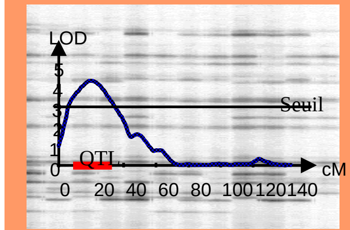
Statistical analysis of forest genetic experiments. Some key points.

Catherine Bastien



Statistical analysis of forest genetic experiments

Some key points

Catherine Bastien
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PROFOREST Workshop, Warsaw, 24-27 August 2004

INTRODUCTION

Objectives of forest genetic field experiments

- Comparison of **different populations** of a given species for *quantitative* and *qualitative* traits expressed in **forest conditions: provenance tests**

- Genetic evaluation in **forest conditions** of **phenotypical selections** : **progeny tests** (« + » trees open-pollinated progenies, polymix progenies, controlled crosses), **clonal tests, multisite experiments**

- **Backward** selection in clonal seed orchard on multitrait evaluation in **forest conditions** of **phenotypical selections** : **progeny tests** (« + » trees open-pollinated progenies, polymix progenies, controlled crosses)

- **Forward** selection on multitrait evaluation in **forest conditions** for long-term breeding strategies : **progeny tests** (« + » trees open-pollinated progenies, polymix progenies, controlled crosses)

- Evaluation of **genetic variability** of natural and artificial populations for *quantitative* and *qualitative* traits expressed in forest conditions : **progeny tests**

INTRODUCTION

forest genetic field experiments

Genotype : provenance, progeny-family, clone

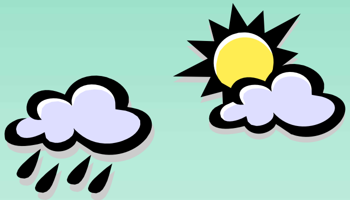
A basic common model : Fisher (1918)

P = G + E + GxE

Genotype → G

Common Environment → E

Interaction between genotype and environment → GxE



Fixed situation

• Precise estimation of genotypic values and genotype stability over a given set of environmental conditions

Random situation

• Precise estimation of genetic and GxE variances in a multitrait context

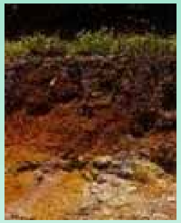
INTRODUCTION

forest genetic field experiments

Prediction of G_i values in a given experiment

$$P_{ij} = G_i + B_{lock}^{*} + R_{ij}$$

Controlled experimental variation



To maximize for a better control of environmental variation

Residual Uncontrolled variation

To minimize for maximum precision (experimental designs)

* Complete or incomplete block design with single or multitree plots

PLAN

forest genetic field experiments

- 1 - **Test** and **adjustment** for local environmental effects:
  - Efficiency of block designs
  - Correction with **spatial analysis** : Papadakis iterative method

INTRODUCTION

forest genetic field experiments

Prediction of Breeding Values A_i
before genetic thinning in clonal seed orchards

Fisher's key insights : Each individual pass to its offspring a fraction of its genetic value which at a minimum is equal to ½ genetic additive value **A**

Evaluation criteria

Breeding objective

Own performance P_1

Performance of offspring P_2

Correlated Traits P_n

Molecular markers M_n

→ Breeding value A_i

Multiple linear regression

$$A = b_1P_1 + b_2P_2 + \dots + b_nP_n + \dots + c_nM_m$$

forest genetic field experiments

PLAN

- 1 - **Test** and **adjustment** for local environmental effects:
  - Efficiency of block designs
  - Correction with **spatial analysis** : Papadakis iterative method
- 2 – **Estimation of breeding values**
  - BLUP's
  - variance components estimation

INRA

INTRODUCTION

forest genetic field experiments

Multitrait selection
and economic weights of the different selection objectives

Adaptation
(biotic & abiotic factors)

Volume production

Stem quality

Wood quality

Selection Index : $I = a_1G_1 + a_2G_2 + \ldots + a_nG_n$

PLAN

forest genetic field experiments

- 1 - **Test** and **adjustment** for local environmental effects:
  - Efficiency of block designs
  - Correction with **spatial analysis** : Papadakis iterative method
- 2 – **Estimation of breeding values**
  - BLUP's
  - variance components estimation
- 3 – **Multi-trait selection**
  - Prediction of response to selection
  - Independent Culling vs. Index
  - Economic vs technical weights in selection index

forest genetic field experiments

Control of environmental variation

Adjustment for local environmental effects

Adjustment for local environmental effects

forest genetic field experiments

Control of environmental variation by block effects

Example : analysis of total height of a clonal test
in a 6 complete block design

ANOVA Table 2003 Total Height

	Df	SSE	MS	F-test	P-value
Bloc	5	603119	120624	72.36	0.000
Genotype	354	1988304	5617	3.3692	0.000
Residuals	1718	2864033	1667		

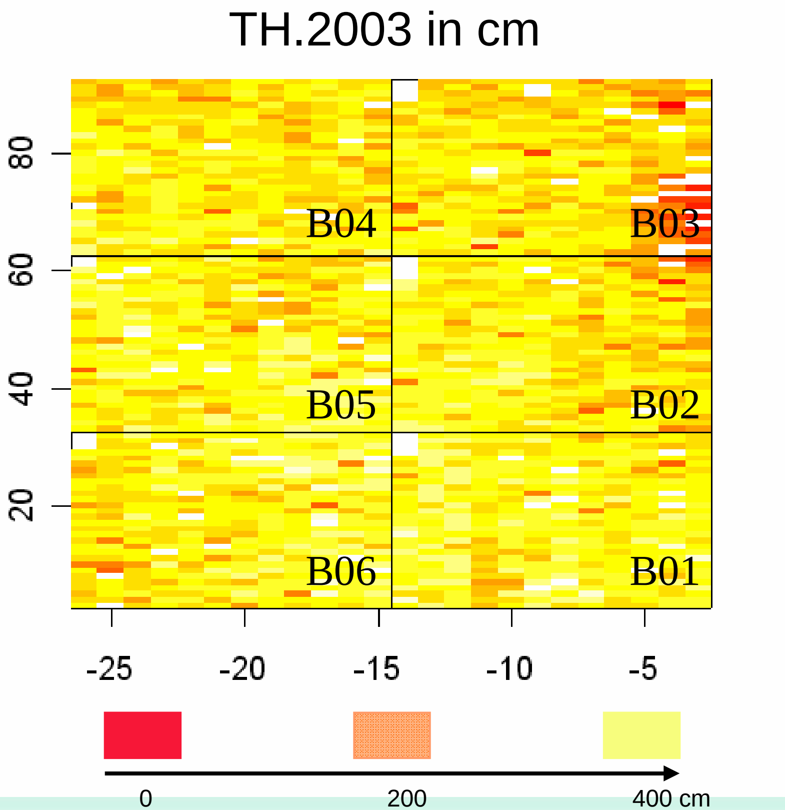
Strong block effects !

