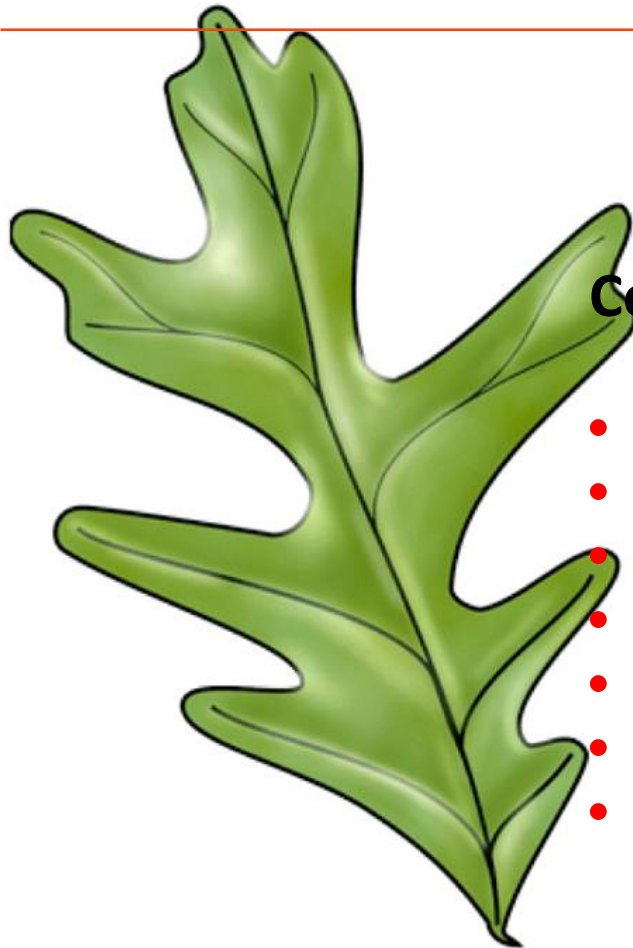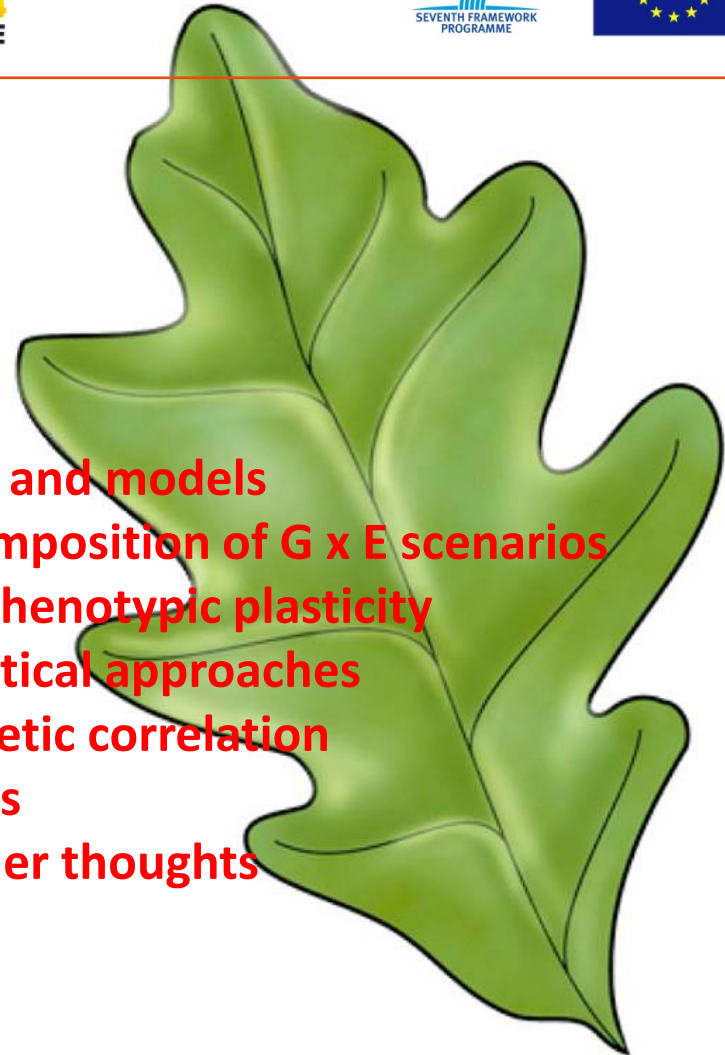Leaves of a white oak

Contents

- **Definitions and models**
- **Basic decomposition of G x E scenarios**
- **G x E and phenotypic plasticity**
- **Basic analytical approaches**
- **Type B genetic correlation**
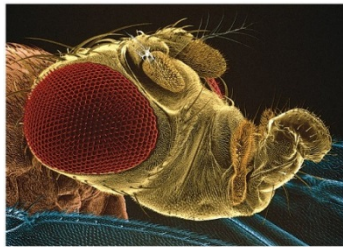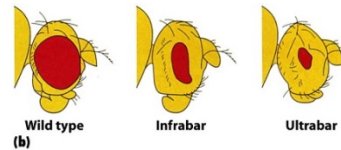- **Ecovalences**
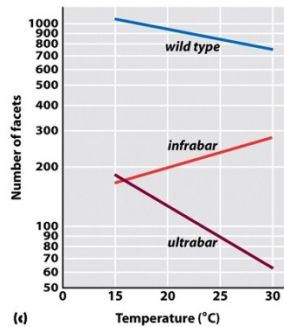- **Some further thoughts**

Grown in sun

Grown in shade

Designing Trees for the Future

G × E occurs when changes in environment do not have the same effect on all genotypes:
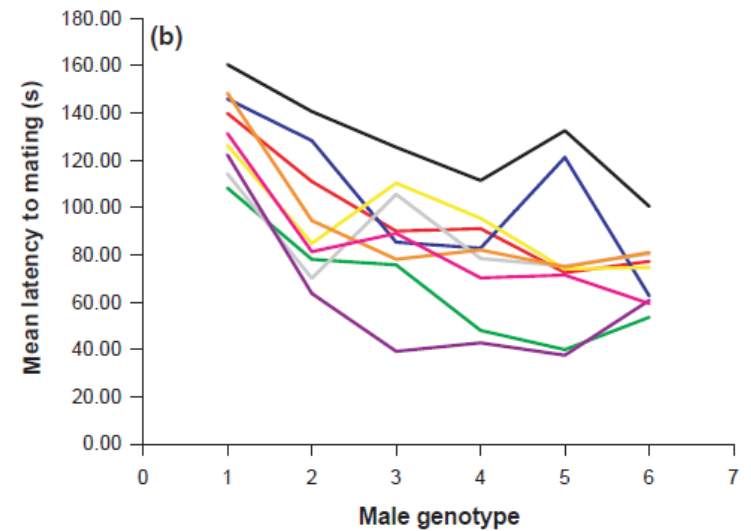

