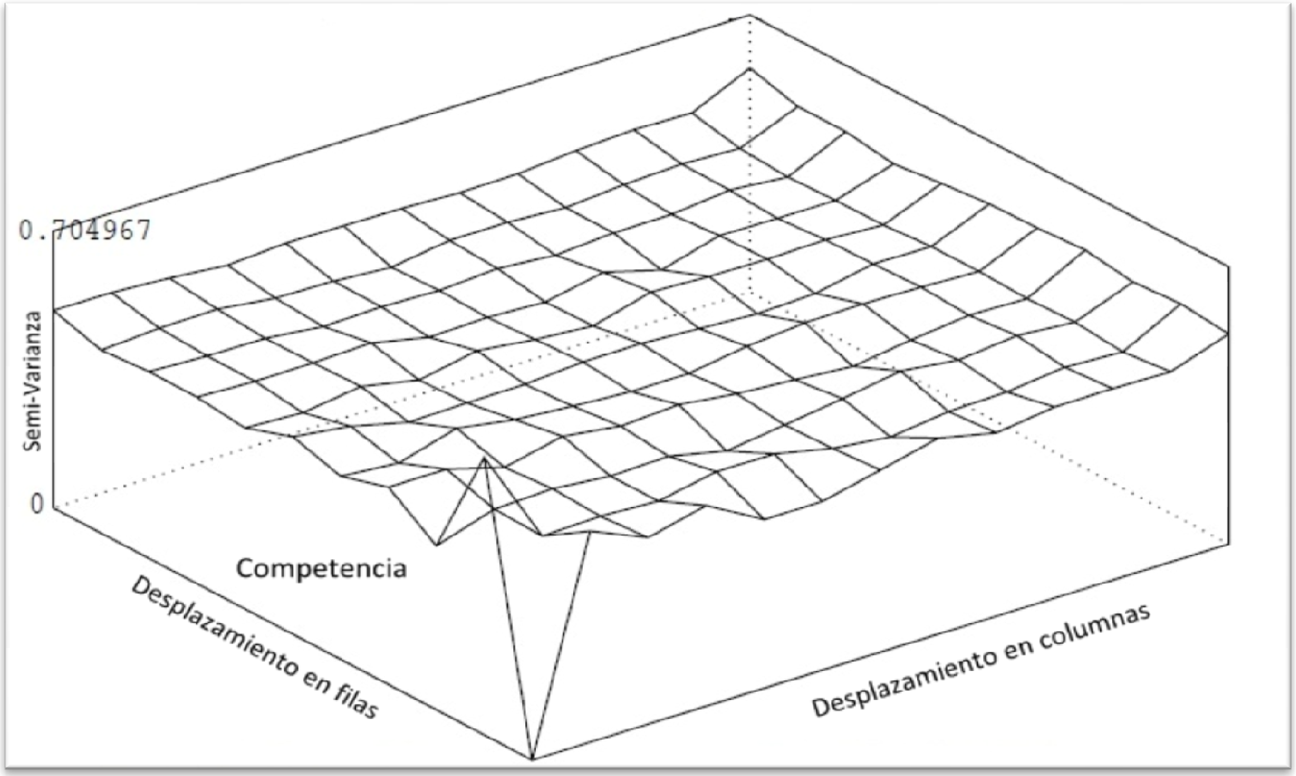
variogram, breed-R
vgram.matrix, R-Fields.



```
# 5. DIAGNOSIS
# 5.3.Variograms of residuals
variogram(res.stdSB)
variogram(res.stdSB, plot = 'perspective')
```

Sample Variogram in Loblolly pine: Competition effects

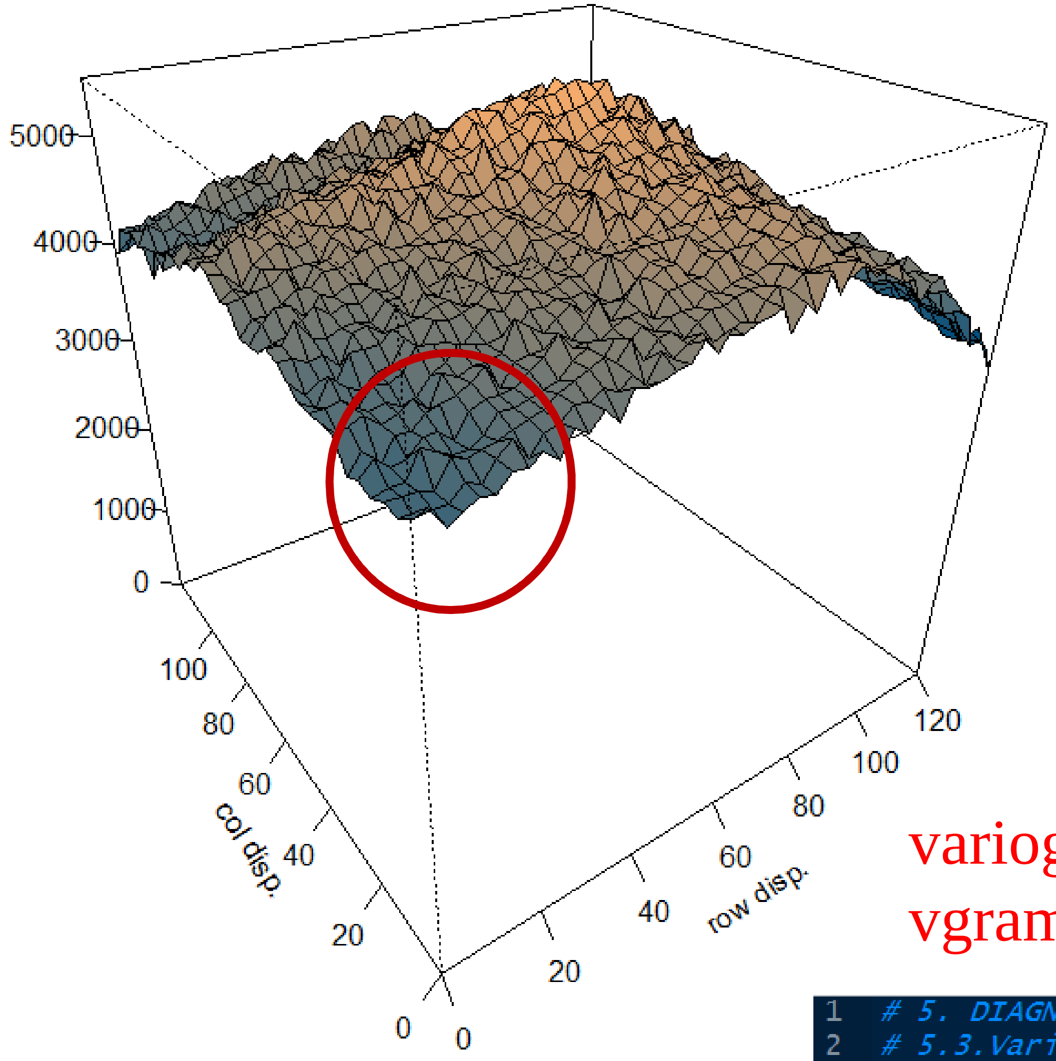
Figura 2. Variograma muestral indicando los efectos de competencia para el carácter diámetro a la altura del pecho (DAP) en la base de datos de *Pinus taeda* L.

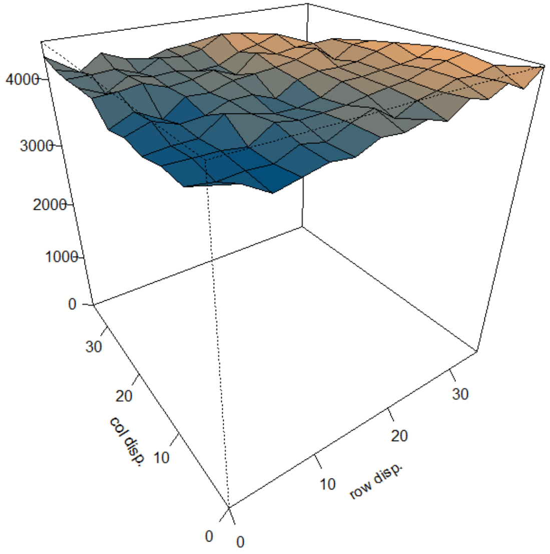


Sample Variogram in Douglas-fir:

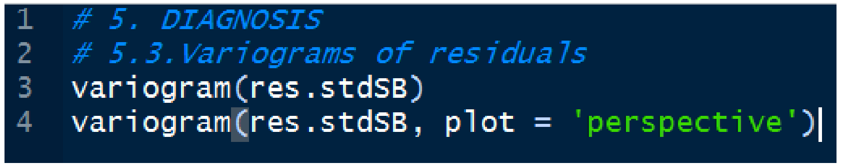
Environmental heterogeneity and competition effects

Figura 1. Variograma muestral indicando los efectos de competencia para el carácter diámetro a la altura del pecho (DAP) en la base de datos de Douglas-fir.



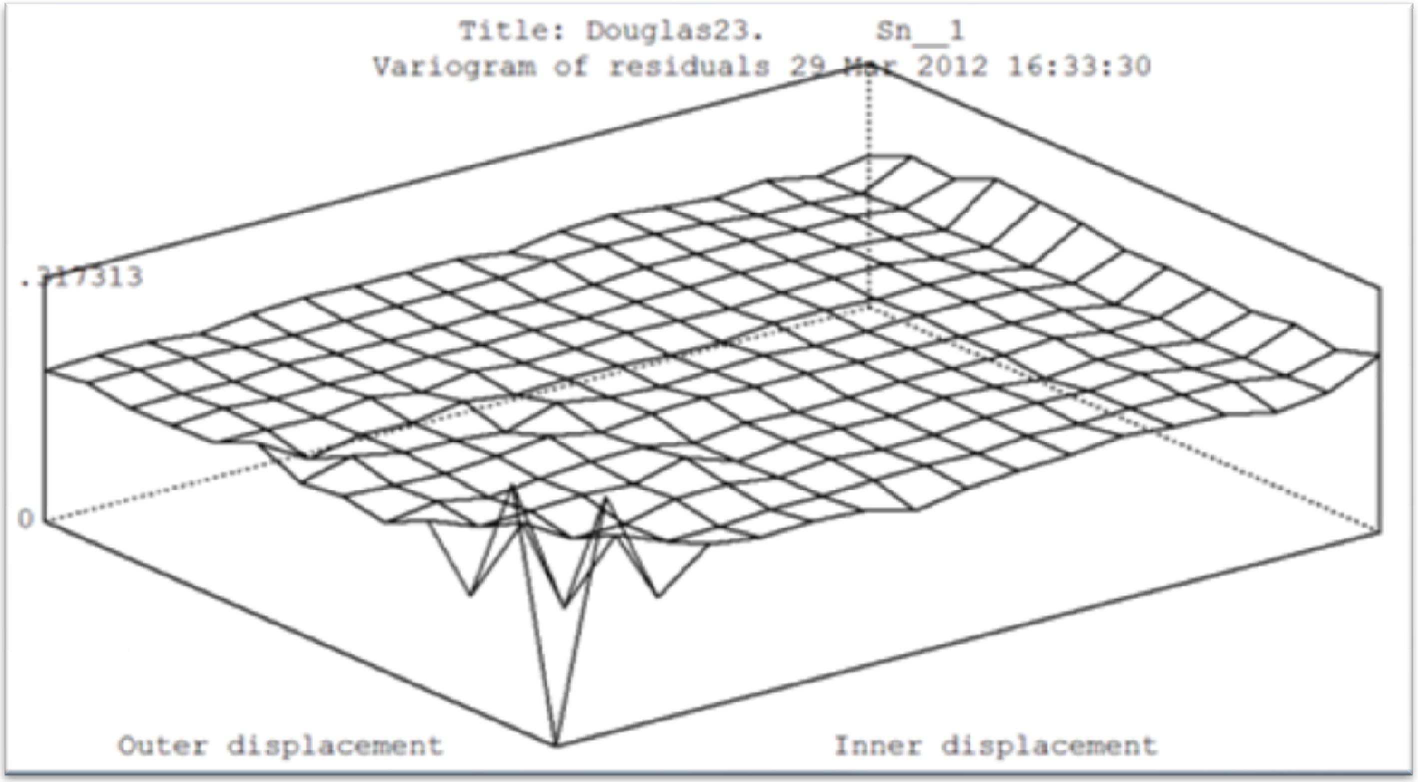


variogram, breed-R
vgram.matrix, R-Fields.



```
# 5. DIAGNOSIS
# 5.3.Variograms of residuals
variogram(res.stdSB)
variogram(res.stdSB, plot = 'perspective')
```

Sample Variogram in Douglas-fir BC: Competition effects



Diagnosis of environmental heterogeneity or/and competition effects

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To indentify the environmental heterogeneity or/and competition effects, we can fitted a spatial models with autoregressive residuals (*I will introduce this model in the next slides*).

"High (say > 0.3) positive auto-correlation coefficients estimates obtained in spatial analysis reveal that spatial trend is predominant over competition, and negative or near zero auto-correlation coefficients estimates reveals strong competition effects probably together with spatial trend."