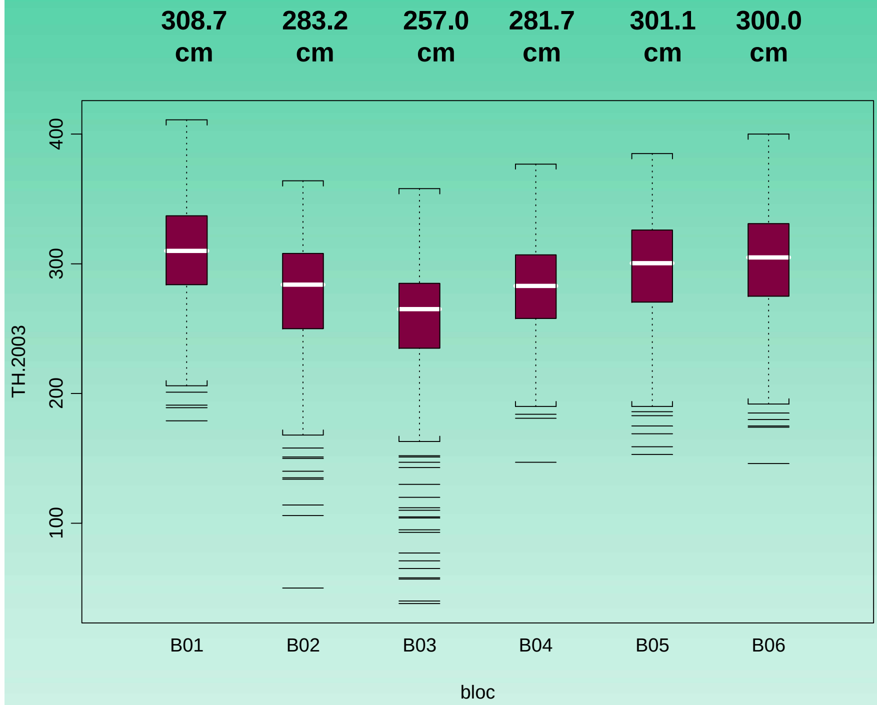
$CV_r = 14.1\%$

Adjustment for local environmental effects

Control of environmental variation by block effects

Example : analysis of total height of a clonal test in a 6 complete block design





block effects will control part of environmental variation. What does remain ?

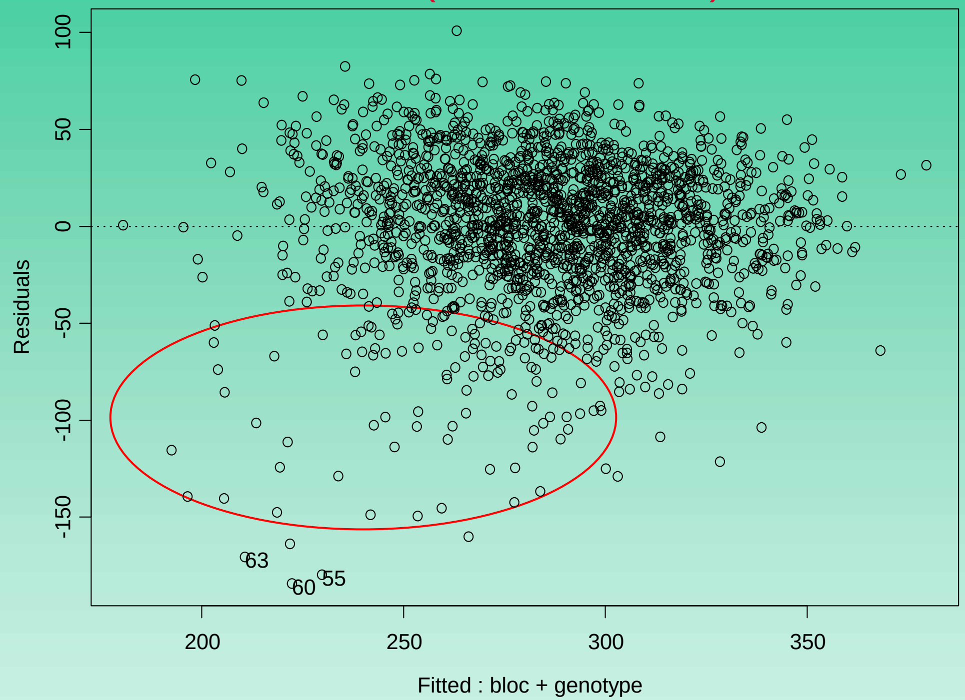
Analysis of microsatellite sequences in Scots pine (p. 145-158). Presented at PROFOREST Workshop on "New approaches in forest tree genetics", Varsovie, POL (2004-08-24 - 2004-08-27). Varsovie, POL : Forest Research Institute.

Adjustment for local environmental effects

Control of environmental variation by block effects

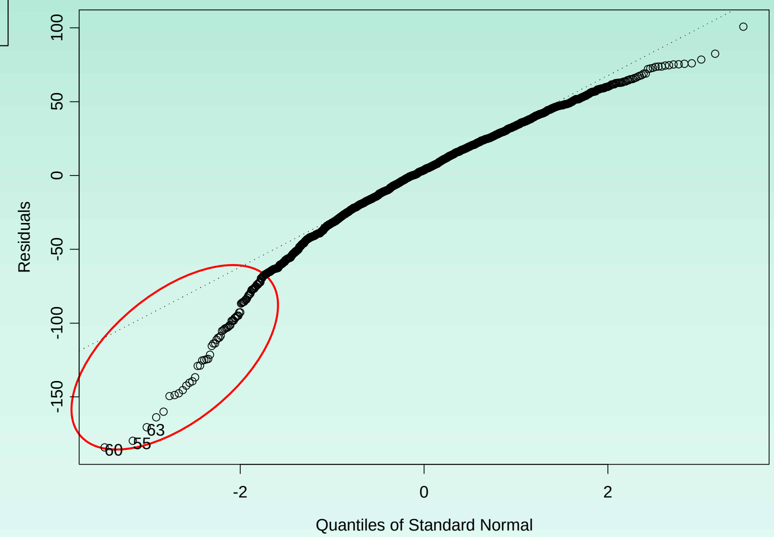
Example : analysis of total height of a clonal test in a 6 complete block design

Plot(fitted,residuals)



Analysis of residual variation

Quantile-Quantile plot of residuals



- **A lot of plants with relative low height**

transplantation effect ?
local environmental effects ?