Figure 1-18
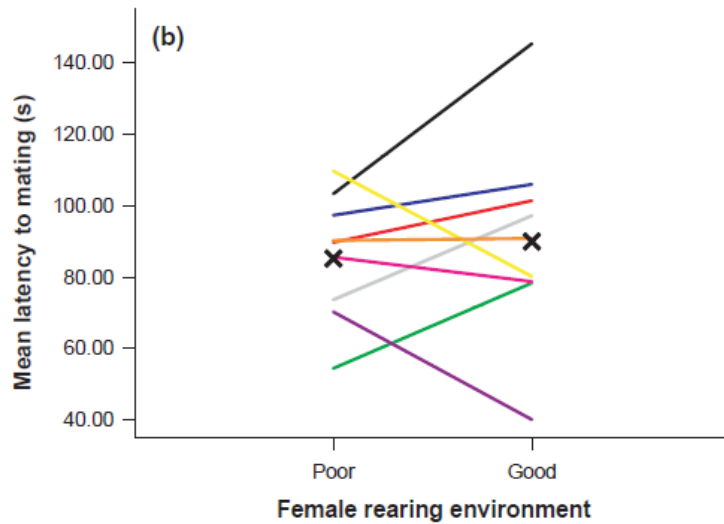Introduction to Genetic Analysis, Ninth Edition
© 2008 W.H. Freeman and Company
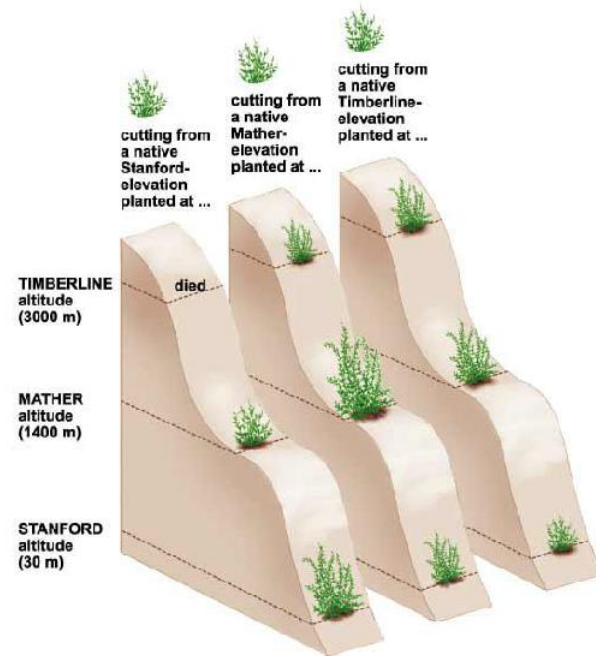
G × E is of great importance for the development of breeds with wide geographical use and/or wide coping capacity to global change

GxE is common phenomenon
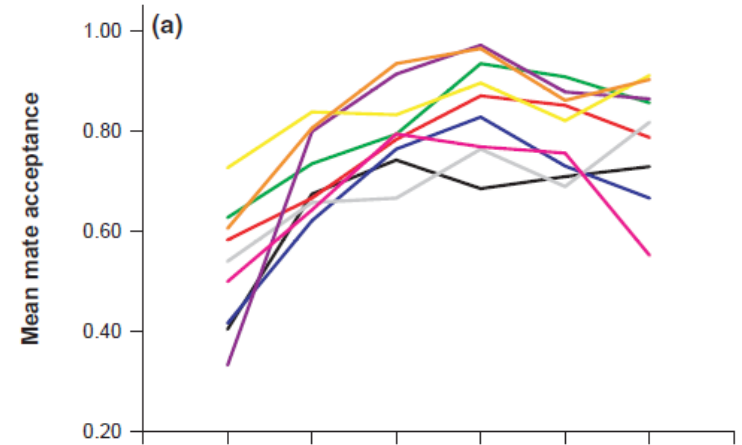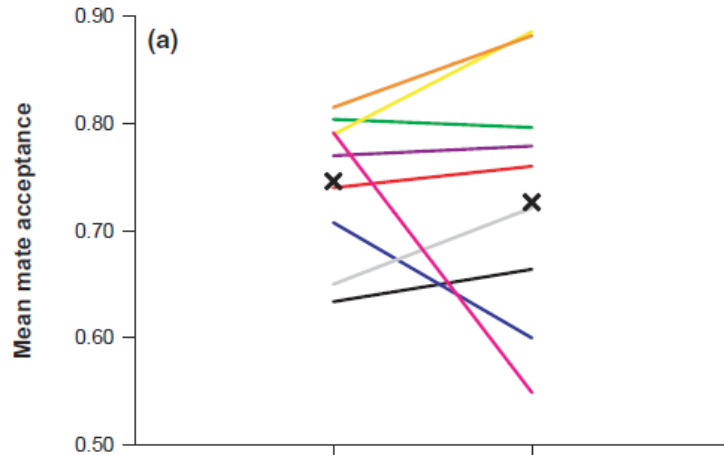
Narraway, C., Hunt, J., Wedell, N., Hosken, D.J., 2010. Genotype-by-environment interactions for female preference. Journal of Evolutionary Biology 23, 2550–2557.

GxE is common phenomenon
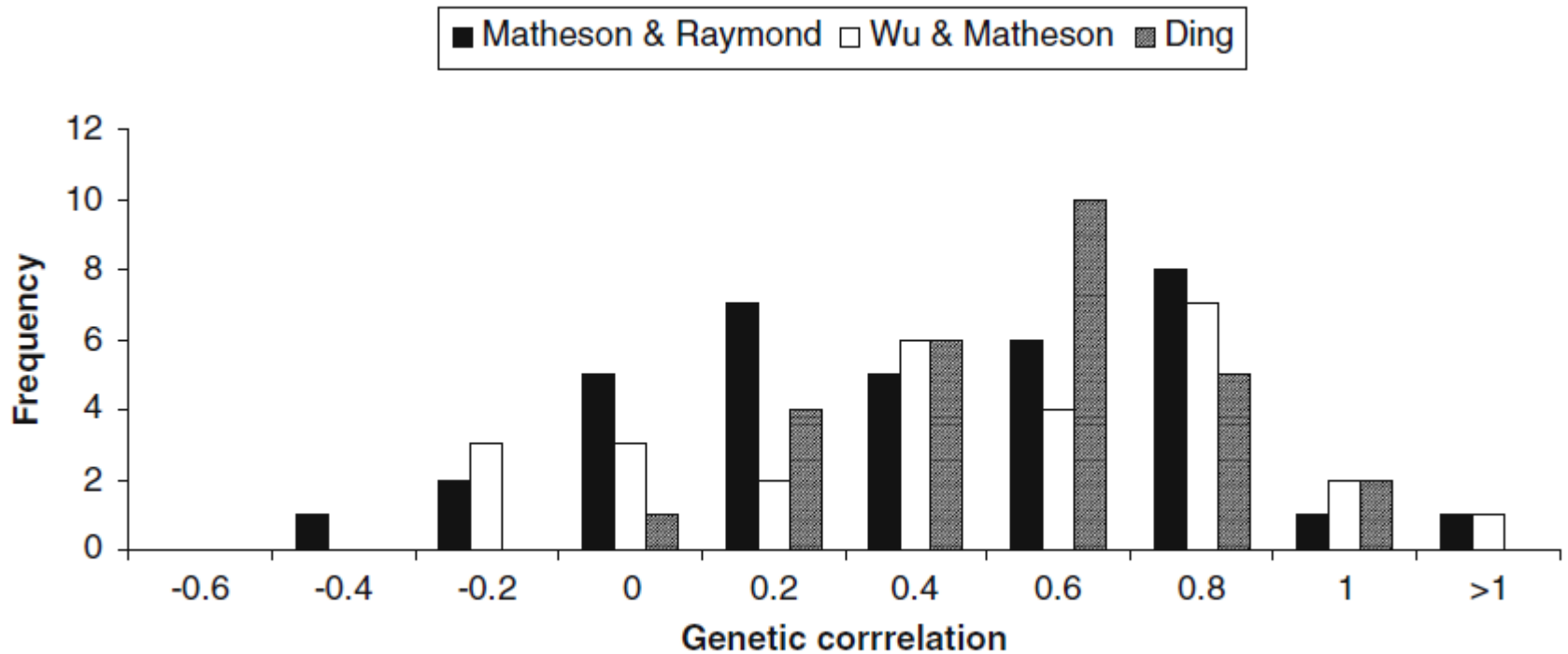
Raymond, C.A., 2011. Genotype by environment interactions for Pinus radiata in New South Wales, Australia. Tree Genetics & Genomes 7, 819–833.