Resende et al. Rev. Mat. Estat. 23: 7-22 (2005)

Autocorrelation coefficients in Douglas-fir BC

Strong spatial patterns of variation could generate positive correlations that reduce the evidence of competition (negative correlations). In this case, a best solution to study competition is fit a spatial model using the de-trended data, i.e., subtracting the fitted spatially dependent residuals from the original data.

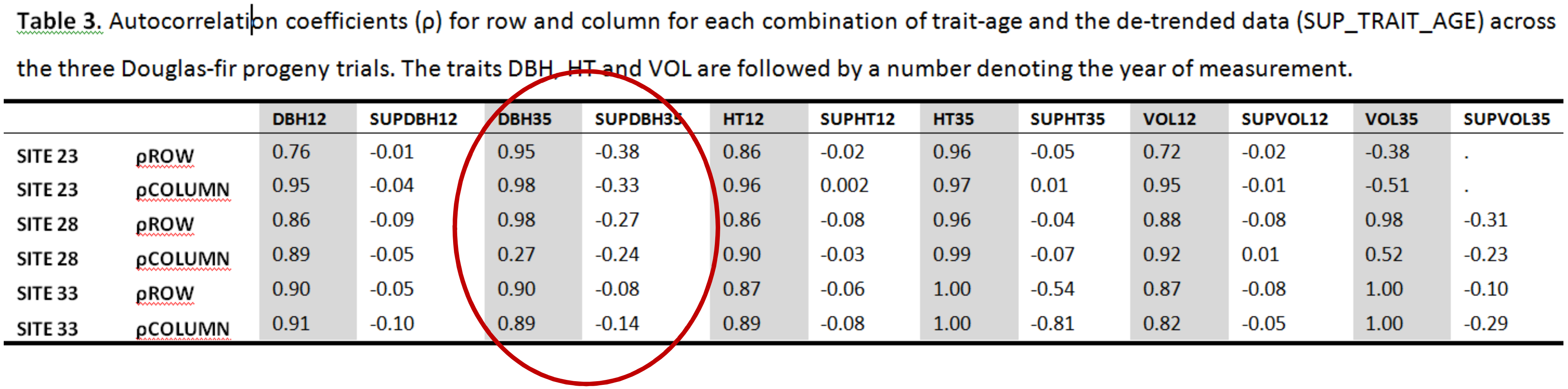


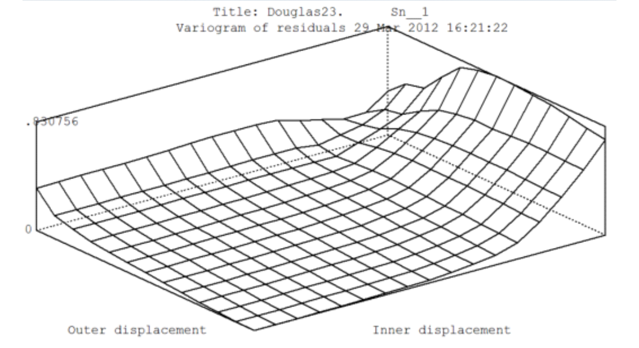
Table 3. Autocorrelation coefficients (ρ) for row and column for each combination of trait-age and the de-trended data (SUP_TRAIT_AGE) across the three Douglas-fir progeny trials. The traits DBH, HT and VOL are followed by a number denoting the year of measurement.

		DBH12	SUPDBH12	DBH35	SUPDBH35	HT12	SUPHT12	HT35	SUPHT35	VOL12	SUPVOL12	VOL35	SUPVOL35
SITE 23	ρROW	0.76	-0.01	0.95	-0.38	0.86	-0.02	0.96	-0.05	0.72	-0.02	-0.38	.
SITE 23	ρCOLUMN	0.95	-0.04	0.98	-0.33	0.96	0.002	0.97	0.01	0.95	-0.01	-0.51	.
SITE 28	ρROW	0.86	-0.09	0.98	-0.27	0.86	-0.08	0.96	-0.04	0.88	-0.08	0.98	-0.31
SITE 28	ρCOLUMN	0.89	-0.05	0.27	-0.24	0.90	-0.03	0.99	-0.07	0.92	0.01	0.52	-0.23
SITE 33	ρROW	0.90	-0.05	0.90	-0.08	0.87	-0.06	1.00	-0.54	0.87	-0.08	1.00	-0.10
SITE 33	ρCOLUMN	0.91	-0.10	0.89	-0.14	0.89	-0.08	1.00	-0.81	0.82	-0.05	1.00	-0.29

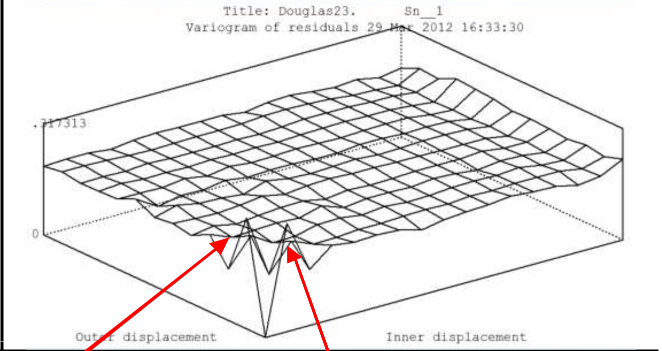
Sample Variogram in Douglas-fir BC: Enviromental heterogeneity - Competition effects

Site 23

Spatial Model for DBH10 at age 35



Spatial model for de-trended DBH10 at age 35

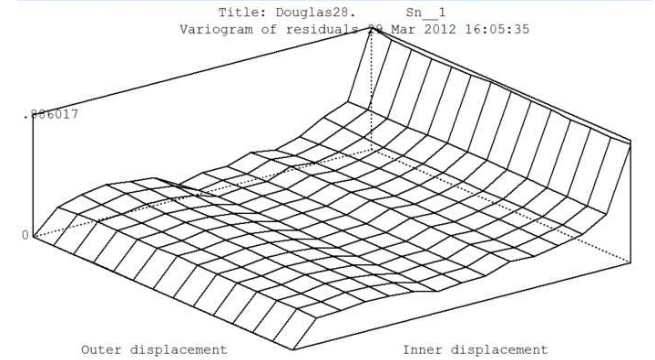


Competition in row

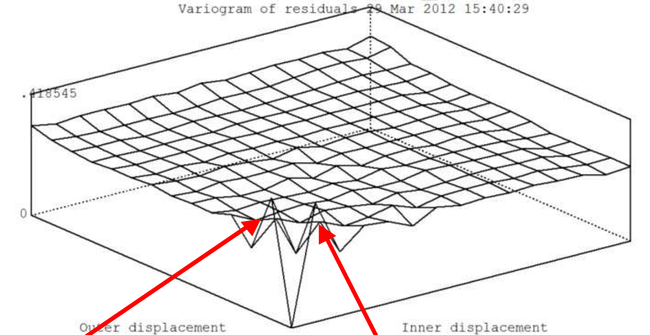
Competition in column

Site 28

Spatial Model for DBH10 at age 35



Spatial model for de-trended DBH10 at age 35



Competition in row

Competition in column

Other ways to identify competition effects

✓ At phenotypic level, **Gould et al. (2011)** calculated the correlation coefficients among pairs of trees (adjacent to one another in the diagonal and/or same planting row or column) for the difference in DBH between two ages (**DBH growth**). It was more sensitive to recent competition than DBH at early age, which is the sum of growth over the entire life of the study. Statistically significant negative correlations provided evidence for antagonistic relationships among families (trees had greater growth in locations where their neighbours had lesser growth, and vice versa).

✓ At genetic level, fitting a competition model (Cappa et al. 2008; *I will introduce this model in the next slides*): **high and negative correlation between direct and competition BV** reveals strong genetic competition (higher than -0.3, Kusnandar 2001). That means, the magnitude of correlation between direct and competition BV measures the intensity of competition.

Other ways to identify competition effects

✓ **Durban et al (2001)** suggested to plot the residuals after fitting genetic and block against means of the neighbouring trees.

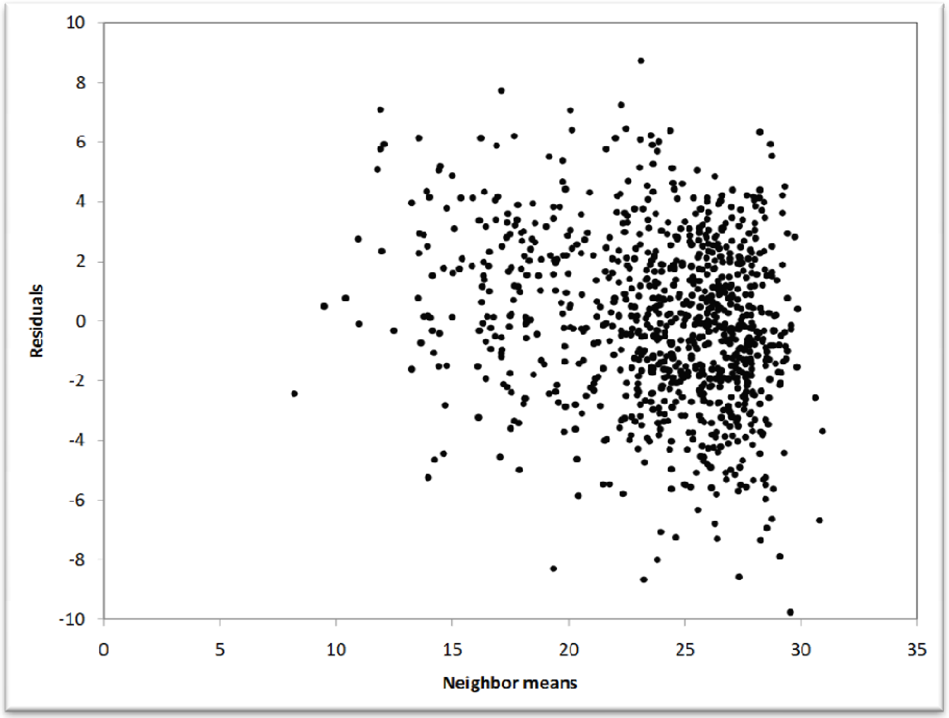
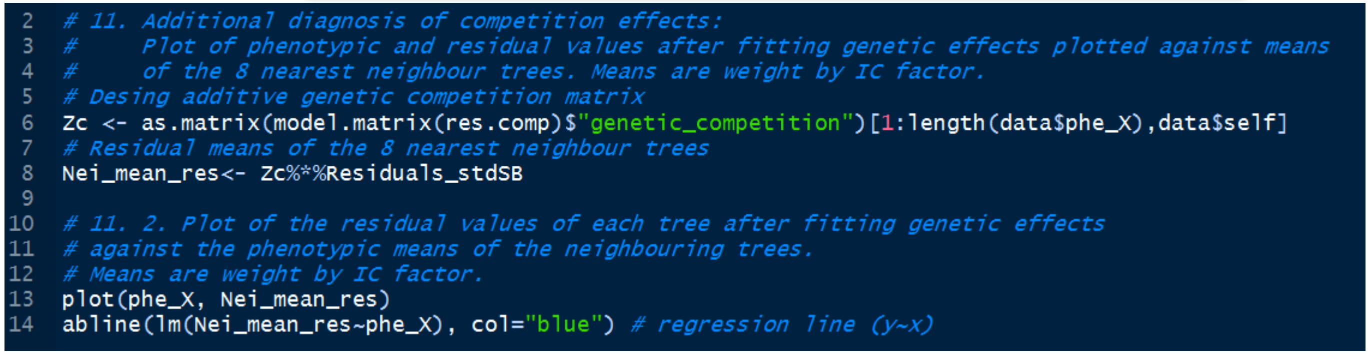


Figure 2: Residuals after fitting fixed overall mean and additive genetic effects plotted against means of the 8 nearest neighbour trees in Loblolly pine.