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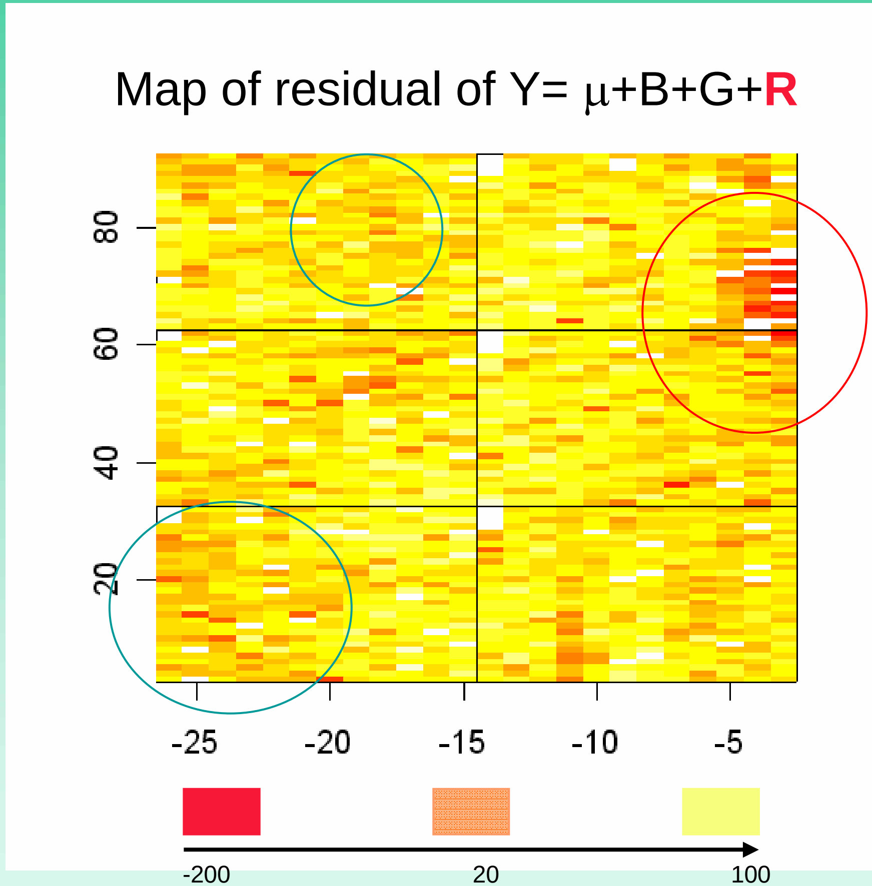
Adjustment for local environmental effects

Control of environmental variation by block effects

Example : analysis of total height of a clonal test in a 6 complete block design

spatial distribution of residual variation

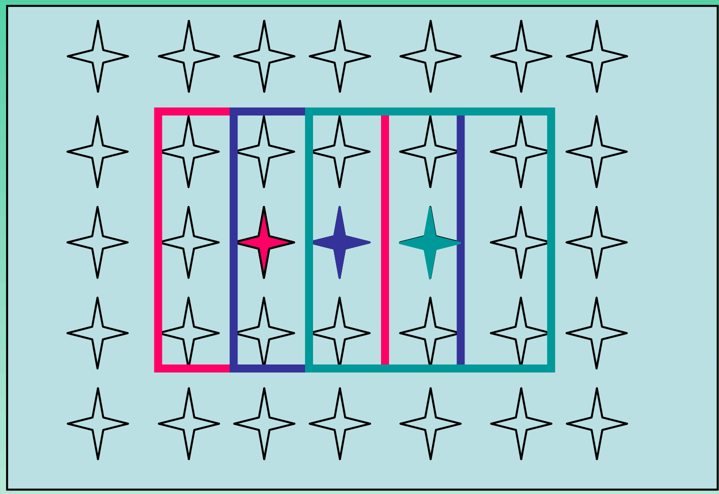


Environmental variation still exist within block !

Control of environmental variation by spatial analysis

Example : analysis of total height of a clonal test in a 6 complete block design

Papadakis iterative method



Environmental variation is measured by the neighborhood residual information **(Ψr)**

$$P_{ij} = \mu + G_i + b\,E(\Psi r) + R'_{ij}$$

$$E(\Psi r) = \sum_{i'j'} R'_{i'j'} \;/\; n_{(r)}$$

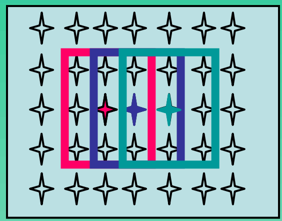
$$P'_{ij} = P_{ij} - b\,E(\Psi r)$$

Iterative procedure

Adjustment for local environmental effects

Control of environmental variation by spatial analysis

Example : analysis of total height of a clonal test in a 6 complete block design



Papadakis iterative method

Neighborhood : 5 trees x 9 trees

ANOVA Table 2003 on Total Height corrected by Papadakis

	Df	SSE	MS	F-test	P-value
Bloc	5	7023	1405	1.0711	0.3745
Genotype	354	1861064	5257	4.0089	<0.0001
Residuals	1718	2252986	1311		

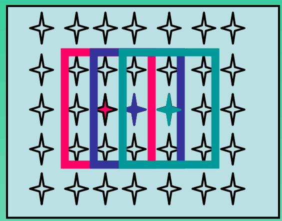
Reduced residual variation

$CV_r = 12.8\%$

Adjustment for local environmental effects

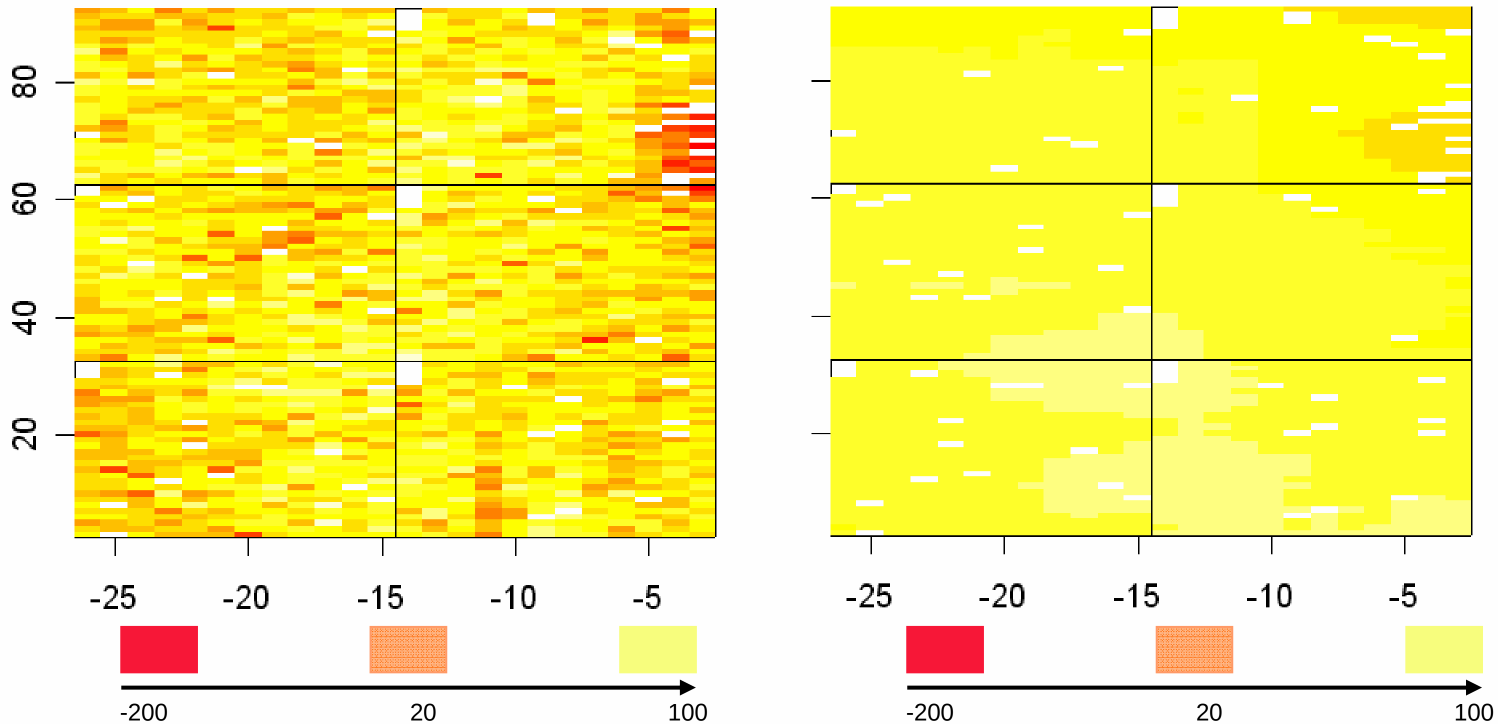
Control of environmental variation by spatial analysis