The basic model

Breed and environmental effects are combined additively

$$P_{ij} = G_i + E_j$$
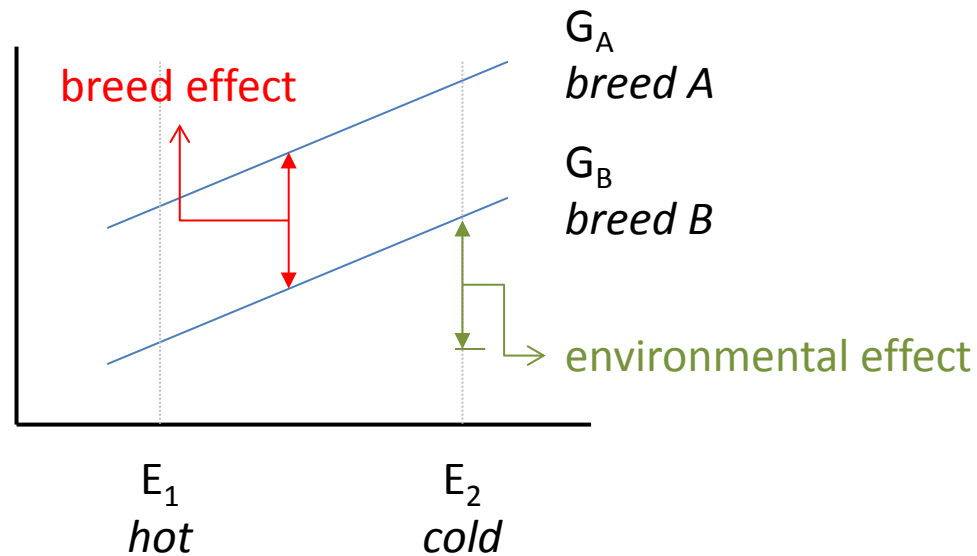
The phenotypic response of a genotype to a change in an environmental factor is often called **Norm of Reaction** (NoR) or simply plasticity

The extended model

Breed and environmental effects have an additional term of interaction
$$P_{ij} = G_i + E_j + G \times E_{ij}$$
G×E may cause changes in breeds' ranking

G_A
breed A

G_B
breed B

E_1
hot

E_2
cold
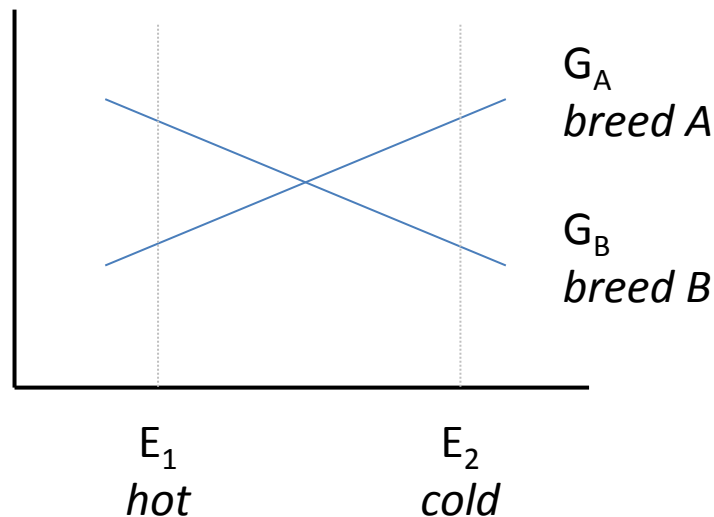
Change in rank:

- there is no universal genotype
- a specific genotype is bred for each environment

The extended model

Breed and environmental effects have an additional term of interaction

$$P_{ij} = G_i + E_j + G \times E_{ij}$$

G×E may cause changes in scale

Change in scale:

- Breed A is environmentally **sensitive**
- Breed B is environmentally **insensitive**
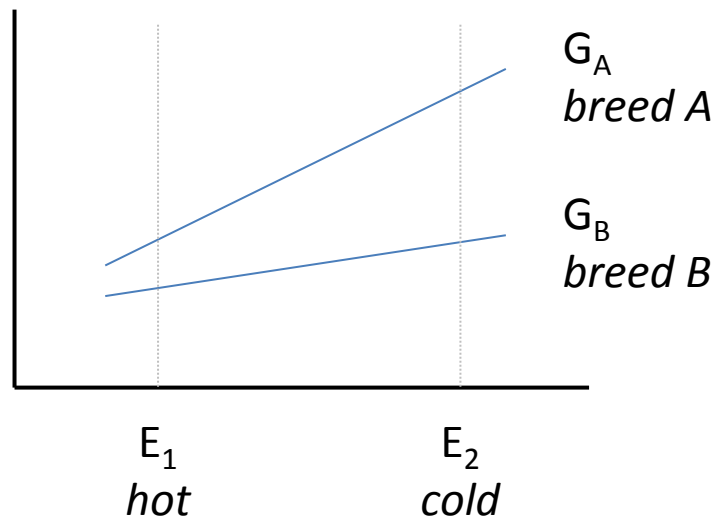
The extended model