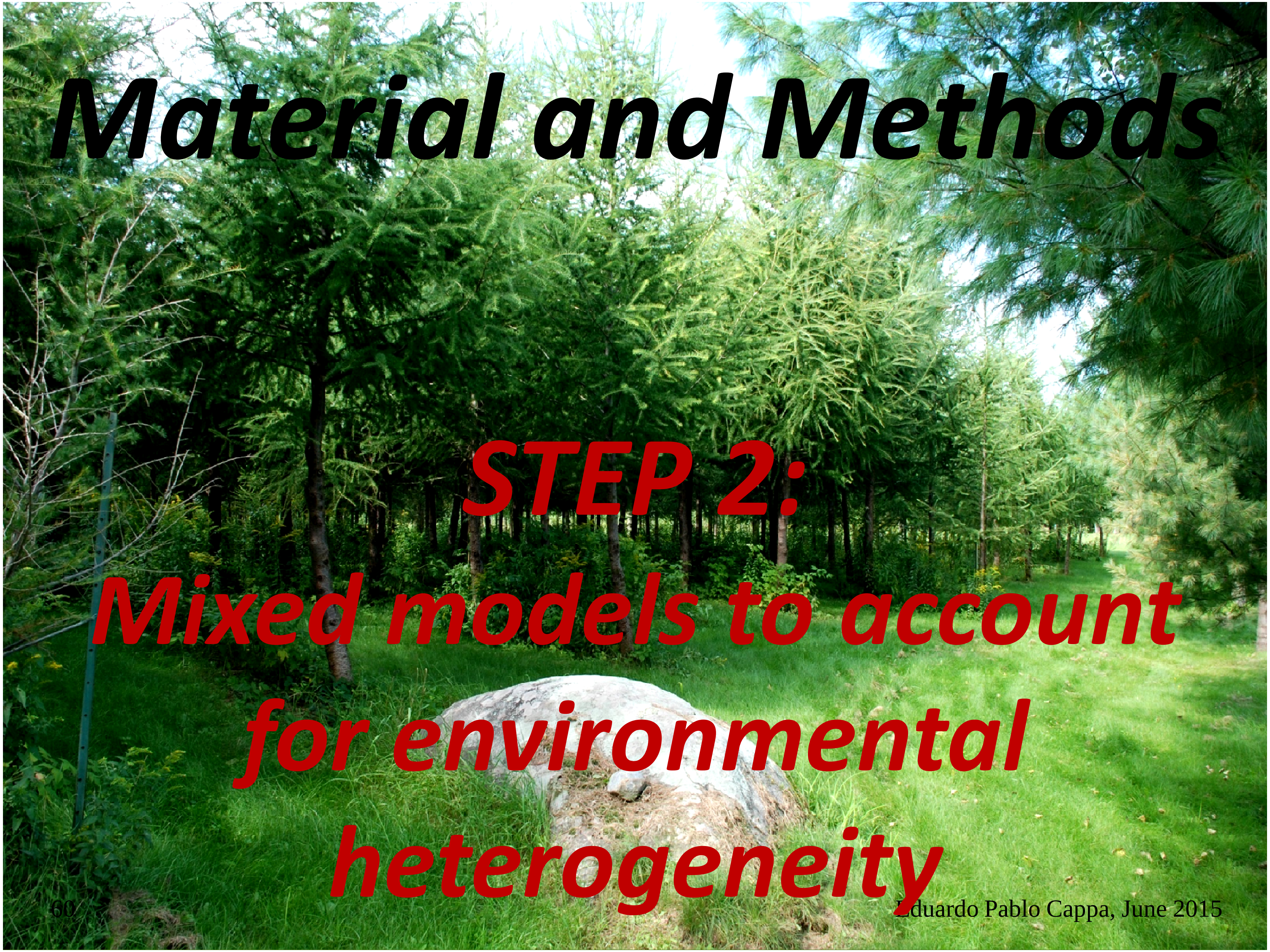
```
# 11. Additional diagnosis of competition effects:
#     Plot of phenotypic and residual values after fitting genetic effects plotted against means
#     of the 8 nearest neighbour trees. Means are weight by IC factor.
# Desing additive genetic competition matrix
Zc <- as.matrix(model.matrix(res.comp)$"genetic_competition")[1:length(data$phe_X),data$self]
# Residual means of the 8 nearest neighbour trees
Nei_mean_res<- Zc%*%Residuals_stdSB

# 11. 2. Plot of the residual values of each tree after fitting genetic effects
# against the phenotypic means of the neighbouring trees.
# Means are weight by IC factor.
plot(phe_X, Nei_mean_res)
abline(lm(Nei_mean_res~phe_X), col="blue") # regression line (y~x)
```

Other ways to identify competition effects

*"… **it is important to gauge the correct number of significant competitors** because if this number is overestimated, there is a risk that genetic competition will not be detected, especially if the signal is already inherently weak. Consequently, **an important step in the analysis of genetic competition will be to pursue a pre-analysis to evaluate the number of neighbours with a significant competitive effect on a focal individual**…"*

Costa e Silva and Kerr TGG, 9: 1-17 (2013)

breedR code should be modified to account for the competition at rows, columns and diagonals.



Material and Methods

STEP 2: Mixed models to account for environmental heterogeneity

Spatial model with autoregressive residuals

Matrix expression of an individual tree mixed model with spatial correlated residuals:

$$\boldsymbol{y} = \boldsymbol{X\beta} + \boldsymbol{Za} + \boldsymbol{w} + \eta$$

Fixed effects

Additive genetic effects

Error:

- ✓***Spatially correlated residual***
  - ✓ ***Spatially uncorrelated residual*** (white noise)

Spatial model with autoregressive residuals

$$\boldsymbol{E(y) = X\beta}$$

$$Var(\boldsymbol{y}) = \begin{bmatrix} \boldsymbol{A}\sigma_A^2 & 0 & 0 \\ 0 & \rho(d_{ij})\sigma_w^2 & 0 \\ 0 & 0 & \boldsymbol{I}\sigma_\eta^2 \end{bmatrix}$$

siendo ***A*** la matriz de relaciones de los efectos genéticos aditivos, ***H=* $\boldsymbol{\rho}$**(d_{ij}) σ^2_w la matriz de (co)varianzas espacial de la tendencia local ***w*** denominada **FUNCIÓN DE COVARIANZA ESPACIAL**.

$$\boldsymbol{R} = \boldsymbol{H} + I\sigma_\eta^2$$

REML APPROACH

First-order autoregressive AR(1) in one dimension

$$\mathbf{R} = \rho^{d_{ij}}\ \sigma_w^2 + I\sigma_\eta^2$$

$$R = \begin{bmatrix} 1 & \rho & \rho^2 & \cdots \rho^{n-1} \\ \rho & 1 & \rho & \cdots \quad \vdots \\ \rho^2 & \rho & 1 & \cdots \quad \vdots \\ \vdots & \vdots & \vdots & \ddots \quad \vdots \\ \rho^{n-1} & \cdots & \cdots & \cdots \quad 1 \end{bmatrix} \sigma_w^2 + I\sigma_\eta^2$$

Separable first-order autoregressive AR(1) in two dimension

Asumiendo separabilidad, *es decir que todos los árboles de una misma fila tienen igual estructura de covarianza para cada columna, y viceversa*:

$$\boldsymbol{R} = \rho^{d_{ij}}\,\rho^{d_{kl}}\ \sigma_w^2 + I\sigma_\eta^2$$

$$\boldsymbol{R} = \left[\mathrm{AR1}\left(\rho_{fila}\right) \otimes \mathrm{AR1}\left(\rho_{col}\right)\right]\sigma_w^2 + \boldsymbol{I}\sigma_\eta^2$$

$$\begin{array}{ccccc} \mathit{Fila} & \begin{array}{ccccc} 1 & 2 & 3 & & n_{fila} \end{array} & \mathit{Col} & \begin{array}{ccccc} 1 & 2 & 3 & & n_{col} \end{array} & \\ R = & \begin{bmatrix} 1 & \rho_f & \rho_f^{2} & \cdots & \rho_f^{n-1} \\ \rho_f & 1 & \rho_f & \cdots & \vdots \\ \rho_f^{2} & \rho_f & 1 & \cdots & \vdots \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ \rho_f^{n-1} & \cdots & \cdots & \cdots & 1 \end{bmatrix} & \otimes & \begin{bmatrix} 1 & \rho_c & \rho_c^{2} & \cdots & \rho_c^{n-1} \\ \rho_c & 1 & \rho_c & \cdots & \vdots \\ \rho_c^{2} & \rho_c & 1 & \cdots & \vdots \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ \rho_c^{n-1} & \cdots & \cdots & \cdots & 1 \end{bmatrix} & \sigma_w^2 + \sigma_\eta^2 I \end{array}$$

Mixed model with two dimensional B-spline

To account for environmental variability, Cappa and Cantet (2007) proposed the use of the tensor products of cubic B-splines based on a mixed model framework using Bayesian techniques via Gibbs sampling to model.

Then, the individual tree mixed model with a with two-dimension B-spline to account for environmental heterogeneity is given by:

$$\boldsymbol{y} = \underbrace{\boldsymbol{X}\beta}_{fixed} + \underbrace{\boldsymbol{Bb} + \boldsymbol{Za} + \boldsymbol{e}}_{random}$$

Smooth surface with a two-dimension cubic B-spline

Moments

$$\mathbf{E}(\boldsymbol{y}) = \boldsymbol{X}\beta$$

$$Var(\boldsymbol{y}) = \begin{bmatrix} \color{red}{\boldsymbol{U}}\sigma_b^2 & 0 & 0 \\ 0 & \mathbf{A}\sigma_A^2 & 0 \\ 0 & 0 & \boldsymbol{I}\sigma_e^2 \end{bmatrix}$$

BAYESIAN or REML APPROACHES

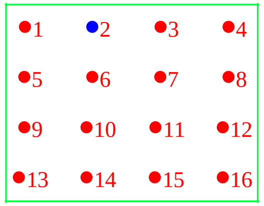
Green and Silverman (1994) *U matrix*

To exemplify, suppose $n_{xr} = n_{xc} = 4$

One-dimensional covariance structure originally suggested by Green and Silverman (1994, page 13) and then used by Durban et al. (2001) to fit a fertility trend. In this matrix, correlations are non-zero for neighbor knots and are 0 otherwise.

$$\boldsymbol{\Sigma}_r = \boldsymbol{\Sigma}_c = \frac{1}{6}\begin{bmatrix} 4 & 1 & 0 & 0 \\ 1 & 4 & 1 & 0 \\ 0 & 1 & 4 & 1 \\ 0 & 0 & 1 & 4 \end{bmatrix}$$

Grid of knots



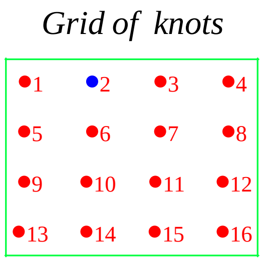
$$\boldsymbol{U} = \boldsymbol{\Sigma}_r \otimes \boldsymbol{\Sigma}_c = \frac{1}{6}\begin{bmatrix}
16 & 4 & 0 & 0 & 4 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
4 & 16 & 4 & 0 & 1 & 4 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 4 & 16 & 4 & 0 & 1 & 4 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 4 & 16 & 0 & 0 & 1 & 4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
4 & 1 & 0 & 0 & 16 & 4 & 0 & 0 & 4 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
1 & 4 & 1 & 0 & 4 & 16 & 4 & 0 & 1 & 4 & 1 & 0 & 0 & 0 & 0 & 0 \\
0 & 1 & 4 & 1 & 0 & 4 & 16 & 4 & 0 & 1 & 4 & 1 & 0 & 0 & 0 & 0 \\
0 & 0 & 1 & 4 & 0 & 0 & 4 & 16 & 0 & 0 & 1 & 4 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 4 & 1 & 0 & 0 & 16 & 4 & 0 & 0 & 4 & 1 & 0 & 0 \\
0 & 0 & 0 & 0 & 1 & 4 & 1 & 0 & 4 & 16 & 4 & 0 & 1 & 4 & 1 & 0 \\
0 & 0 & 0 & 0 & 0 & 1 & 4 & 1 & 0 & 4 & 16 & 4 & 0 & 1 & 4 & 1 \\
0 & 0 & 0 & 0 & 0 & 0 & 1 & 4 & 0 & 0 & 4 & 16 & 0 & 0 & 1 & 4 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 4 & 1 & 0 & 0 & 16 & 4 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 4 & 1 & 0 & 4 & 16 & 4 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 4 & 1 & 0 & 4 & 16 & 4 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 4 & 0 & 0 & 4 & 16
\end{bmatrix}$$

More explicitly, if ς_{ij} is element *ij* of any of the matrices $\boldsymbol{\Sigma}_r$ or $\boldsymbol{\Sigma}_c$, diagonals are $\varsigma_{ii} = 4/6$, whereas off-diagonals are either $\varsigma_{i+1,i} = \varsigma_{i,i+1} = 1/6$ or $\varsigma_{ij} = 0$ for $|i - j| \geq 2$, $i = j = 1, 2, \ldots, nx_r$ or nx_c. Thus, besides being **positive definite**, $\boldsymbol{U} = \boldsymbol{\Sigma}_r \otimes \boldsymbol{\Sigma}_c$ is also **tri-diagonal** and **strictly diagonally dominant** as $|\varsigma_{ii}| > \sum_{j \neq i} |\varsigma_{ij}|$ for every *i*.