Example : analysis of total height of a clonal test in a 6 complete block design



Papadakis iterative method

Adjustment to block effects | Adjustment by spatial analysis



Final choice : *adjustment by spatial analysis and elimination of five rows in block 03*

Control of environmental variation by spatial analysis

Adjustment for local environmental effects

Papadakis iterative method

Kempton RA and Howes CW 1981. The use of neighbouring plot values in the analysis of variety trials. Applied Statistics 30 (1), 59-70

Dagnélie P. 1989. The method of Papadakis in Agricultural Experimentations. An overview Bulletyn Oceny Odmian, 21-22, 111-122.

Besag J and Kempton R. 1986. Statistical Analysis of Field Experiments Using neighbouring plots. Biometrics 42, 231-251.

Bartlett MS. 1978. Nearest neighbour models in the Analysis of Field Experiments.J.R. Statist. Soc. 2, 147-174.

Analysis of microsatellite sequences in Scots pine (p. 145-158). Presented at PROFOREST Workshop on "New approaches in forest tree genetics", Varsovie, POL (2004-08-24 - 2004-08-27). Varsovie, POL : Forest Research Institute.

Estimation of breeding values

forest genetic field experiments

Estimation of breeding values and phenotypic variance components

VG

VR

VA

h2

rG

Estimation of breeding values

forest genetic field experiments

Prediction of Breeding Values A_i before genetic thinning in clonal seed orchards

Finding the optimal regression coefficients b_n

$$A = b1P1 + b2P2 + \ldots + bnPn$$

$$Y = f(X) = b\,X \qquad b = \frac{cov(X,Y)}{var(X)}$$

BLUP = **B**est **l**inear **u**nbiased **p**rediction

Evaluation criteria

Own performance P_1

$$b_1 = Cov(P_1, A) / var(P_1)$$

$$b_1 = Cov(A + \cancel{D} + \cancel{I} + \cancel{E}, A) / var(P_1)$$

$$b_1 = Cov(A, A) / var(P_1)$$

$$b_i = h^2$$

Analysis of microsatellite sequences in Scots pine (p. 145-158). Presented at PROFOREST Workshop on "New approaches in forest tree genetics", Varsovie, POL (2004-08-24 - 2004-08-27). Varsovie, POL : Forest Research Institute.

Estimation of breeding values

Prediction of Breeding Values A_i before genetic thinning in clonal seed orchards

Evaluation criteria

Open pollinated progeny performance P_2

$$A = b_2 P_2$$

n = nb. ind in progeny

Var(mean) = common variance + specific / n

$$b_2 = Cov(P_2, A) / var(P_2)$$

$$b_2 = \tfrac{1}{2} V_A / var(P_2)$$

$$b_2 = \tfrac{1}{2} V_A / (V_{Fam} + V_{resid} / n)$$

Heritability of progeny test

$$b_2 = h^2_{Fam} = \frac{2n}{n + \frac{4 - h^2}{h^2}}$$

b_2 depends on the number of progeny and on the heritability

Estimation of breeding values

Prediction of Breeding Values A_i before genetic thinning in clonal seed orchards

Evaluation criteria — Open pollinated progeny performance P_2

k traits measured

$$A = b_2^1 P_2^1 + b_2^2 P_2^2 + \dots + b_2^k P_2^k$$

M_P = matrix of phenotypic variances-covariances

M_A = matrix of additive genetic variances-covariances

$$b_2 = ½ M_A M_P^{-1}$$

Traits	b_2 for $A_{\text{Total height age 15}}$
Total height age 15	0.562
Total height age 15 Total height age 10 Girth age 15 Branch angle age 10	0.714

From Bastien 1999, unpublished data

Estimation of breeding values

Prediction of Breeding Values A_i before genetic thinning in clonal seed orchards

- *Efficiency* of **BLUP** estimation proved in many animal and plant breeding programs

- **BLUP** estimation is always superior to phenotypical selection on progeny means

- Measuring **correlated traits** could increase significantly precision of breeding values estimation

- **BLUP** could be easily calculated with all softwares including linear model predictions [SAS, ASREML, Splus,….]

- **BLUP** needs only accurate estimation of M_A (heritabilities and additive genetic correlations)

Estimation of variance components

Estimation of variance components

- Two key statistical ANOVA identities
  - Total variance = between-group variance (V_{Fam}) + within-group variance (V_W)
  - Variance(between groups) = covariance (within groups)

- One key genetic property of Fisher model (Kempthorne 1957)

  X and Y , two individuals

$$Cov(X, Y) = 2\, r_{XY}\, V_A + u_{XY}\, V_D$$

In practice

Open-pollinated progenies collected **randomly** in most Scots pine stands could be considered as a **random** sample of **half-sib progenies**

$$\mathbf{V_{Fam}} = Cov\ (HS)$$
$$\mathbf{V_{Fam}} = \mathbf{V_A} \;/ 4$$

4 V_{Fam} gives an estimation of $\mathbf{V_A}$

Estimation of variance components according to the experimental design

Estimation of variance components

Estimation of variance components

Two methods

Expected means squares of Analysis of Variance (ANOVA) Henderson III	Restricted maximum likelihood estimation (REML)
• Independent estimation of fixed and random effects	•Simultaneous estimation of fixed and random effects
• Biaised estimation in case of non-orthogonal (unbalanced) designs	• no demand on design or balance of data
• difficulty to analyze jointly variety of relatives	• no demand on design or balance of data
	• **now available** in most statistical softwares

Estimation of variance components

Estimation of variance components

Example : analysis of total height and branch angle in a Scots pine progeny test

Expected means squares of Analysis of Variance (ANOVA)

ANOVA Table on Total Height adjusted to block effects Y'= Y - Block

		Df	SSE	MS	E(MS)
Fixed	**Bloc**	41	100978	2463	$V_R + k\phi_{bloc}$
Random	**Genotype**	64	1039806	16247	$V_R + nV_{Fam}$
Random	**Residuals**	1935	7260365	3752	V_R

Average **n = 31.4** trees per progeny

$$\hat{V}_R = 3752$$

$$\hat{V}_{Fam} = (16247 – 3752)/31.4 = 397.9$$

$$\hat{V}_A = 4*\hat{V}_F = 1591.7$$

$$\hat{h}^2 = 1591.7 / (397.9 + 3752) = 0.383$$

Estimation of variance components

Estimation of variance components

Example : analysis of total height and branch angle in a Scots pine progeny test

Expected means squares of Analysis of Variance (ANOVA)