Breed and environmental effects have an additional term of interaction

$$P_{ij} = G_i + E_j + G \times E_{ij}$$

G×E may cause changes in ranking and scale simultaneously

G_A
breed A

G_B
breed B

E_1
hot

E_2
cold
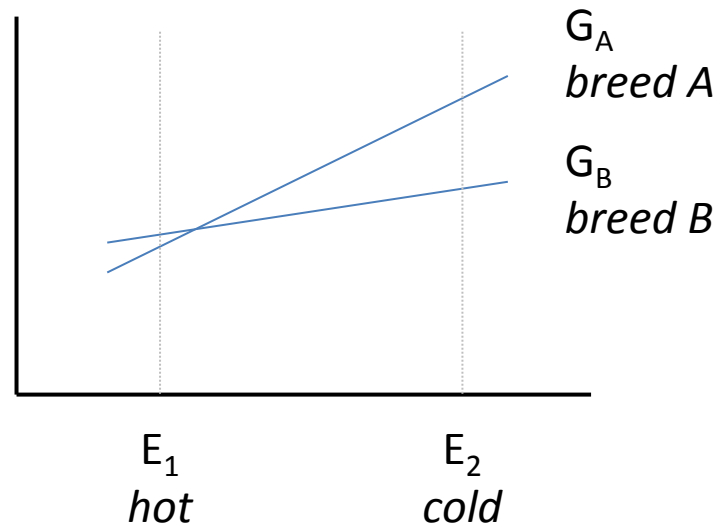
Changes in ranking and scale:

- Breed A is environmentally **sensitive** and **specially suited to cold**
- Breed B is environmentally **insensitive** but **better suited to hot**

Genotype, environmental and interaction effects
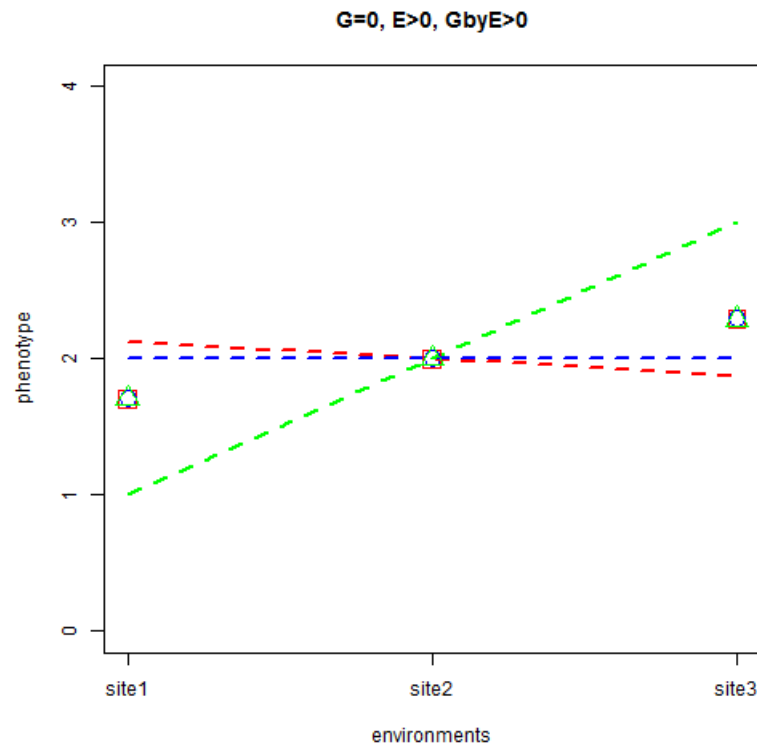
G=0, E>0, GbyE>0

G>0, E=0, GbyE=0

G>0, E>0, GbyE=0

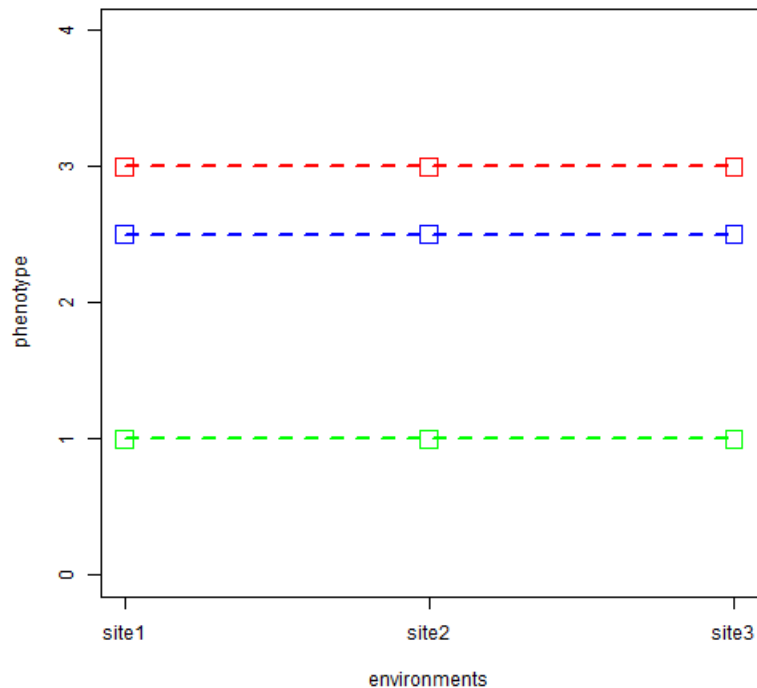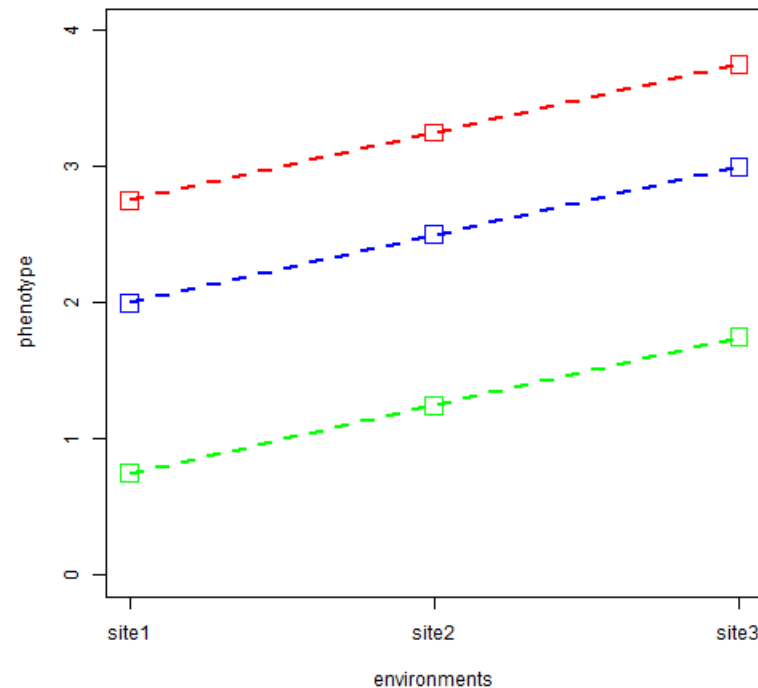$$g_i = \bar{X}_{i.} - \bar{X}_{..}$$