Cantet et al. (2005) *U matrix*

To exemplify, suppose $n_{xr} = n_{xc} = 4$, but now the lag row = 1 and lag col = 1.2

One-dimensional covariance structure originally suggested by Cantet et al. (2005) to fit contemporary group in a AM. This matrix modeling a gradual linear decay in correlation as knots are separated farther in the direction of rows or of the columns. This dense correlation structure accounts for different spacing between knots. Diagonal element are equal to 1 and off-diagonal elements are function of spacing lag *sj* - *si* between the row (column) knots *i* and *j*.



$$\boldsymbol{U} = \boldsymbol{\Sigma}_r \otimes \boldsymbol{\Sigma}_c = \begin{bmatrix}
1 & 0.7 & 0.4 & 0.1 & 0.75 & 0.525 & 0.3 & 0.075 & 0.5 & 0.35 & 0.2 & 0.05 & 0.25 & 0.175 & 0.1 & 0.025 \\
\boxed{0.7} & 1 & \boxed{0.7} & 0.4 & 0.525 & \boxed{0.75} & 0.525 & 0.3 & 0.35 & 0.5 & 0.35 & 0.2 & 0.175 & 0.25 & 0.175 & 0.1 \\
0.4 & 0.7 & 1 & 0.7 & 0.3 & 0.525 & 0.75 & 0.525 & 0.2 & 0.35 & 0.5 & 0.35 & 0.1 & 0.175 & 0.25 & 0.175 \\
0.1 & 0.4 & 0.7 & 1 & 0.075 & 0.3 & 0.525 & 0.75 & 0.5 & 0.2 & 0.35 & 0.5 & 0.025 & 0.1 & 0.175 & 0.25 \\
0.75 & 0.525 & 0.3 & 0.075 & 1 & 0.7 & 0.4 & 0.1 & 0.75 & 0.525 & 0.3 & 0.075 & 0.5 & 0.35 & 0.2 & 0.05 \\
0.525 & 0.75 & 0.525 & 0.3 & 0.7 & 1 & 0.7 & 0.4 & 0.525 & 0.75 & 0.525 & 0.3 & 0.35 & 0.5 & 0.35 & 0.2 \\
0.3 & 0.525 & 0.75 & 0.525 & 0.4 & 0.7 & 1 & 0.7 & 0.3 & 0.525 & 0.75 & 0.525 & 0.2 & 0.35 & 0.5 & 0.35 \\
0.075 & 0.3 & 0.525 & 0.75 & 0.1 & 0.4 & 0.7 & 1 & 0.075 & 0.3 & 0.525 & 0.75 & 0.05 & 0.2 & 0.35 & 0.5 \\
0.5 & 0.35 & 0.2 & 0.5 & 0.75 & 0.525 & 0.3 & 0.075 & 1 & 0.7 & 0.4 & 0.1 & 0.75 & 0.525 & 0.3 & 0.075 \\
0.35 & 0.5 & 0.35 & 0.2 & 0.525 & 0.75 & 0.525 & 0.3 & 0.7 & 1 & 0.7 & 0.4 & 0.525 & 0.75 & 0.525 & 0.3 \\
0.2 & 0.35 & 0.5 & 0.35 & 0.3 & 0.525 & 0.75 & 0.525 & 0.4 & 0.7 & 1 & 0.7 & 0.3 & 0.525 & 0.75 & 0.525 \\
0.05 & 0.2 & 0.35 & 0.5 & 0.075 & 0.3 & 0.525 & 0.75 & 0.1 & 0.4 & 0.7 & 1 & 0.075 & 0.3 & 0.525 & 0.75 \\
0.25 & 0.175 & 0.1 & 0.25 & 0.5 & 0.35 & 0.2 & 0.05 & 0.75 & 0.525 & 0.3 & 0.075 & 1 & 0.7 & 0.4 & 0.1 \\
0.175 & 0.25 & 0.175 & 0.1 & 0.35 & 0.5 & 0.35 & 0.2 & 0.525 & 0.75 & 0.525 & 0.3 & 0.7 & 1 & 0.7 & 0.4 \\
0.1 & 0.175 & 0.25 & 0.175 & 0.2 & 0.35 & 0.5 & 0.35 & 0.3 & 0.525 & 0.75 & 0.525 & 0.4 & 0.7 & 1 & 0.7 \\
0.025 & 0.1 & 0.175 & 0.25 & 0.05 & 0.2 & 0.35 & 0.5 & 0.075 & 0.3 & 0.525 & 0.75 & 0.1 & 0.4 & 0.7 & 1
\end{bmatrix}$$

$$\Sigma_r = \begin{bmatrix}
1 & 0.75 & 0.5 & 0.25 \\
0.75 & 1 & 0.75 & 0.5 \\
0.5 & 0.75 & 1 & 0.75 \\
0.25 & 0.5 & 0.75 & 1
\end{bmatrix}$$

$$\Sigma_c = \begin{bmatrix}
1 & 0.7 & 0.4 & 0.1 \\
0.7 & 1 & 0.7 & 0.4 \\
0.4 & 0.7 & 1 & 0.7 \\
0.1 & 0.4 & 0.7 & 1
\end{bmatrix}$$

Hyndman et al. (2001)

This matrix modeling a non linear decay in correlation between knots. Inverting this matrix is computationally problem.

Material and Methods

STEP 2:

Mixed model to account for competition effects

Spatial model with autoregressive residuals

"An **AR(1) ⊗ AR(1)** ***process is very flexible****, as it can model local and global trend, competition, and row or column effects"*

Dutkowski *et al*. CJFR 2002.

However, the autoregressive residual approach fit the competition only at residual level and this is not sufficient in the case that competition is also due to genetic causes (Resende et al. 2005).

Cappa and Cantet (2008) showed an additive genetic individual tree mixed model for FGE that includes direct and competition effects plus environmental competition effects, accounting for the number and position of competitor trees.

Individual tree model with competition effects

Matrix expression:

$$\boldsymbol{y} = \boldsymbol{X\beta} + \boldsymbol{Z}_d \boldsymbol{a}_d + \boldsymbol{Z}_c \boldsymbol{a}_c + \boldsymbol{Z}_p \boldsymbol{p}_c + \boldsymbol{e}$$

DUE TO THE INDIVIDUAL'S GENES : Classical BV

FROM CONTRIBUTIONS FROM OTHER GENOTYPES

The total additive genetic competition that is exerted over plant *i* from trees j_1, j_2, …, j_{im} is equal to

$$\boldsymbol{Z}_c \boldsymbol{a}_c = \sum_{j=1}^{m_i} f_{ij} \boldsymbol{a}_{c_j} = f_{i1} \boldsymbol{a}_{c_1} + f_{i2} \boldsymbol{a}_{c_2} + \ldots + f_{im} \boldsymbol{a}_{c_m}$$

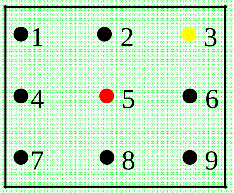
Additive genetic effects of competition

To account for different number of competitors and also additive relationship between competitors

$$\sum_{j=1}^{m_i} f_{ijk}^{2} = n_{\text{R-C}}\ f_{ij\,\text{R-C}}^{2} + n_{\text{D}}\ f_{ij\,\text{D}}^{2} = 1$$

If $\sqrt{2}\, f_{ijD} = f_{ijR-C}$, replacing this expression in the previous:

$$f_{ij\text{R-C}} = \sqrt{\frac{2}{2\, n_{\text{R-C}} + n_{\text{D}}}} \qquad\qquad f_{ij\text{D}} = \frac{1}{\sqrt{2\, n_{\text{R-C}} + n_{\text{D}}}}$$



$$\left[\, {}^{1}\!/\!_{\sqrt{11}} \quad {}^{\sqrt{2}}\!/\!_{\sqrt{11}} \quad {}^{\sqrt{2}}\!/\!_{\sqrt{11}} \quad 0 \quad {}^{\sqrt{2}}\!/\!_{\sqrt{11}} \quad {}^{1}\!/\!_{\sqrt{11}} \quad {}^{\sqrt{2}}\!/\!_{\sqrt{11}} \quad {}^{1}\!/\!_{\sqrt{11}} \,\right]$$

$f_{ij\text{D}} = 1/\,[2*4 + 3]^{1/2} = 1/(11)^{1/2}$

$f_{ij\text{R-C}} = [2/(2*4 + 3)]^{1/2} = (2/11)^{1/2}$

Additive genetic effects of competition

Costa e Silva et al. (2013; TGG 9: 1-17) extended this approach to cases where inter-row spacing is not equal to inter-column spacing, by introducing a parameter *p*, which is the ratio of inter-row to inter-column spacing ($p = d_c/d_r$).

$$f_{ij\mathrm{D}} = \frac{p}{\sqrt{n_\mathrm{R}\, p^4 + n_\mathrm{R}\, p^2 + n_C\, p^2 + n_\mathrm{D}\, p^2 + n_C}}$$

$$f_{ij\mathrm{R}} = f_{ij\mathrm{D}}\sqrt{1+p^2} \qquad f_{ij\mathrm{C}} = \frac{f_{ij\mathrm{D}}\sqrt{1+p^2}}{p}$$

The FORTRAN code should be modified to calculate the IC at rows, columns and diagonals.

Moments

$$\mathrm{E}(\boldsymbol{y}) = \boldsymbol{X}\beta$$

Additive variance for direct BV

$$\mathrm{Var}\begin{bmatrix} \boldsymbol{a}_d \\ \boldsymbol{a}_c \\ \boldsymbol{p}_c \\ \boldsymbol{e} \end{bmatrix} = \begin{bmatrix} \boldsymbol{G}_0 \otimes \boldsymbol{A} & 0 & 0 \\ 0 & \boldsymbol{I}\sigma_p^2 & 0 \\ 0 & 0 & \boldsymbol{R} \end{bmatrix} = \begin{bmatrix} \boldsymbol{A}\sigma_{\mathrm{A}d}^2 & \boldsymbol{A}\sigma_{\mathrm{AdA}c} & 0 & 0 \\ \boldsymbol{A}\sigma_{\mathrm{AdA}c} & \boldsymbol{A}\sigma_{\mathrm{A}c}^2 & 0 & 0 \\ 0 & 0 & \boldsymbol{I}\sigma_p^2 & 0 \\ 0 & 0 & 0 & \boldsymbol{I}\sigma_e \end{bmatrix}$$

Covariance between direct and competition breeding values

Additive variance for competition BV

BAYESIAN and REML APPROACHES

Results

Individual-tree mixed model with a smoothed surface

Some papers

1- Eduardo P. Cappa, and Rodolfo J. C. Cantet. (2007). Bayesian estimation of a surface to account for a spatial trend using penalized splines in an individual-tree mixed model. Canadian Journal of Forest Research, 37: 2677-2688.

2- Eduardo, P. Cappa (2007). Inferencia Bayesiana en modelos mixtos con datos faltantes, efectos de competencia genética y tendencias espaciales para la evaluación genética forestal. PhD. thesis. Facultad de Agronomia, Universidad de Buenos Aires, Buenos Aires - Argentina.

3- Eduardo P. Cappa, Milan Lstiburek, Alvin D. Yanchuk and Yousry A. El-Kassaby. (2011). Two-dimensional penalized splines via Gibbs sampling to account for spatial variability in forest genetic trials with small amount of information available. Silvae Genetica, 60(1): 25-35.

4- Eduardo P. Cappa, Alvin D. Yanchuk and Charlie V. Cartwright (2013). Estimation of genetic parameters using spatial analysis in *Tsuga heterophylla* full-sibling family trials in British Columbia (Silvae Genetica, minor revision).

5- Eduardo, P. Cappa, Facundo Muño, Leopoldo Sanchez, Rodolfo J. C. Cantet. (2015). A novel individual-tree mixed model with competition effects and environmental heterogeneity: a Bayesian approach. Tree Genetics & Genomes (below revision).