MANOVA Total Height , Branch angle adjusted to block effects Y'= Y - Block

		Df	SCPE	MCP	E(MCP)
Fixed	**Bloc**	41	-232.27	-5.66	$Cov_R + k\phi_{bloc}$
Random	**Genotype**	64	722.97	11.30	$Cov_R + nCov_{Fam}$
Random	**Residuals**	1911	2423.75	1.27	Cov_R

Average **n = 31.2** trees per progeny

$$\hat{Cov}_R = 1.27$$

$$\hat{Cov}_{Fam} = (11.30-1.27)/31.2 = 0.32$$

$$\hat{Cov}_A = 4*\hat{Cov}_F = 1.28$$

$$\hat{r}_A = 1.28 / \sqrt{(1591.7 *0.45)} = 0.047$$

Analysis of microsatellite sequences in Scots pine (p. 145-158). Presented at PROFOREST Workshop on "New approaches in forest tree genetics", Varsovie, POL (2004-08-24 - 2004-08-27). Varsovie, POL : Forest Research Institute.

Estimation of variance components

Estimation of variance components

Example : analysis of total height and branch angle in a Scots pine progeny test

Restricted maximum likelihood estimation (REML)

Model : $Y_{adj} = \mu + B_{lock} + F_{amily} + R_{esidual}$

Fixed (Block), Random (Family), Random (Residual)

	Total Height	**Branch angle**
V_{Fam}	411.86	0.116
$Sd(V_{Fam})$	95.21	0.024
V_R	3753	0.609
$Sd(V_R)$	29.33	0.020
h^2	0.395	0.640
$Sd(h^2)$	0.085	0.051

Precision of variance component estimations depends on nb. of progenies

Estimation of variance components

Example : analysis of total height and branch angle in a Scots pine progeny test

Restricted maximum likelihood estimation (REML)

Model : $Y_{adj} = \mu + B_{lock} + F_{amily} + R_{esidual}$

Fixed Random Random

Estimation of Covariance components

$$Cov(X+Y) = V_X + V_Y + 2\,Cov(X,Y)$$

$$Cov(X,Y) = ½\,(Cov(X+Y) - (V_X + V_Y))$$

	Total Height-Branch angle
Cov_{Fam}	-0.120
Cov_R	3753
r_A	**-0.017**

Multi-trait selection

3- Multitrait selection and economic weights of the different selection objectives

Adaptation
(biotic & abiotic factors)

Volume production

Stem quality

Wood quality

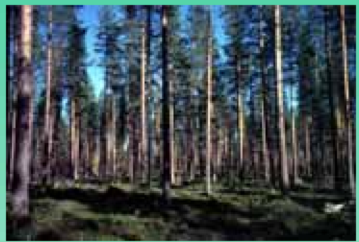
Selection Index : $I = a_1G_1 + a_2G_2 + \ldots + a_nG_n$

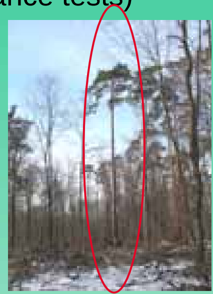
forest genetic field experiments

Prediction of response to selection

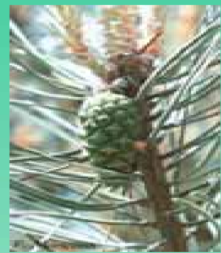
Multitrait selection

« + » tree selection
(natural stands, provenance tests)





Seed collection



Multisite evaluation
progeny testing

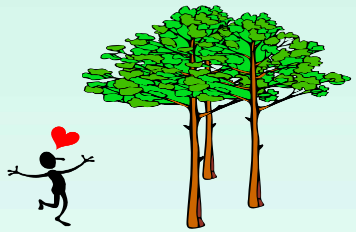
Grafting

Clonal Collection for recombination

Clonal seed orchard

Forward selection
Genetic thinning in seed orchard

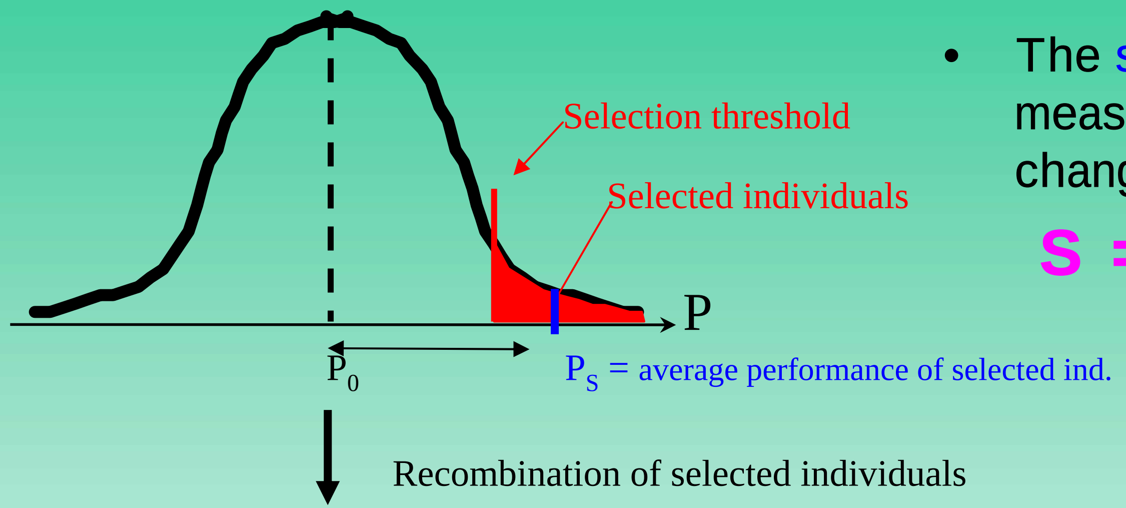
Realized genetic gain

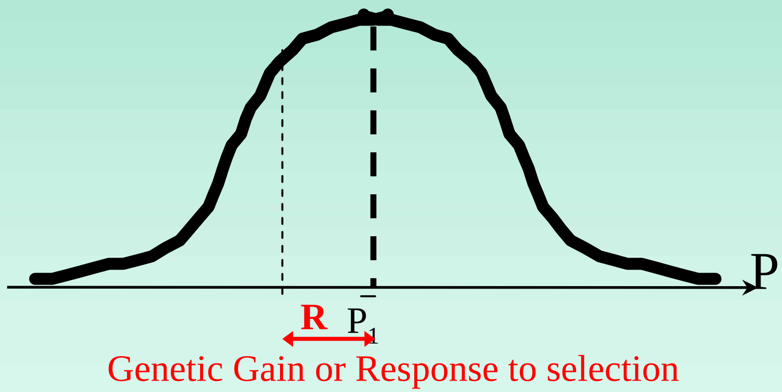


Response to selection

forest genetic field experiments

Prediction of response to selection





- The selection differential **S** measures the within-generation change in the mean

$$S = P_s - P_0$$

- The response **R** is the between-generation change in the mean

$$R = P_1 - P_0$$

Response to selection

forest genetic field experiments

Prediction of response to selection

- Selection can change the distribution of phenotypes. We typically measure this by changes in mean.