	s1	s2	s3	mean g	g effect
g1	3.00	3.00	3.00	3.00	0.83
g2	2.50	2.50	2.50	2.50	0.33
g3	1.00	1.00	1.00	1.00	-1.17
mean s	2.17	2.17	2.17	2.17	
s effect	0.00	0.00	0.00		
	Interactions g x s				
g1	0.00	0.00	0.00		
g2	0.00	0.00	0.00		
g3	0.00	0.00	0.00		

	s1	s2	s3	mean g	g effect
g1	2.75	3.25	3.75	3.25	0.92
g2	2.00	2.50	3.00	2.50	0.17
g3	0.75	1.25	1.75	1.25	-1.08
mean s	1.83	2.33	2.83	2.33	
s effect	-0.50	0.00	0.50		
	Interactions g x s				
g1	0.00	0.00	0.00		
g2	0.00	0.00	0.00		
g3	0.00	0.00	0.00		

$$s_j = \bar{X}_{.j} - \bar{X}_{..}$$
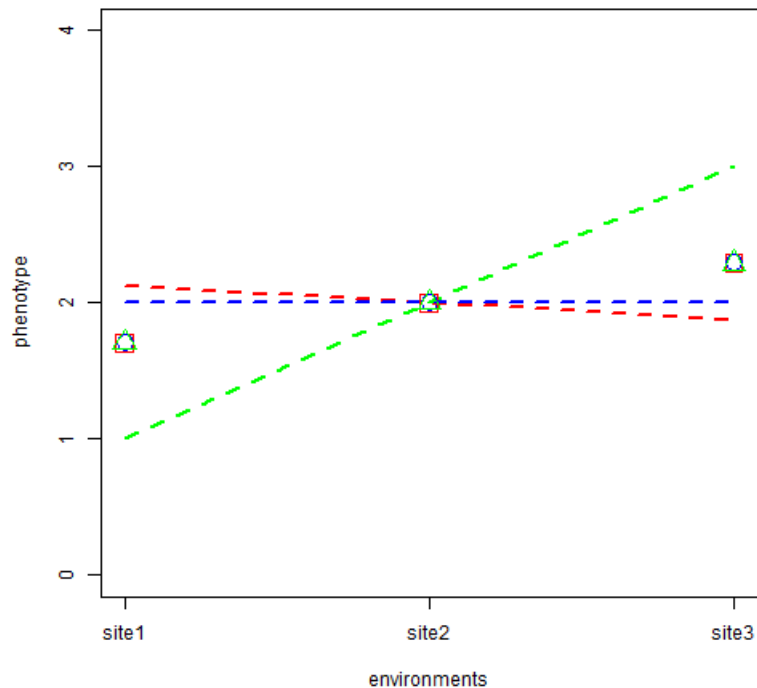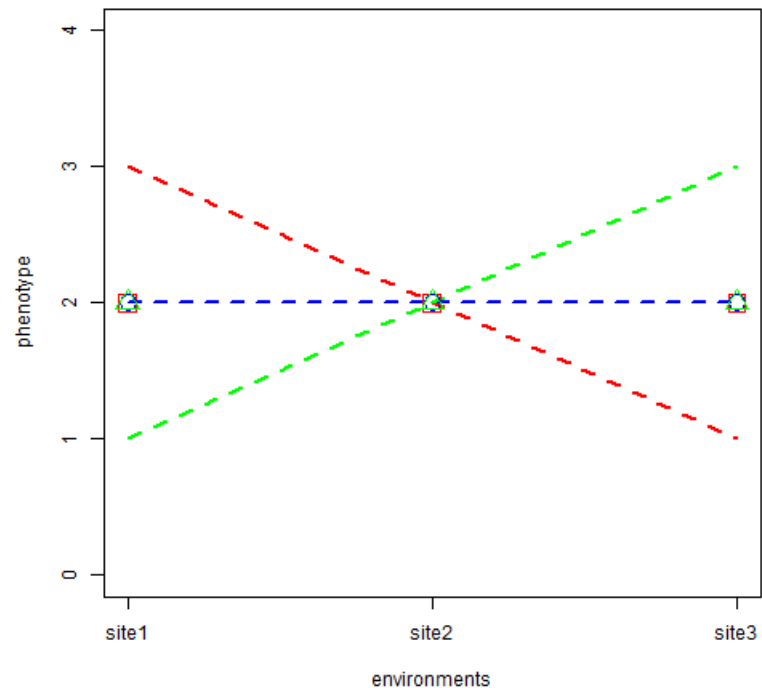
	s1	s2	s3	mean g	g effect
g1	2.13	2.00	1.88	2.00	0.00
g2	2.00	2.00	2.00	2.00	0.00
g3	1.00	2.00	3.00	2.00	0.00
mean s	1.71	2.00	2.29	2.00	
s effect	-0.29	0.00	0.29		
		Interactions g x s			
g1	0.42	0.00	-0.42		
g2	0.29	0.00	-0.29		
g3	-0.71	0.00	0.71		

	s1	s2	s3	mean g	g effect
g1	3.00	2.00	1.00	2.00	0.00
g2	2.00	2.00	2.00	2.00	0.00
g3	1.00	2.00	3.00	2.00	0.00
mean s	2.00	2.00	2.00	2.00	
s effect	0.00	0.00	0.00		
		Interactions g x s			
g1	1.00	0.00	-1.00		
g2	0.00	0.00	0.00		
g3	-1.00	0.00	1.00		