Spatial model with B-splines in E. globulus

Data

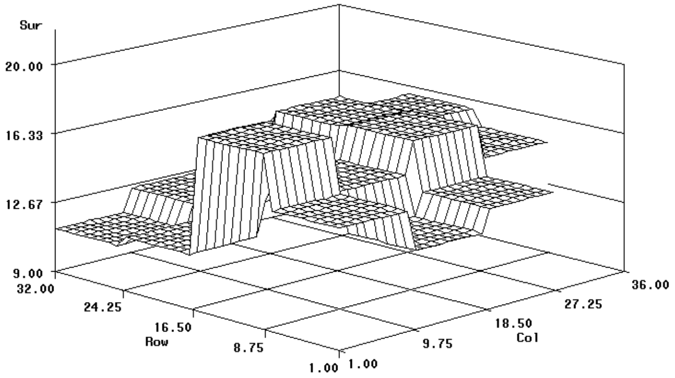
- **36 open pollinated families of *Eucalyptus globulus.***
- **The soil was a Petrocalcic Paleudoll. It is characterized by a fine texture and a subsuperficial petrocalcic horizon starting at 0.81 m from surface and with variable depth.**
- **DBH (1080) measured at age 6.**
- **Trees were planted in single-tree plots on a rectangular grid of 32 rows and 36 columns (93 m × 105 m) arrayed in squares of 3 by 3 meters.**

Models of analyses

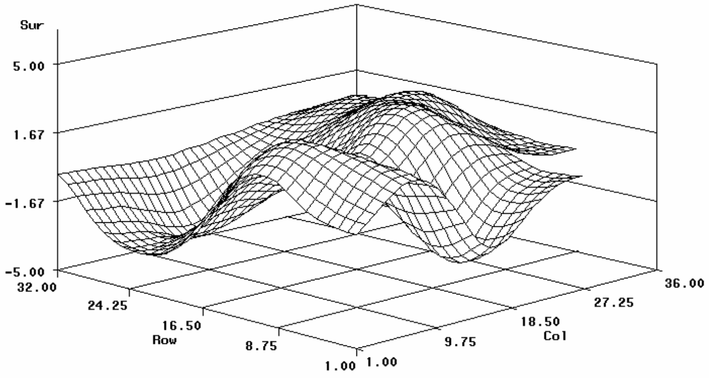
- **Four individual additive tree models were evaluated.**
- **The DIC (Spiegelhalter *et al*. 2002) was employed to compare the fit from different models.**
- **Further model comparison was provided by the accuracy of prediction of breeding values and genetic gain.**

Spatial model with B-splines in E. globulus

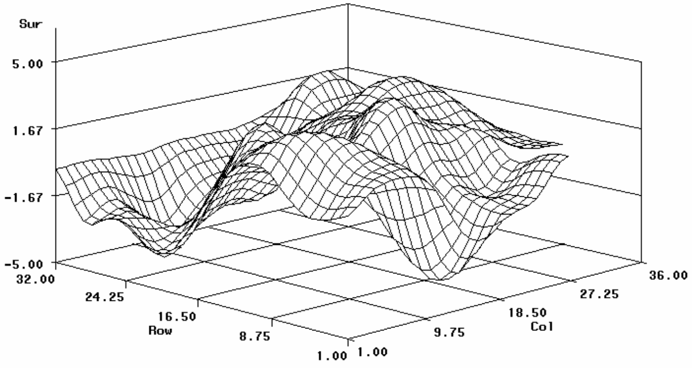
Blocks



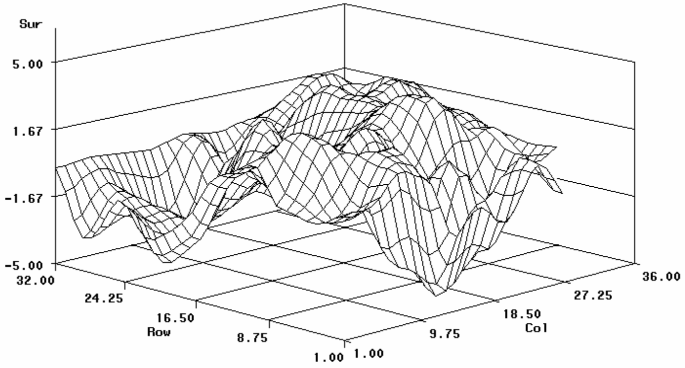
8 × 8



12 × 12



18 × 18



Cuadro 5.1. Criterio de Información de la Desviación (DIC), para los cuatro modelos analizados.

Modelo[a]	**Bloques**	**8 × 8**	**12 × 12**	**18 × 18**
DIC	**3152.660**	**2868.6380**	**2833.463**	**2835.1230**

Spatial model with B-splines in E. globulus

Table 1: Posterior statistics for the additive genetic variance (σ^2_A), the variance of the RKE (σ^2_b), the error variance (σ^2_e), and the heritability of DBH (h^2_{DBH}).

Model[a]	**Parm.**[b]	**Mean**	**Median**	**Mode**	**SD**[c]	**95% HPD**[d]	**ESS**[e]
1	σ^2_A	1.835	1.801	1.609	0.37149	1.291 – 2.503	24119
	σ^2_e	23.043	20.144	14.070	8.69251	15.182 – 40.520	87274
	h^2_{DBH}	0.080	0.079	0.084	0.02520	0.040 – 0.123	43572
3	σ^2_A	3.754	3.643	2.933	1.00390	2.310 – 5.573	16474
	σ^2_b	22.317	21.649	23.716	5.47972	14.682 – 32.132	109973
	σ^2_e	10.275	10.301	9.900	1.01309	8.558 - 11.871	23568
	h^2_{DBH}	0.267	0.261	0.244	0.06872	0.167 - 0.389	16519

Table 2: Accuracy of prediction of breeding values from models 1 and 3 and Spearman correlation between predicted breeding values from models 1 and 3.

Accuracy of breeding values for parents		**Accuracy of breeding values for offspring**		**Spearman correlation of breeding values**	
Model 1	**Model 3**	**Model 1**	**Model 3**	**Parents**	**Offspring**
0.40	0.61	0.32	0.54	0.97	0.94

+ 66 %

+ 60 %

(0.23 cm) – (0.77 cm)

Spatial model with B-splines in E. globulus

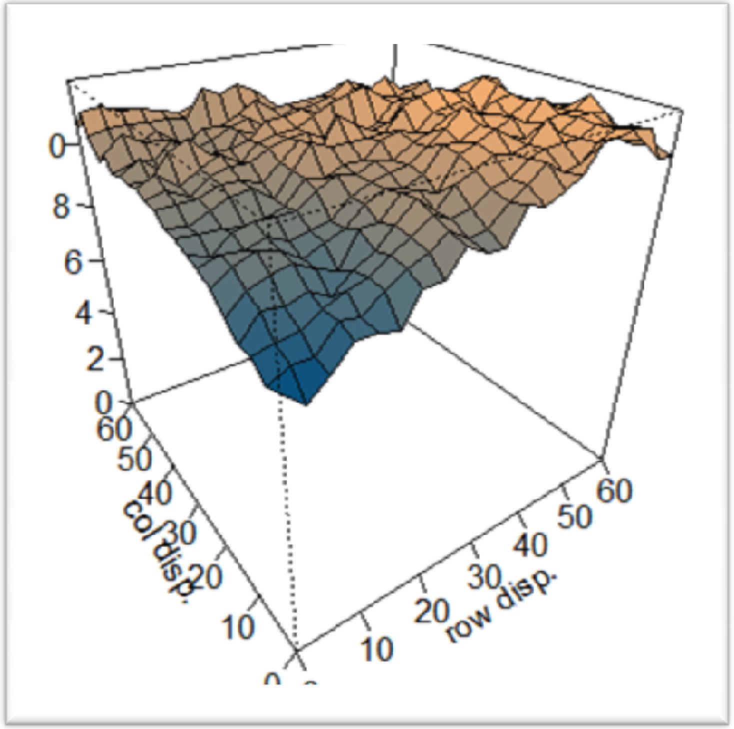
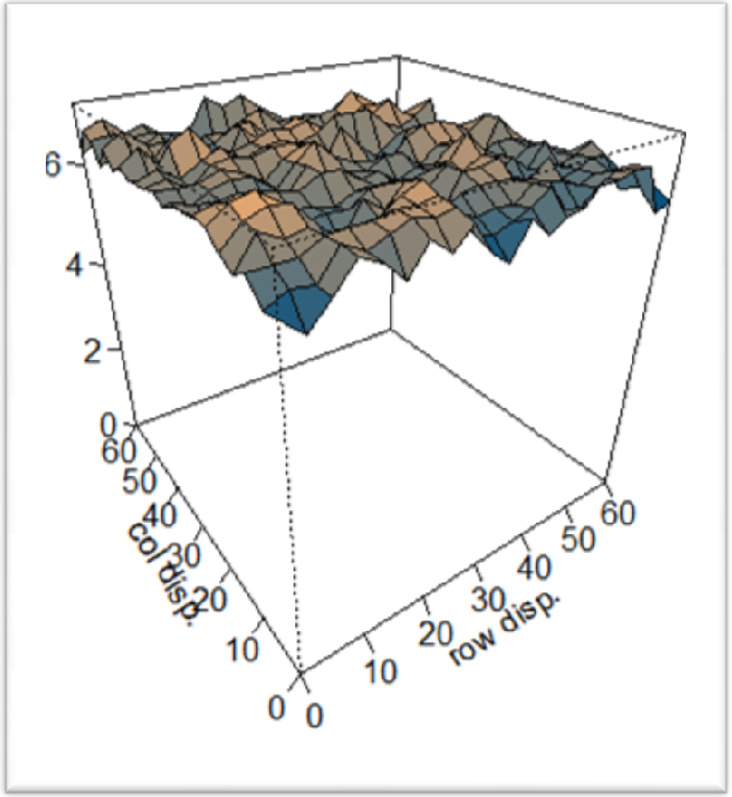
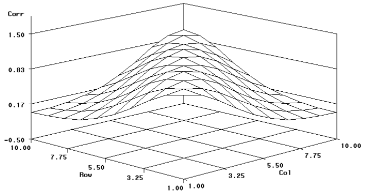
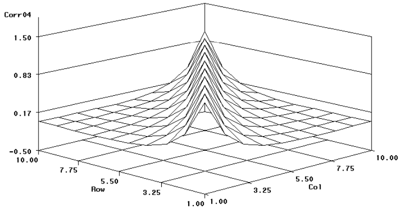
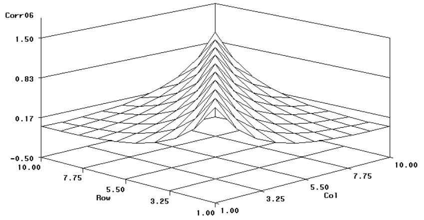
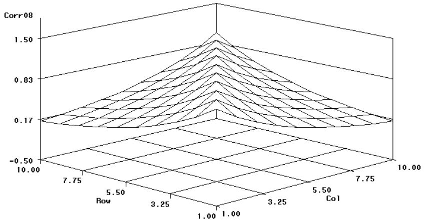


Figura 6.2. Variograma muestral indicando la eliminación de la variación espacial continua producida por el modelo con 12 nodos para filas y 12 para columnas.

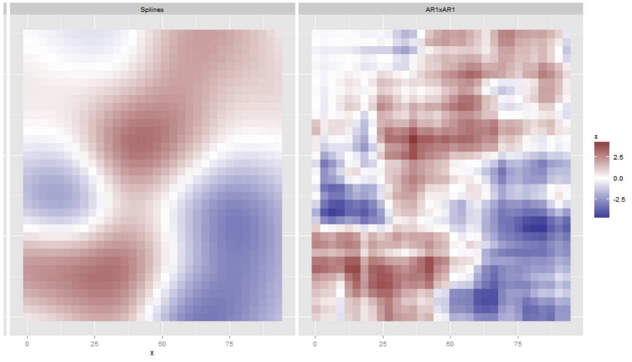


Spatial model with B-splines and autoregressive residuals in E. globulus

Figura 6.3. Matriz de correlación y función de correlación para el modelo propuesto: ***BUB'*** y las estructuras autregresivas de primer orden para filas y columnas: $\mathrm{AR1}(\rho_{fila}) \otimes \mathrm{AR1}(\rho_{col})$ con $\rho_{fila} = \rho_{col} = 0.4$, 0.6 y 0.8.