This is a within-generation change measured by $S = P_s - P_0$

- Selection can also change the distribution of breeding values (changes in allele frequencies).

This is a the response to selection, the change in the trait in the next generation (between-generation change) measured by

$R = P_1 - P_0$

Response to selection

Prediction of response to selection

The Breeder's Equation

$$R = h^2 S$$

- Note that no matter how strong **S**, if **h²** is small, the response is small
- **S** is a measure of selection, **R** the actual response. One can get lots of selection but no response

Applications

- In agriculture and forestry breeding
- Construction of divergent pedigree for QTL mapping and gene expression (microarray) analysis : inferences about nb. Of loci, effects and frequencies
- Evolutionary inferences : correlated charcaters, effects on fitness, long-term response

Response to selection

Prediction of response to selection

The Selection Intensity, i

Populations with the same selection differential (**S**) may experience very different amounts of selection

The selection intensity i provided a suitable measure for comparisons between populations,

$$\mathbf{i} = \frac{\mathbf{S}}{\sigma_p}$$

$$R = h^2 S = i\,h^2 \sigma_p = \mathbf{i}\ \mathbf{h}\ \sigma_A$$

- Since **h** = correlation between phenotypic and breeding values

Response = Intensity * Accuracy * Spread in V_A

The correlated response

Selection on Trait 1, predicting response of Trait 2

$$R_2 = i_1 \, r_{A_{1,2}} \, h_1 \, h_2 \, \boldsymbol{\sigma}_{\mathbf{p2}}$$

Response to selection

Prediction of response to selection

A general formulation

X = trait selected Y= trait measured

$$R = i\,\rho\,\sigma_{A_X}$$

$$\rho = 2.\ r.\ r_{A_{X,Y}}.\ h'_Y.\sqrt{(n/[1+(n-1)t])}$$

Ollivier,2002

r = coancestry coefficient between candidate and ind. measured
(OP progeny → parent-offspring → r=1/4)

$r_{A_{X,Y}}$ = genetic correlation between X and Y if different

h'_Y = heritability of the selection criterion
(ind. Values, progeny means)

n = nb. of measures on the candidate (nb. offspring per parent)

t = correlation between observations on the same candidate
(OP progeny → h^2 / 4)

Response to selection

Response to selection with progeny testing

Forward selection

$$\rho = 2 . r . r_{AX,Y} . h'_Y . \sqrt{(n/[1+(n-1)t])}$$

Ollivier,2002

	Response X	Response Y
r	¼	¼
$r_{AX,Y}$	1	$r_{AX,Y}$
h'_Y	h_X	h_X

n = nb. of measures on the candidate (nb. offspring per parent)

t	$h^2_X/4$	$h^2_x/4$

Response to selection

Response to selection with progeny testing

Forward selection

$$R_X = 0.5\ i\ h_x . \sqrt{(n/[1+(n-1)h^2_x/4])}\ \ \sigma_{Ax}$$

$$R_{Y/X} = 0.5\ i\ r_{Ax,Y}\ h_x . \sqrt{(n/[1+(n-1)h^2_x/4])}\ \sigma_{AY}$$

	Response X Total height	Response Y Branch angle
h^2	0.395	0.640
$\sigma^2_A=4*\sigma^2_{Fam}$	1647.44	0.464

$r_{Ax,Y}$= -0.210
n= 30
i=1.755 (10%)

Forward selection on X	Phenotypic selection on X
R_X = 62.4 cm	R_X = 44.8 cm
$R_{Y/X}$ = -0.43	$R_{Y/X}$ = -0.16

Bastien, C. (2004). Statistical analysis of forest genetic experiments: Some key points. In: Analysis of microsatellite sequences in Scots pine (p. 145-158). Presented at PROFOREST Workshop on "New approaches in forest tree genetics", Varsovie, POL (2004-08-24 - 2004-08-27). Varsovie, POL : Forest Research Institute.

Response to selection with progeny testing

Forward selection

$$R = 2\ h^2_f\ S_f = 2\ i\ h^2_f\ \sigma_{Pf}$$

Selection on 2 parents (male and female)

$$h^2_f = \frac{\sigma^2_f}{\sigma^2_f + \sigma^2_R/n}$$

$$\sigma^2_{Pf} = \sigma^2_f + \sigma^2_R/n$$

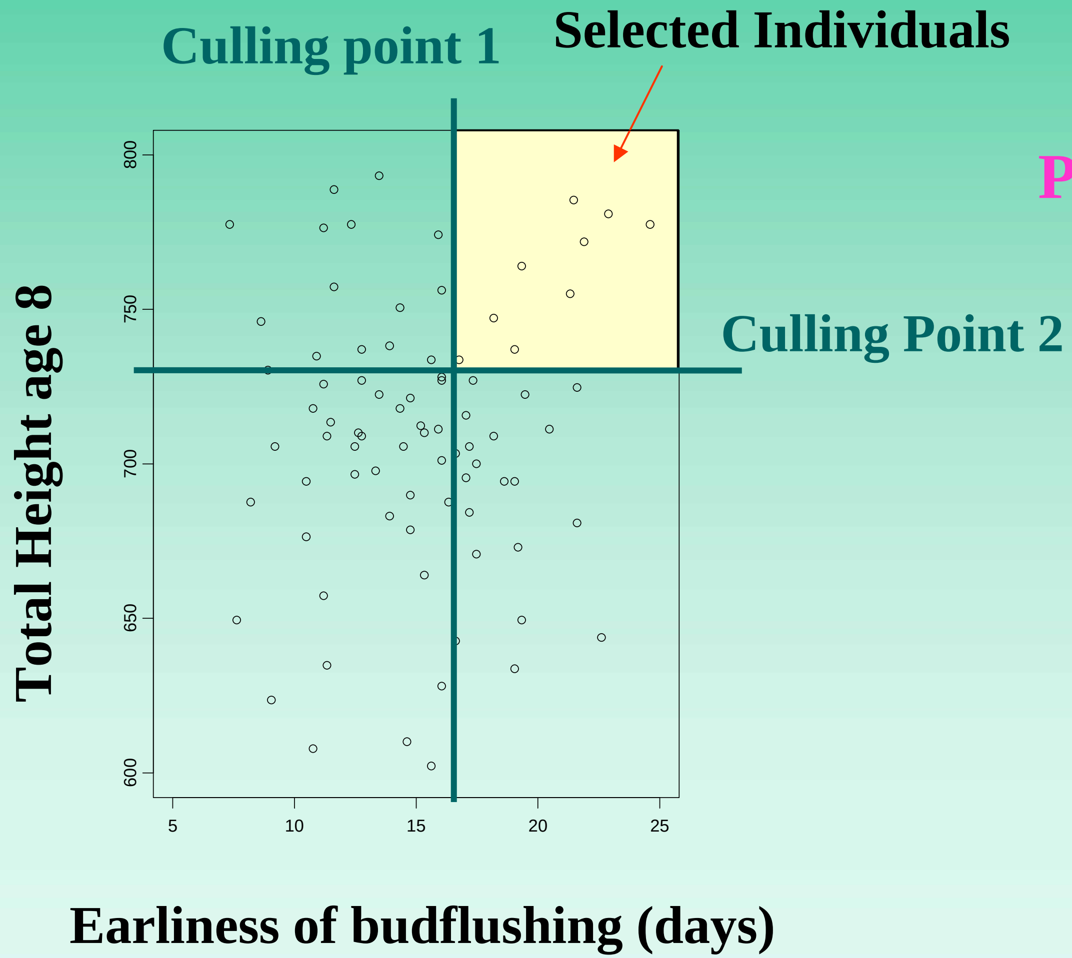
	Response X Total height	
h^2	0.395	
σ^2_{Fam}	411.86	h^2_f = 0.767
σ^2_R	3753	σ^2_{Pf} =537