$$g \times s_{ij} = X_{ij} - \bar{X}_{i.} - \bar{X}_{.j} + \bar{X}_{..}$$

G>0, E>0, GbyE>0 (left)
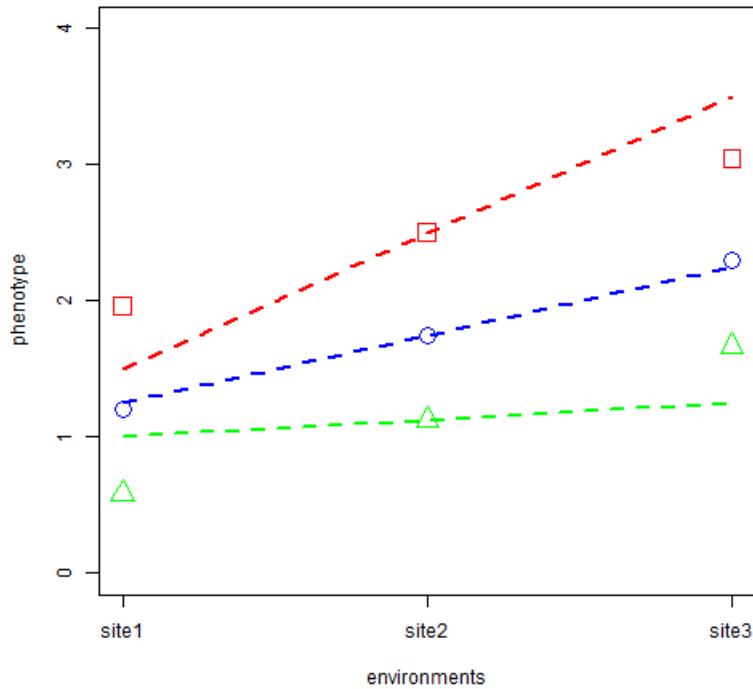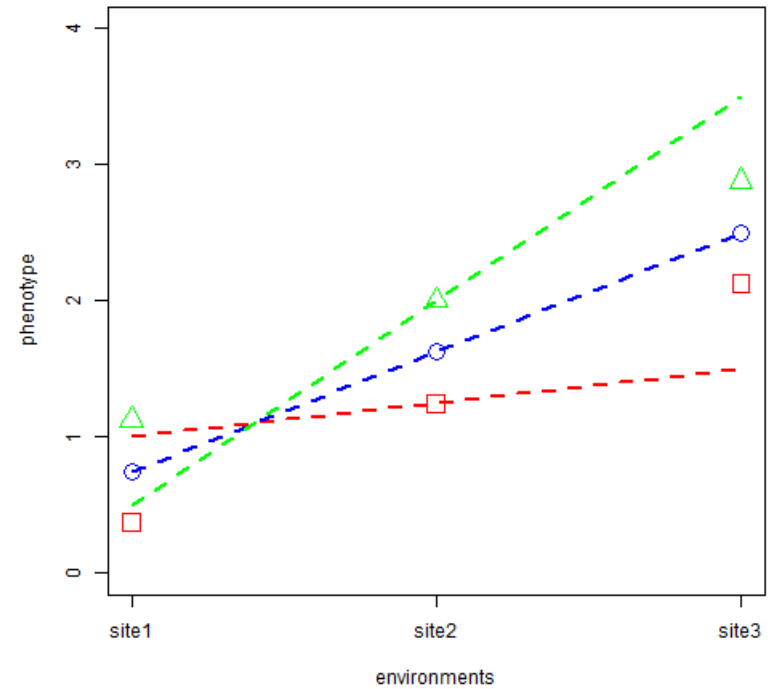
	s1	s2	s3	mean g	g effect
g1	1.50	2.50	3.50	2.50	0.71
g2	1.25	1.75	2.25	1.75	-0.04
g3	1.00	1.13	1.25	1.13	-0.67
mean s	1.25	1.79	2.33	1.79	
s effect	-0.54	0.00	0.54		
		Interactions g x s			
g1	-0.46	0.00	0.46		
g2	0.04	0.00	-0.04		
g3	0.42	0.00	-0.42		

G>0, E>0, GbyE>0 (right)

	s1	s2	s3	mean g	g effect
g1	1.00	1.25	1.50	1.25	-0.38
g2	0.75	1.63	2.50	1.63	0.00
g3	0.50	2.00	3.50	2.00	0.38
mean s	0.75	1.63	2.50	1.63	
s effect	-0.88	0.00	0.88		
		Interactions g x s			
g1	0.63	0.00	-0.63		
g2	0.00	0.00	0.00		
g3	-0.63	0.00	0.63		

G x E and phenotypic plasticity

- G x E implies plasticity in at least one genotype

- Plasticity need not imply G x E

- Phenotypic plasticity is a change in phenotype due to changes in environment

- NoR is the function of phenotypes over environmental changes of a given genotype

- The genetic variation in phenotypic plasticity is G x E and it is identified whenever there are intercrossing NoRs


G>0, E>0, GbyE>0
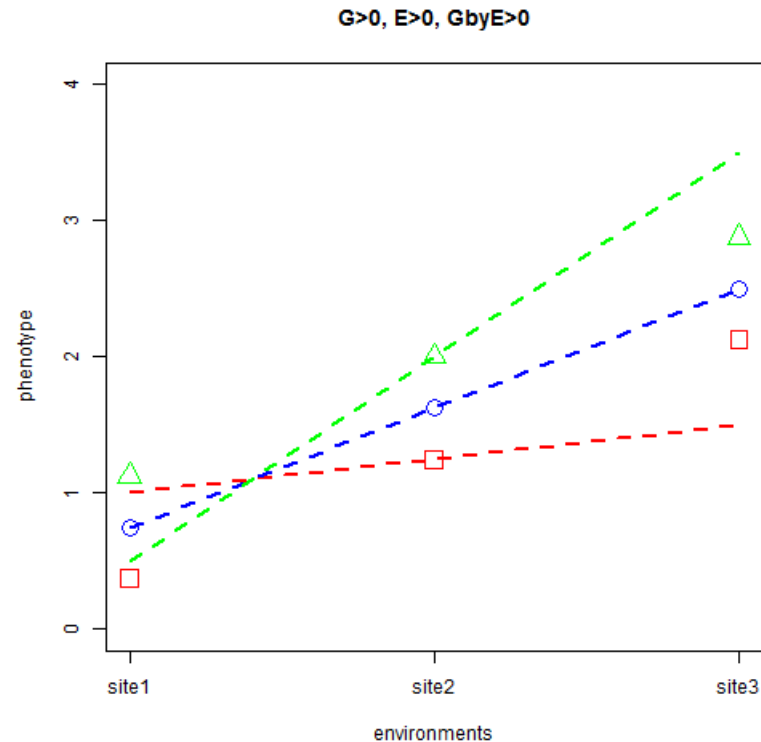
Assessing G x E

- Two-way (factorial) designs are one of the simplest experimental layouts to detect and assess G x E

- Often genetic groups (families) are sampled randomly from a larger founder population, whose genetic variation we intent to gauge

Analysis of Variance

Table 1. Analysis of variance and expected mean squares

| Source	df	Sum of squares	Mean square	Expected mean square
Environ-ments (E)	e-1			
Genotypes (G)	g-1			
G × E	(g-1) (e-1)	SS (G × E)	MS (GE)	$\sigma^2 + n\sigma^2_{GE}$
Individuals within	ge (n-1)	SS (within)	MS (E)	σ^2

genotypic values
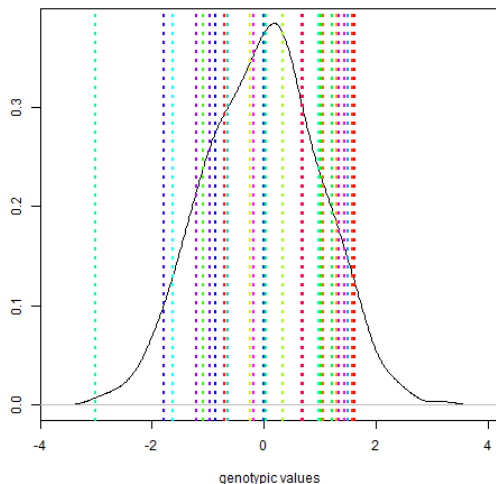
genotypes (families) are assumed to be random effects in the model