Matriz de correlación	**Función de correlación para filas y columnas**
BUB'	***BUB'***
$\begin{bmatrix} 1,000 & 0,924 & 0,746 & 0,536 & 0,350 & 0,201 & 0,099 & 0,043 & 0,017 & 0,005 \\ 0,924 & 0,964 & 0,898 & 0,752 & 0,557 & 0,358 & 0,199 & 0,099 & 0,043 & 0,015 \\ 0,746 & 0,898 & 0,973 & 0,931 & 0,768 & 0,548 & 0,345 & 0,198 & 0,099 & 0,042 \\ 0,536 & 0,752 & 0,931 & 0,997 & 0,916 & 0,741 & 0,539 & 0,353 & 0,202 & 0,099 \\ 0,350 & 0,557 & 0,768 & 0,916 & 0,959 & 0,902 & 0,759 & 0,559 & 0,355 & 0,198 \\ 0,201 & 0,358 & 0,548 & 0,741 & 0,902 & 0,983 & 0,934 & 0,763 & 0,542 & 0,345 \\ 0,099 & 0,199 & 0,345 & 0,539 & 0,759 & 0,934 & 0,990 & 0,907 & 0,740 & 0,544 \\ 0,043 & 0,099 & 0,198 & 0,353 & 0,559 & 0,763 & 0,907 & 0,957 & 0,909 & 0,765 \\ 0,017 & 0,043 & 0,099 & 0,202 & 0,355 & 0,542 & 0,740 & 0,909 & 0,992 & 0,934 \\ 0,005 & 0,015 & 0,042 & 0,099 & 0,198 & 0,345 & 0,544 & 0,765 & 0,934 & 0,980 \end{bmatrix}$	
$\mathrm{AR1}(0.4) \otimes \mathrm{AR1}(0.4)$	$\mathrm{AR1}(0.4) \otimes \mathrm{AR1}(0.4)$
$\begin{bmatrix} 1,000 & 0,400 & 0,160 & 0,064 & 0,026 & 0,010 & 0,004 & 0,002 & 0,001 & 0,000 \\ 0,400 & 1,000 & 0,400 & 0,160 & 0,064 & 0,026 & 0,010 & 0,004 & 0,002 & 0,001 \\ 0,160 & 0,400 & 1,000 & 0,400 & 0,160 & 0,064 & 0,026 & 0,010 & 0,004 & 0,002 \\ 0,064 & 0,160 & 0,400 & 1,000 & 0,400 & 0,160 & 0,064 & 0,026 & 0,010 & 0,004 \\ 0,026 & 0,064 & 0,160 & 0,400 & 1,000 & 0,400 & 0,160 & 0,064 & 0,026 & 0,010 \\ 0,010 & 0,026 & 0,064 & 0,160 & 0,400 & 1,000 & 0,400 & 0,160 & 0,064 & 0,026 \\ 0,004 & 0,010 & 0,026 & 0,064 & 0,160 & 0,400 & 1,000 & 0,400 & 0,160 & 0,064 \\ 0,002 & 0,004 & 0,010 & 0,026 & 0,064 & 0,160 & 0,400 & 1,000 & 0,400 & 0,160 \\ 0,001 & 0,002 & 0,004 & 0,010 & 0,026 & 0,064 & 0,160 & 0,400 & 1,000 & 0,400 \\ 0,000 & 0,001 & 0,002 & 0,004 & 0,010 & 0,026 & 0,064 & 0,160 & 0,400 & 1,000 \end{bmatrix}$	
$\mathrm{AR1}(0.6) \otimes \mathrm{AR1}(0.6)$	$\mathrm{AR1}(0.6) \otimes \mathrm{AR1}(0.6)$
$\begin{bmatrix} 1,000 & 0,600 & 0,360 & 0,216 & 0,130 & 0,078 & 0,047 & 0,028 & 0,017 & 0,010 \\ 0,600 & 1,000 & 0,600 & 0,360 & 0,216 & 0,130 & 0,078 & 0,047 & 0,028 & 0,017 \\ 0,360 & 0,600 & 1,000 & 0,600 & 0,360 & 0,216 & 0,130 & 0,078 & 0,047 & 0,028 \\ 0,216 & 0,360 & 0,600 & 1,000 & 0,600 & 0,360 & 0,216 & 0,130 & 0,078 & 0,047 \\ 0,130 & 0,216 & 0,360 & 0,600 & 1,000 & 0,600 & 0,360 & 0,216 & 0,130 & 0,078 \\ 0,078 & 0,130 & 0,216 & 0,360 & 0,600 & 1,000 & 0,600 & 0,360 & 0,216 & 0,130 \\ 0,047 & 0,078 & 0,130 & 0,216 & 0,360 & 0,600 & 1,000 & 0,600 & 0,360 & 0,216 \\ 0,028 & 0,047 & 0,078 & 0,130 & 0,216 & 0,360 & 0,600 & 1,000 & 0,600 & 0,360 \\ 0,017 & 0,028 & 0,047 & 0,078 & 0,130 & 0,216 & 0,360 & 0,600 & 1,000 & 0,600 \\ 0,010 & 0,017 & 0,028 & 0,047 & 0,078 & 0,130 & 0,216 & 0,360 & 0,600 & 1,000 \end{bmatrix}$	
$\mathrm{AR1}(0.8) \otimes \mathrm{AR1}(0.8)$	$\mathrm{AR1}(0.8) \otimes \mathrm{AR1}(0.8)$
$\begin{bmatrix} 1,000 & 0,800 & 0,640 & 0,512 & 0,410 & 0,328 & 0,262 & 0,210 & 0,168 & 0,134 \\ 0,800 & 1,000 & 0,800 & 0,640 & 0,512 & 0,410 & 0,328 & 0,262 & 0,210 & 0,168 \\ 0,640 & 0,800 & 1,000 & 0,800 & 0,640 & 0,512 & 0,410 & 0,328 & 0,262 & 0,210 \\ 0,512 & 0,640 & 0,800 & 1,000 & 0,800 & 0,640 & 0,512 & 0,410 & 0,328 & 0,262 \\ 0,410 & 0,512 & 0,640 & 0,800 & 1,000 & 0,800 & 0,640 & 0,512 & 0,410 & 0,328 \\ 0,328 & 0,410 & 0,512 & 0,640 & 0,800 & 1,000 & 0,800 & 0,640 & 0,512 & 0,410 \\ 0,262 & 0,328 & 0,410 & 0,512 & 0,640 & 0,800 & 1,000 & 0,800 & 0,640 & 0,512 \\ 0,210 & 0,262 & 0,328 & 0,410 & 0,512 & 0,640 & 0,800 & 1,000 & 0,800 & 0,640 \\ 0,168 & 0,210 & 0,262 & 0,328 & 0,410 & 0,512 & 0,640 & 0,800 & 1,000 & 0,800 \\ 0,134 & 0,168 & 0,210 & 0,262 & 0,328 & 0,410 & 0,512 & 0,640 & 0,800 & 1,000 \end{bmatrix}$	

En todos los casos la estructura propuesta (***U** matrix)* produce mucho más suavizado que las estructuras autoregresivas. Al considerar dos árboles contiguos, por ejemplo los ubicados en la fila 3 columnas 4 y 5, la diferencia en correlación para la estructura propuesta es 0.1635, mientras que en el caso del AR(1) con *ρfila* = *ρcol* = 0.6 dicha diferencia es igual a 0.384. La caída de la correlación producida por el modelo con B-splines es similar a la de una estructura Gausiana.



Spatial model with B-splines in E. globulus

Conclusions:

- The three models with B-splines displayed a sizeable lower value of the DIC than the model with blocks. Therefore, analysis of data displaying large scale continuous spatial variation, by spatial models will most likely improve the accuracy of selection as compared with an analysis using a model with blocks;
- The mixed models used to fit a surface in *E. globulus* progeny data displayed: a consistent reduction in the posterior mean of σ^2_e , an increase in the posterior means of σ^2_A and h^2DAP, and an increase of 66 % and 0.23 cm. (for parents) or 60% and 0.77 cm (for offspring) in the accuracy of breeding values and genetic gain, respectively.

Spatial model with B-splines in western hemlock

Data

- The western hemlock full-sib second-generation program was composed of 149 parents, 498 families and 38,948 progeny trees with two different mating structures: 1) 'Local Diallels' (LD) series, representing five geographic populations, and 2) 'Elites' (E) series, 30 'best' parents, 6 best from each geographic population.
- Planted on six (LD series) and four (E series) sites across the Vancouver Island.
- The families of the LD and E series were arranged in a 'Sets in Replicates', with families within a local diallel grouped together in a set ('genetic group') and each replicate included all the sets, and incomplete block design (Alpha design).
- The trait analyzed was Total Height (HT, cm) measured at age 10.

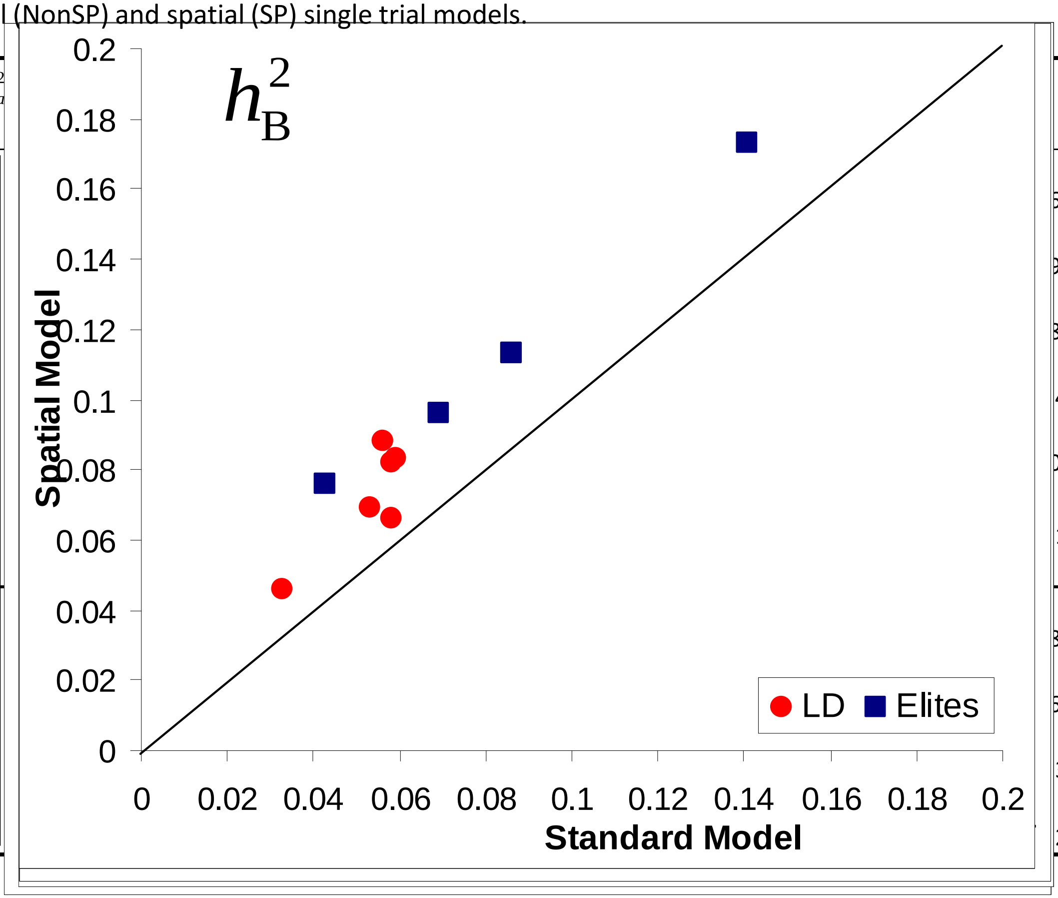
Models of analyses

- Four individual additive tree models were evaluated (Non-spatial and Spatial with 10, 20 and 30 knots).
- The DIC (Spiegelhalter *et al*. 2002) was employed to compare the fit from different models.
- Further model comparison was provided by the accuracy of prediction of breeding values and genetic gain.

Spatial model with B-splines in western hemlock

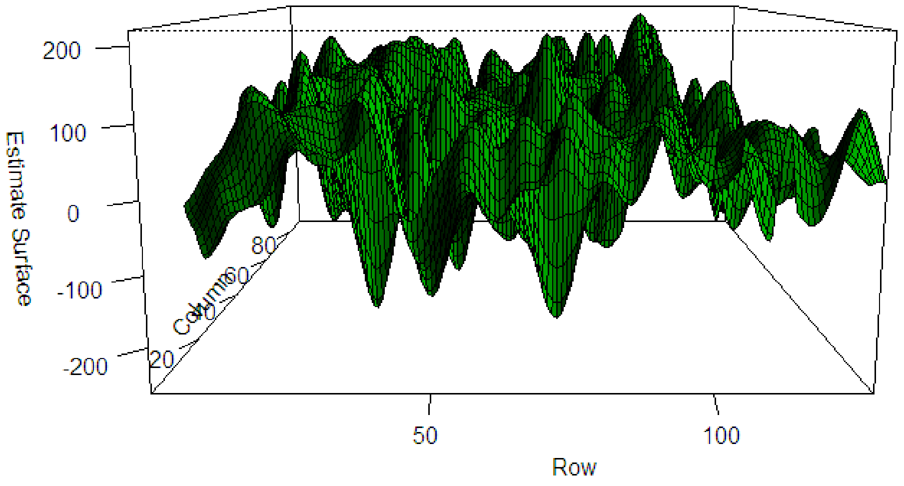
Table 2. Deviance Information Criterion (DIC, expressed as differences from the DIC for the non-spatial model), posterior means (Mean) and standard deviations (SD) of the additive genetic variance ( ), dominance genetic variance ( ), error variance ( ), individual narrow-sense heritability (h2N), individual broad-sense heritability (h2B), dominance to additive variance ratio ( ), knot effects variance ( ), replicates variances ( ) and incomplete block variance ( ) from the non-spatial (NonSP) and spatial (SP) single trial models.