R_x = 62.4

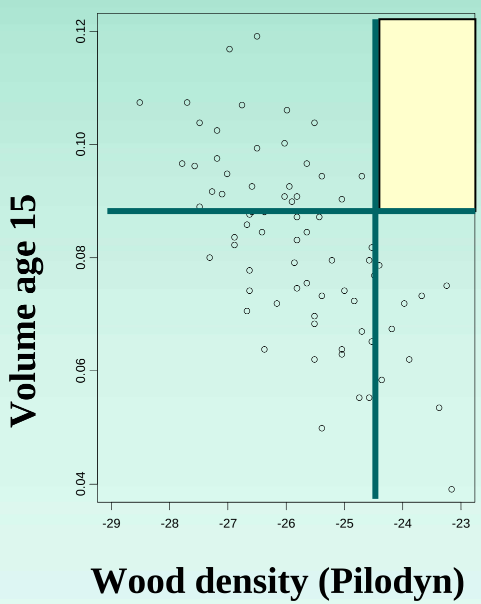
Multitrait selection : Independent Culling vs. Index

Multi-trait selection

Independent Culling



Problem if unfavourable correlation



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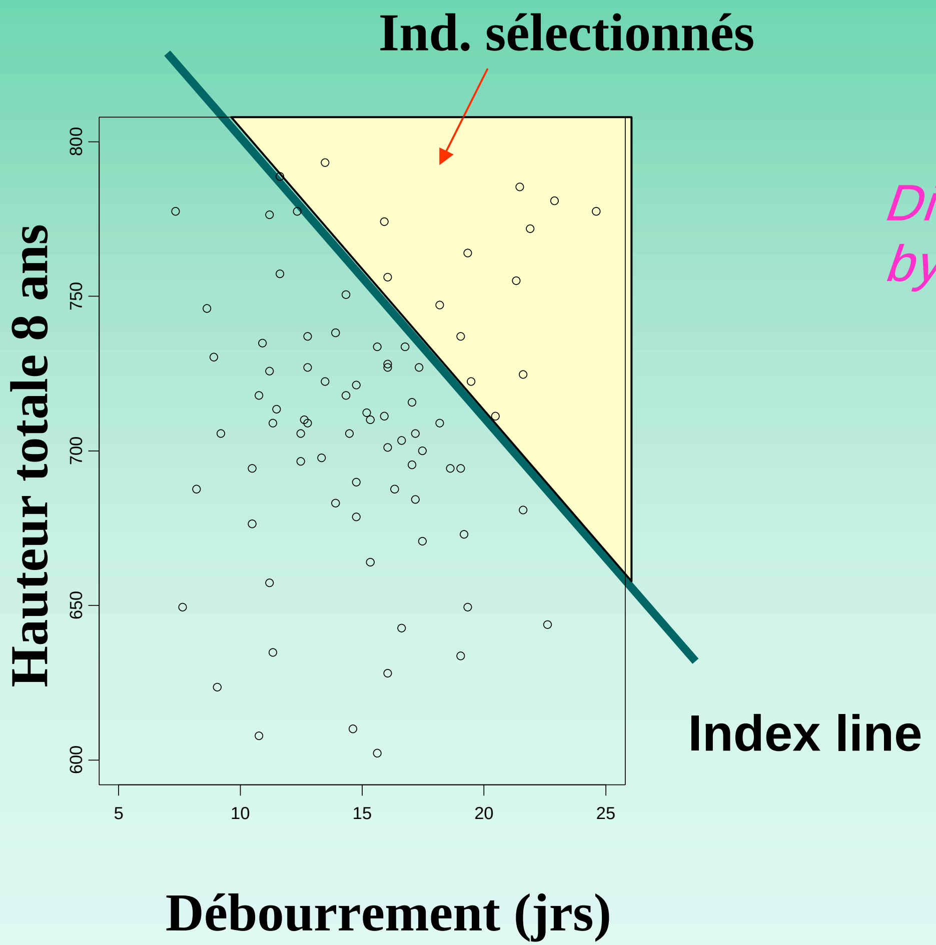
Multitrait selection : Independent Culling vs. Index

Multi-trait selection

Index Selection

$$I = w_1 A_1 + w_2 A_2 + \ldots w_q A_q$$



Disadvantage in one trait off set by advantage in the other

Multitrait selection : Independent Culling vs. Index

Index Selection vs. Independent Culling

Theoretical comparisons

If same total of nb. of individuals measured on all traits:

genetic gain

Index S > Independent Culling > Tandem selection

Practical considerations

- Index selection:
  - -must keep all individuals until all traits measured
  - -cull in one stage
- Traits differ greatly in costs to measure
- Traits differ greatly in age of evaluation
- Selection intensity may be greater for multistage (culling) selection

Index Selection and technical weights

Index Selection

$$I = w_1 A_1 + w_2 A_2 + \ldots w_q A_q = [w'A]$$

w = vector of technical or economical weights

$$I = b_1 P_1 + b_2 P_2 + \ldots b_q P_q = [b'P]$$

b = vector of weights for phenotypic predictors

BLUP properties : $A = M_P^{-1} M_A Z_{centered}$

$$b = [M_P^{-1} M_A w]$$

Example	σ_P	h^2	r_A	w		b
Wood density	0.4	0.3	0.5	5	→	0.53
Volume	0.2	0.5	0.5	-1		-0.31

In general, weights on phenotypic information sources are not esay to « recognize »

Index Selection and technical weights

Response to Index Selection

$$I = w_1 A_1 + w_2 A_2 + \ldots w_q A_q = [w'A]$$

w = vector of technical or economical weights

$$R = \begin{matrix} R_1 \\ R_2 \\ . \\ R_k \end{matrix} = \frac{i\, w'\, M_A}{\sqrt{w'\, M_P\, w}}$$

Index Selection and technical weights

Response to Index Selection

Forward selection

Example : HUMPTULIPS Population

$$I = w_1\ \text{BudFlush} + w_2\ \text{TH} + w_3\ \text{Ang} + w_4\ \text{Br} + w_5\ \text{Def}$$