The *issue* with environments being fixed or random
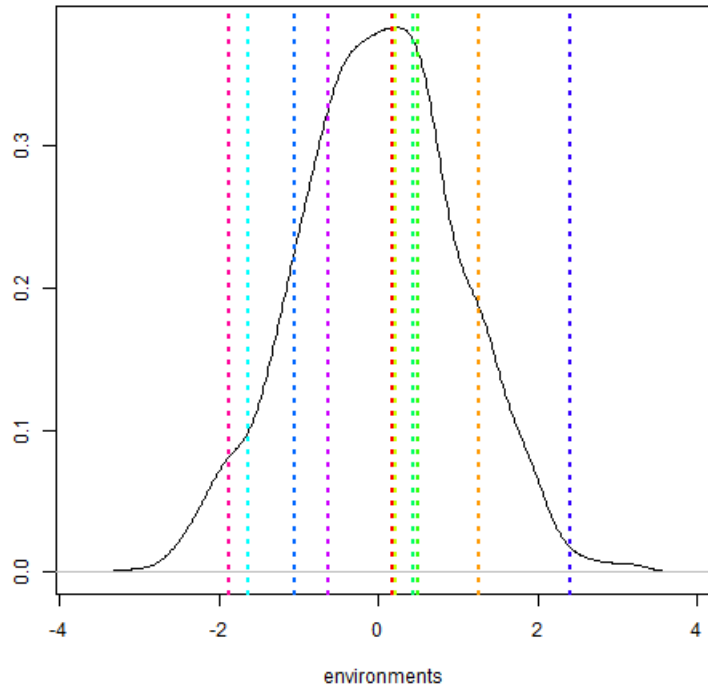
If environments are random samples from *universe* of possible environments & are usually many : niches in a species distribution area, gradient of a climate index, …
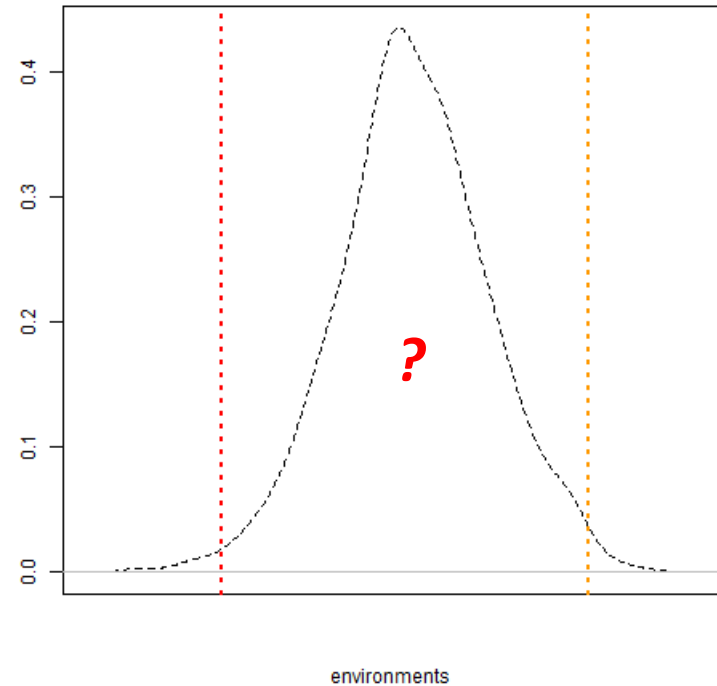
If environments are explicitly selected & are the ones of interest & are often few: typically treatments like irrigated *vs*. non irrigated, *old trusted* testing sites, …

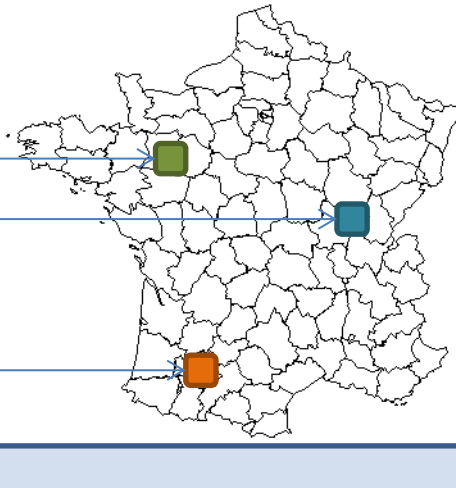# ANOVA: single step *or* double step

step 1: by *macroenv*

$macroenv.1$ $y = \mu + spatial + family + \varepsilon$

$macroenv.k$ $y = \mu + spatial + family + \varepsilon$

step 2 on spatially adjusted data

$\grave{y} = \mu + \textcolor{red}{macroenv} + family$
$\qquad\qquad + macroenv \times family + \varepsilon$

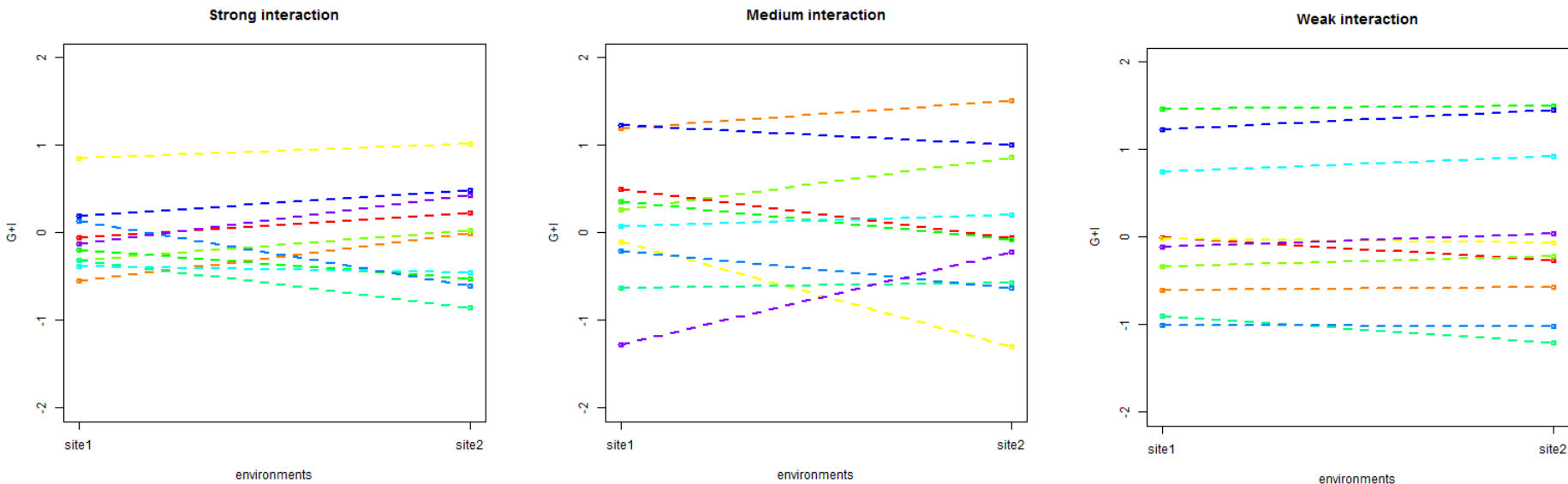$y = \mu + macroenv + spatial: macroenv + family + family \times macroenv + \varepsilon$

genetic correlations between traits measured in different environments

- Same trait measured in two or more environments over same genetic composition can be treated as two different genetically correlated traits