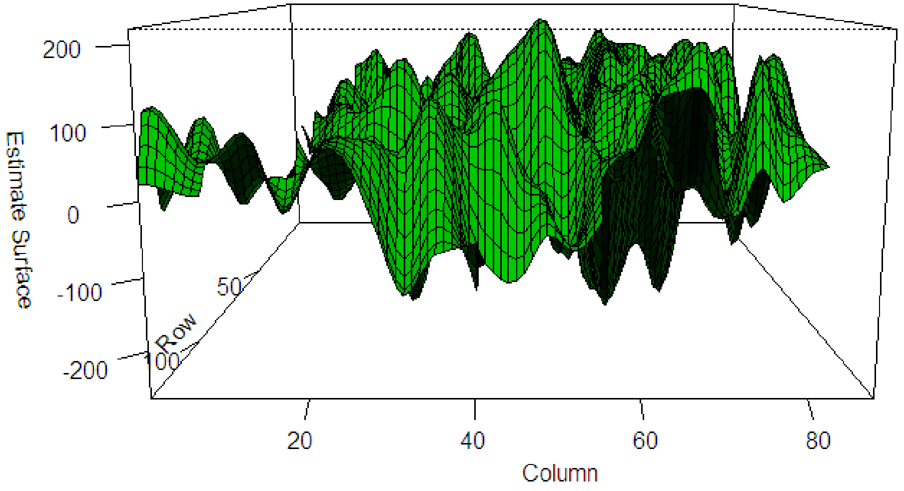
Sites	Model^a	DIC	σ^2_a		σ^2_r		σ^2_s	
'Local Diallels'			Mean	SD	Mean	SD	Mean	SD
Jordan 2	NonSP		887.2	-	2608.0	740.7	-	-
	SP30	1132.29	896.8	523.0	-	-	-	-
Kiyu	NonSP		624.6	-	3258.5	926.3	-	-
	SP30	297.41	554.8	971.0	-	-	-	-
Jordan 3	NonSP		799.2	-	3118.9	891.0	-	-
	SP30	251.98	873.2	358.0	-	-	-	-
Rupert 1	NonSP		1721.6	-	5012.7	1485.0	-	-
	SP10	321.25	1812.2	466.0	-	-	-	-
Russell	NonSP		543.5	-	1682.2	615.5	-	-
	SP30	394.46	528.0	097.0	-	-	-	-
Humptulips	NonSP		1174.2	-	8154.9	2309.0	-	-
	SP10	28.86	1116.3	160.0	-	-	-	-
'Elites Crosses'								
Klanawa	NonSP		1225.2	-	4816.7	1198.0	2786.9	1011.0
	SP30	69.09	1235.5	307.0	-	-	-	-
Stove	NonSP		1834.8	-	1237.1	323.9	952.5	345.7
	SP30	458.07	1883.2	565.0	-	-	-	-
Tlupana	NonSP		1710.6	-	4121.4	1015.0	2783.7	1007.0
	SP10	40.11	1665.6	391.0	-	-	-	-
Michelsen	NonSP		841.1	-	1237.1	322.2	943.8	342.6
	SP10	107.12	914.0	296.0	-	-	-	-

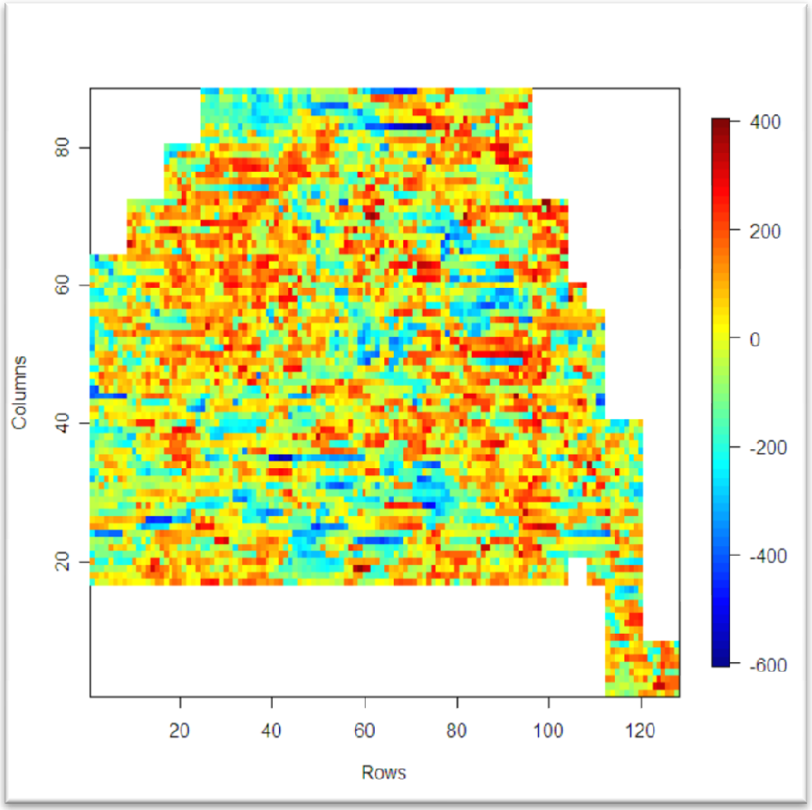


Spatial model with B-splines in western hemlock

Kiyu: small-scale variation.

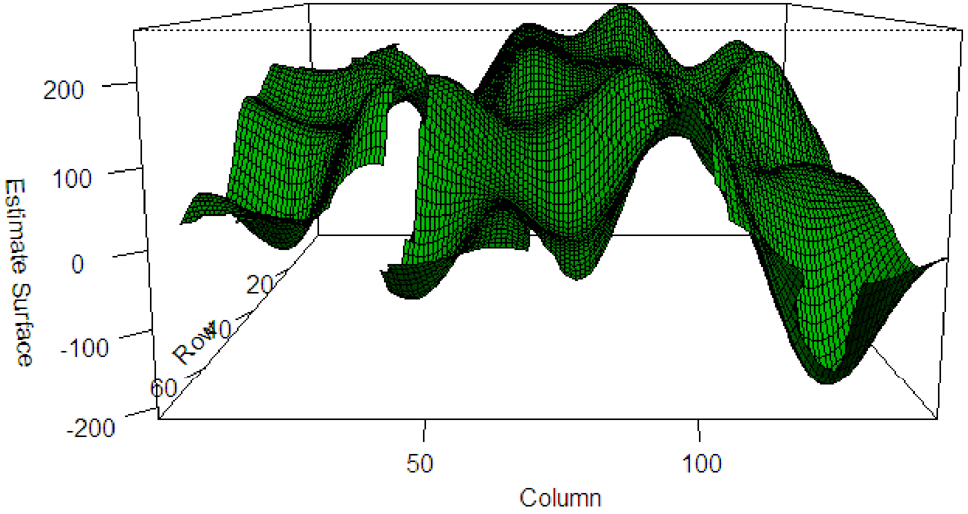


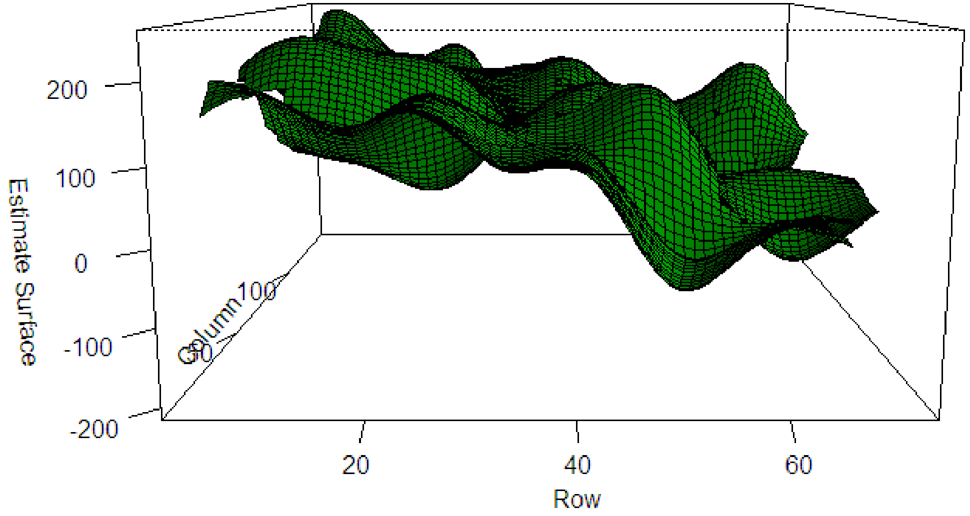


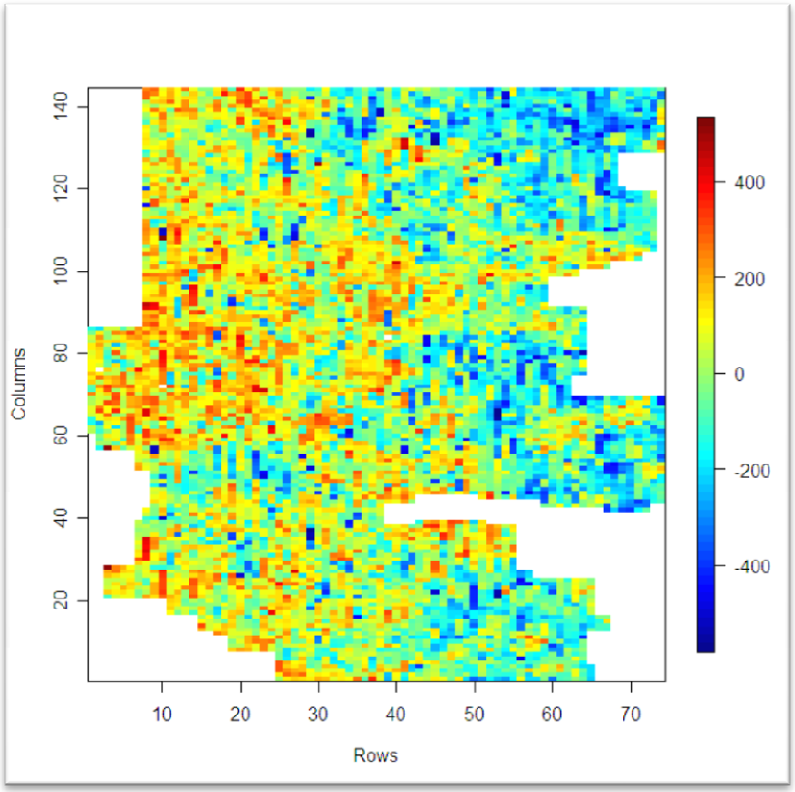


Spatial model with B-splines in western hemlock

Humptulips: large-scale variation in one dimension together with small-scale variation.

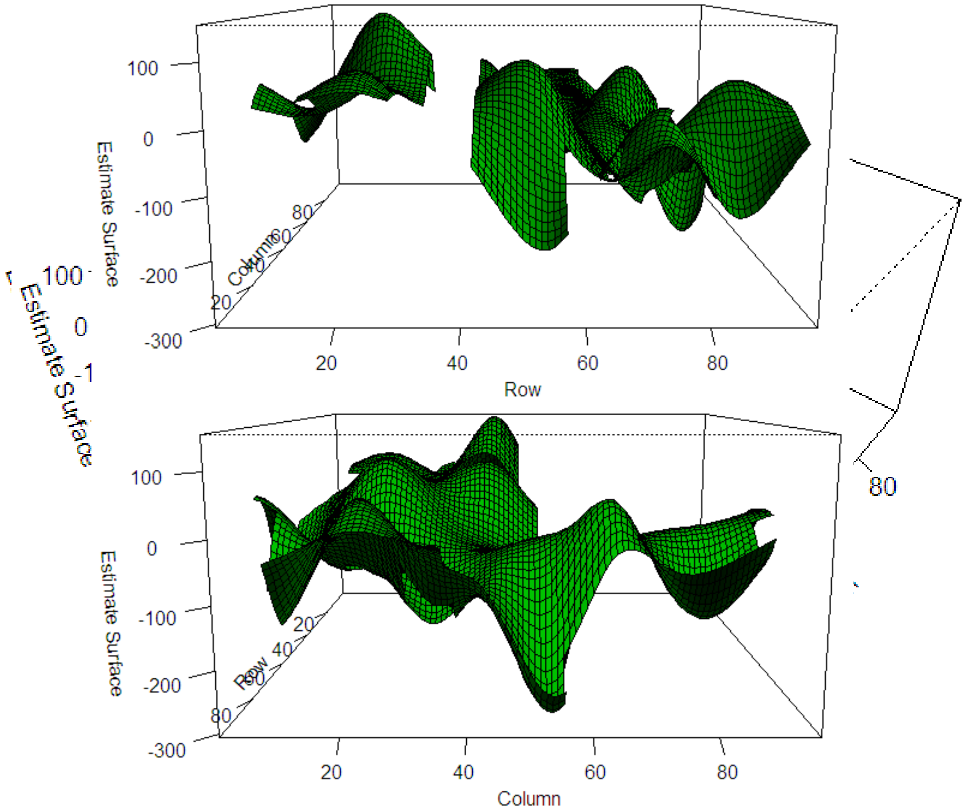


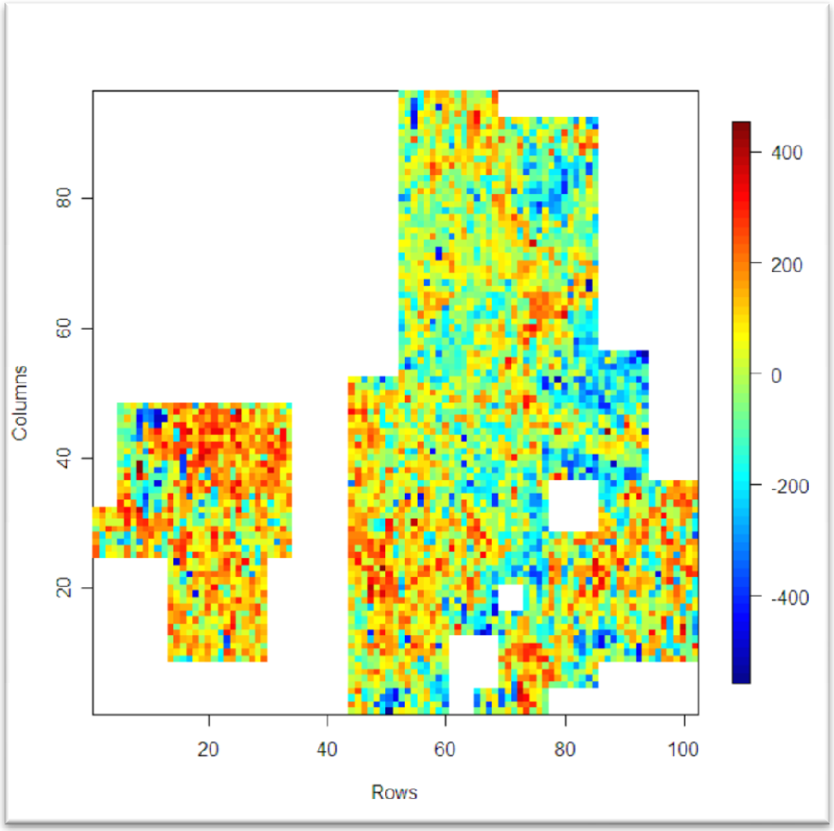




Spatial model with B-splines in western hemlock

Tlupana: large-scale variation in two dimension together with small-scale variation.