Estimation of maximum relative genetic expected gains

W	BudFlush	TH	Ang	Br	Def
(-1,0,0,0,0)	**-55%**	8.9%	1.8%	12%	-19%
(0,1,0,0,0)	-24.4%	**20%**	-0.5%	-0.4%	9.9%
(0,0,1,0,0)	-4.4%	-0.4%	**22.5%**	11.0%	-3.9%
(0,0,0,1 0)	-32.2%	-0.4%	12.1%	**20.5%**	-16.3%
(0,0,0,0,-1)	-34%	-6.4%	2.8%	10.8%	**-31%**

Index Selection and technical weights

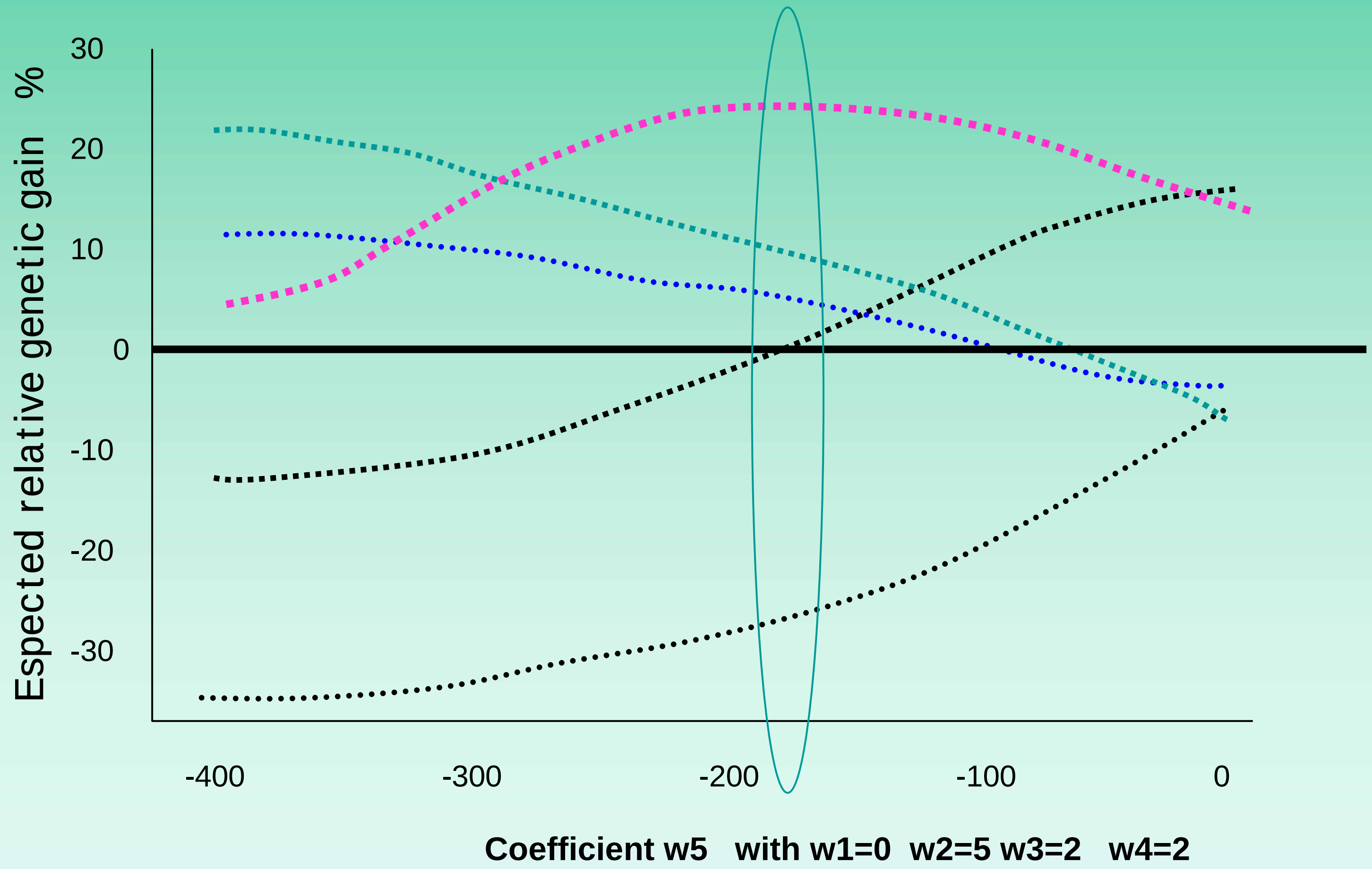
Response to Index Selection

Simulation of expected genetic gains with varying w

Forward selection

Example : HUMPTULIPS Population

$$I = w_1 \textbf{ BudFlush} + w_2 \textbf{ TH} + w_3 \textbf{ Ang} + w_4 \textbf{ Br} + w_5 \text{ Def}$$



Index Selection and technical weights

Response to Index Selection

Forward selection

$$I = w_1 A_1 + w_2 A_2 + \dots w_q A_q = [w'A]$$

w = vector of technical or economical weights

BLUP :

$$\mathbf{A} = \tfrac{1}{2} M_A M_{Pf}^{-1} P$$

$$\mathbf{I} = \tfrac{1}{2} w' M_A M_{Pf}^{-1} P$$

$$R = \frac{2i\, w' M_{Fam}}{\sqrt{w' M_{PFam} w}}$$

$$\sigma^2_{PFam} = \sigma^2_{Fam} + \sigma^2_R / n$$

M_{Fam} =

	Total height	Branch angle
	411.86	-1.451
	-1.451	0.116

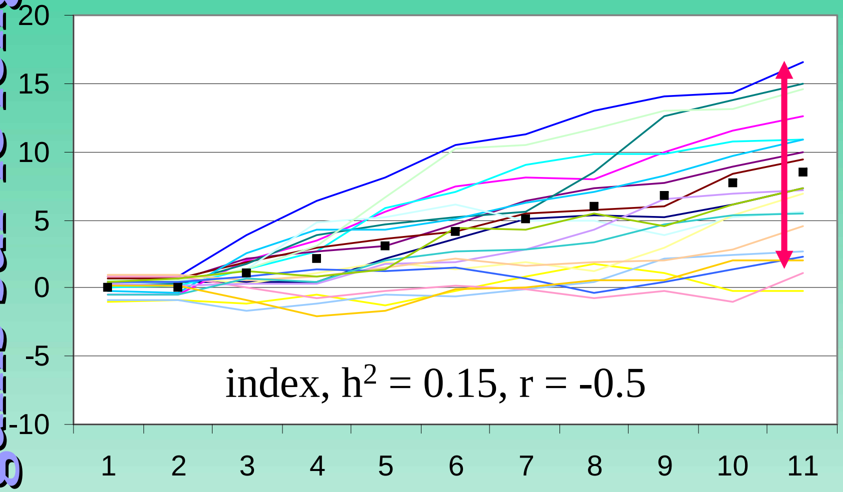
M_{PFam} =

	Total height	Branch angle
	537	-1.528
	-1.528	0.136

Optimisation des gains sur le long terme

Sélection multi-caractères et Liaisons génétiques défavorables

Quels sont les effets?



•Augmentation de la variation du progrès génétique (imprévisibilité)

• Perte du mérite général

Comment diminuer ces effets?

• Choix de la méthode de sélection