Spatial model with B-splines in western hemlock

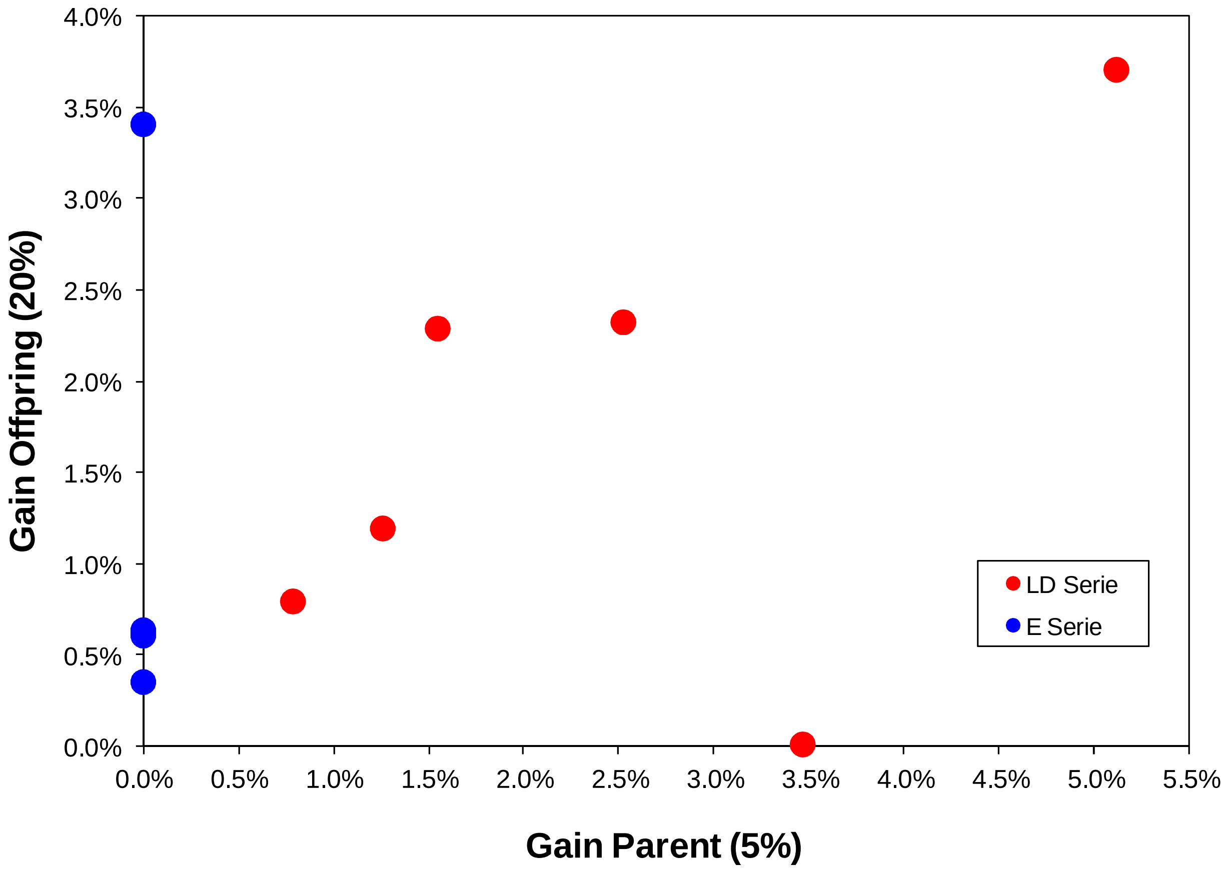
Table 4: Accuracy of prediction of breeding values (BV), and Spearman correlation between predicted breeding values from the estimates random design effects (Models 2) and from the best fitting of tensor product B-splines with 10 (Models 3: Rupert 1, Humptulips and Michelsen) or 20 (Model 5: Jordan 2, Kiyu, Jordan 3, Russell, Klanawa and Stove) knots.

Sites	**Accuracy of BV for**						**Spearman correlation of BV for**		
	Families		**Parents**		**Offspring**		**Families**	**Parents**	**Offspring**
	ST	**SP**	**ST**	**SP**	**ST**	**SP**			
Jordan 2	0.270	0.288	0.556	0.589	0.381	0.404	0.970	0.980	0.977
Kiyu	0.285	0.325	0.422	0.452	0.303	0.325	0.919	0.942	0.945
Jordan 3	0.260	0.292	0.496	0.530	0.358	0.384	0.968	0.980	0.978
Rupert 1	0.074	0.041	0.580	0.604	0.419	0.437	0.986	0.990	0.988
Russell	0.000	0.001	0.361	0.373	0.295	0.303	0.957	0.938	0.933
Humptulips	0.258	0.257	0.606	0.608	0.434	0.435	0.988	0.990	0.988
Klanawa	0.000	0.000	0.833	0.855	0.609	0.625	0.892	0.917	0.956
Stove	0.494	0.494	0.875	0.882	0.641	0.647	0.977	0.996	0.994
Tuplana	0.261	0.278	0.870	0.872	0.634	0.637	0.955	0.992	0.989
Michelsen	0.451	0.484	0.805	0.812	0.586	0.593	0.987	0.990	0.993
AVERAGE	**0.235**	**0.246**	**0.640**	**0.658**	**0.466**	**0.479**	**0.960**	**0.972**	**0.974**

NOTE: *Probability values < 0.0001

Spatial model with B-splines in western hemlock

Relative selection gain from spatial analysis of western hemlock trials.



Spatial model with B-splines in western hemlock

Conclusions:

- Reduce the posterior mean of the error variance from 3.4 to 48.2 %.
- Increase the posterior mean of the h^2_N from 25.0 to 76.7 %.
- Increases the precision (i.e. lower standard deviations) of the error variance from 1.9 to 34.3 % and the h^2_N from 14.3 to 77.8 %.
- Increase the accuracy of breeding values from parents, families and offspring in 4.3, 3.1 and 3.2 %, respectively.
- Increase the genetic gain up to 5.0 % and to 3.5 % for parents and offspring, respectively.

Spatial model with B-splines in western hemlock

The results from the present study show the utility of the tensor product of B-splines in accommodating different patterns of spatial heterogeneity, which had: a) small-scale variations, b) large-scale variation in one dimension (i.e., across the row or column), and c) two dimensions (i.e., across row and column) or both together, in large forest genetics trails.

Results

Individual-tree mixed model with competition effects

Papers

1- Eduardo P. Cappa, and Rodolfo J. C. Cantet. (2008). Direct and competition additive effects in tree breeding: Bayesian estimation from an individual tree mixed model. Silvae Genetica, 57(2): 45-59.

2- Eduardo, P. Cappa, Facundo Muñoz, Leopoldo Sanchez, and Rodolfo J. C. Cantet. (2015). A novel individual-tree mixed model with competition effects and environmental heterogeneity: a Bayesian approach. Tree Genetic and Genomes (enviado).

Competition model in Loblolly pine

Data

- **20 open-pollinated families of Loblolly pine (*Pinus taeda* L.), originary from Marion (Florida, USA)**

- **DBH (932) measured at age 13.**

- **The design was a RCB with 8 replicates of 5 trees in line per plot. The spacing was 3.5 m × 3.5 m.**

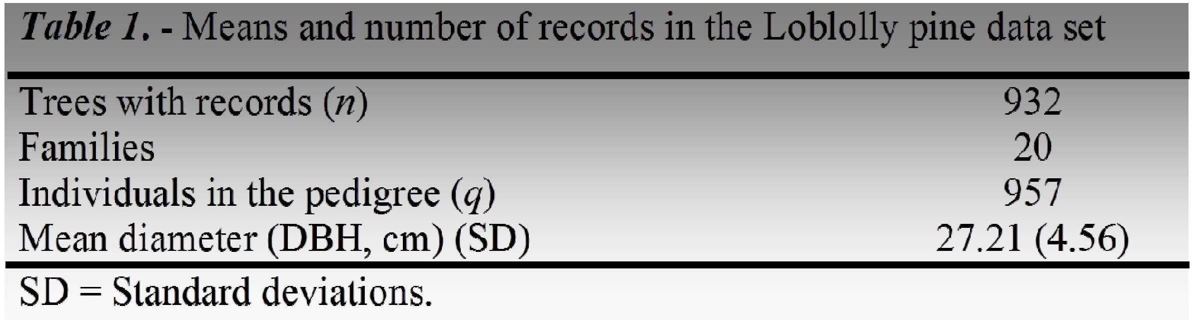


Table 1. **-** Means and number of records in the Loblolly pine data set

Trees with records (n)	932
Families	20
Individuals in the pedigree (q)	957
Mean diameter (DBH, cm) (SD)	27.21 (4.56)

SD = Standard deviations.

Competition model in Loblolly pine

Table 1: Deviance Information Criterion (DIC) and posterior statistics for additive genetic variance $\boldsymbol{\sigma}^2_{\mathbf{A}}$, direct additive variance $\boldsymbol{\sigma}^2_{\boldsymbol{Ad}}$, competition additive variance $\boldsymbol{\sigma}^2_{\boldsymbol{Ac}}$, direct and competition additive correlation $\boldsymbol{r}_{\mathbf{AdAc}}$, knots effects variance $\boldsymbol{\sigma}^2_{\boldsymbol{b}}$, permanent environmental variance $\boldsymbol{\sigma}^2_{\boldsymbol{p}}$, and error variance $\boldsymbol{\sigma}^2_{\boldsymbol{e}}$.

Model[a]	DIC	Parm.[b]	Mean	Median	Mode	SD[c]	95% HPD[d]
TM	2686.24	$\sigma^2_{\mathrm{A}d}$	5.76	5.57	4.74	1.52	3.62 – 8.54
		σ^2_t	20.72	18.80	15.39	8.74	10.66 – 37.33
		σ^2_e	12.44	12.52	12.55	1.41	10.00 – 14.63
CM	2515.20	$\sigma^2_{\mathrm{A}d}$	8.04	7.98	7.95	1.43	5.78 – 10.48
		$\sigma^2_{\mathrm{A}c}$	1.56	1.54	1.39	0.33	1.08 – 2.14
		$\rho_{\mathrm{A}d\mathrm{A}c}$	-0.85	-0.86	-0.87	0.05	-0.91 - -0.76
		σ^2_p	1.21	1.17	1.20	0.30	0.79 – 1.76
		σ^2_t	19.39	17.59	14.85	8.19	9.98 – 34.96
		σ^2_e	8.25	8.22	7.63	1.26	6.23 – 10.36
SP	2593.88	$\sigma^2_{\mathrm{A}d}$	8.52	8.34	8.32	2.22	5.18 – 12.46
		σ^2_b	3.00	2.87	2.92	0.88	1.83 – 4.63
		σ^2_t	16.30	14.80	11.32	6.80	8.46 – 29.29
		σ^2_e	10.19	10.26	10.84	1.85	7.02 – 13.11
CSM	2481.25	$\sigma^2_{\mathrm{A}d}$	8.75	8.70	10.09	1.52	6.35 – 11.33
		$\sigma^2_{\mathrm{A}c}$	1.62	1.59	1.77	0.33	1.12 – 2.19
		$\rho_{\mathrm{A}d\mathrm{A}c}$	-0.85	-0.86	-0.86	0.05	-0.92 - -0.77
		σ^2_b	2.88	2.75	2.25	0.83	1.78 – 4.41
		σ^2_p	0.98	0.95	1.05	0.24	0.65 – 1.42
		σ^2_t	19.45	17.65	13.13	8.20	10.01 – 35.00
		σ^2_e	7.54	7.51	6.17	1.27	5.51 – 9.67

Competition model in Loblolly pine

Conclusions:

- Using the competition model the value of σ^2_{Ad} *was* almost ten times higher than the magnitude of σ^2_{Ac}, whereas the magnitude of the genetic correlation between direct and competitive effects was sizable (-0.85).
- The mixed model with competition genetics effects displayed a consistent increase in the accuracy of BV. Genetic gains of 4 and 16 % (for parents) and 27 and 30 % (for offspring), were achieved.

Spatial and Competition models in Douglas-fir Fr

Data

- …

Models of analyses

- **Time to play!**

Muchas Gracias

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