- The resulting correlation between these two traits is often denoted as **type B genetic correlation**

- The simplest formulation is $\sigma^2_f / (\sigma^2_f + \sigma^2_i)$ [1]

Medium interaction
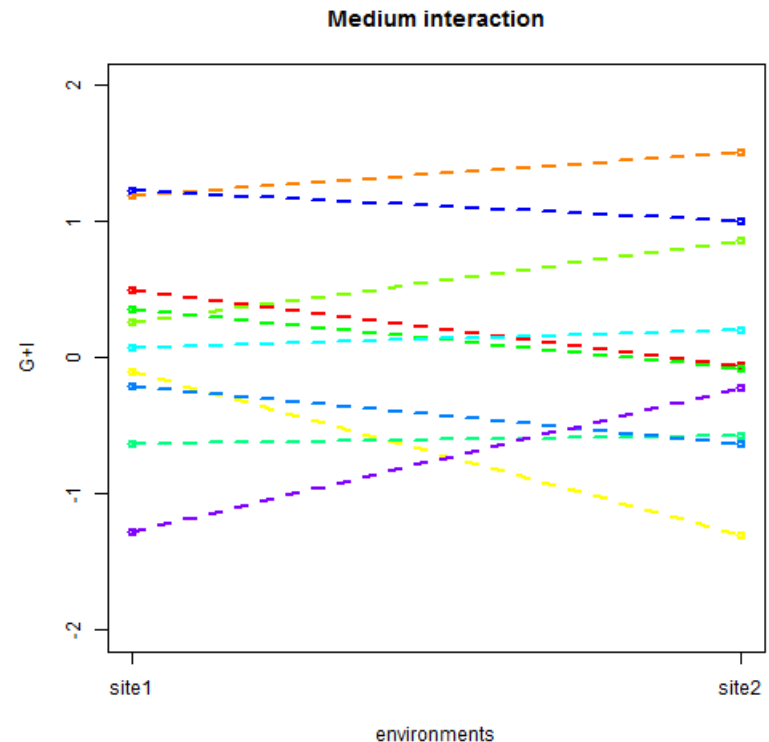
[1] **Yamada, Y.** 1962. Genotype by environment interaction and genetic correlation of the same trait under different environments. Jap. J. Genet. 37: 498-509.

genetic correlations between traits measured in different environments

	Strong interaction	Medium interaction	Weak interaction
σ^2_f	0.1397	0.4600	0.6701
σ^2_i	0.1101	0.1961	0.0219
σ^2_e	0.2465	0.2441	0.2441
cor B	**0.5592**	**0.7011**	**0.9684**
pearson	0.5959	0.7145	0.9852

Source on Save   Run   Source

```r
1
2  library(breedR)
3
4  # family effects
5  num_fam <- 12
6  mean_eff_fam <- 0
7  sd_eff_fam <- 0.5
8  fam_eff <- rnorm(num_fam,mean_eff_fam,sd_eff_fam)      #generate some random normal deviates
9
10 # family size and residuals
11 fam_size <- 20
12 mean_residuals <- 0
13 sd_residuals <- 0.5
14
15 # site effects
16 num_sites <- 2
17 mean_eff_site <- 0
18 site_eff <- c(-0.5,0.5)
19
20 # global_mean
21 global_mean <- 0
```

1:1   (Top Level)   R Script

```r
> samplesize <- 1000
> sub_sample <- 30
> theta <- rnorm(samplesize,0,1)        #generate some random normal deviates
> colores <- rainbow(sub_sample)
> s_theta <- sample(theta)
> plot(density(theta), main = " ",       xlab="genotypic values",          ylab=" ")
> for (i in 1:sub_sample){
+   abline(v = s_theta[i], col = colores[i], lty = 3, lwd = 2)
+ }
> samplesize <- 1000
> sub_sample <- 30
> theta <- rnorm(samplesize,0,1)        #generate some random normal deviates
```

genetic correlations between traits measured in different environments

- type B genetic correlation (*corr B*) = $\sigma^2_f / (\sigma^2_f + \sigma^2_i)$
  when variance among genetic groups (families) is the same in both environments;

- obtained from a two-way mixed model decomposition;

- any *corr B* < 1 indicates G × E and some changes in ranking: the lower the *corr B*, the greater the G × E;

- *corr B* = 1 do not necessarily imply absence of G × E: there can be scale effects;

- *corr B* matrix can be used to delineate breeding or deployment zones: threshold levels $\sigma^2_i > 0.5 \times \sigma^2_f$, which is a *corr B* of 0.67 [1].

[1] **Raymond, C.A.,** 2011. Genotype by environment interactions for Pinus radiata in New South Wales, Australia. Tree Genetics & Genomes 7, 819–833.

how families contribute differently to G x E?

Wricke's **ecovalence**: sum of squared interactions, for a given genotype from a factorial genotype (family) by environment experiment

$$W_i{}^2 = \sum (X_{ij} - \overline{X_{i.}} - \overline{X_{.j}} + \overline{X_{..}})^2$$

it can be made relative to total sum of squared interactions
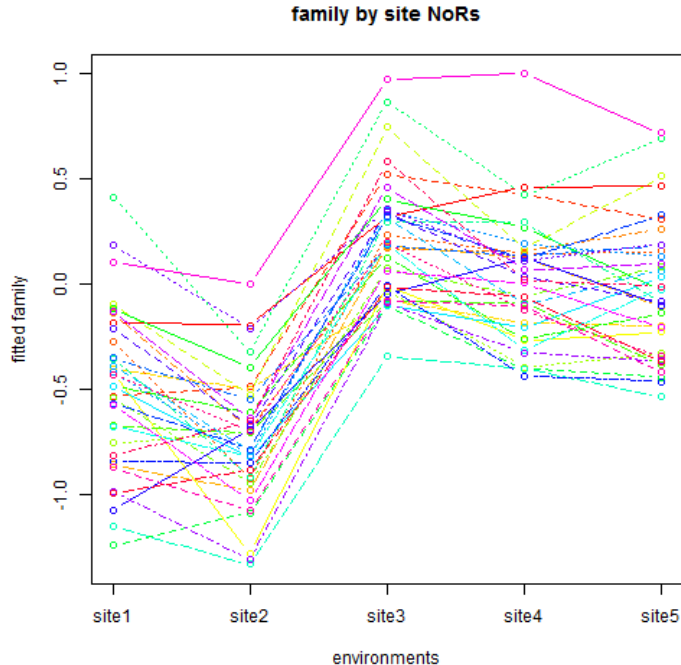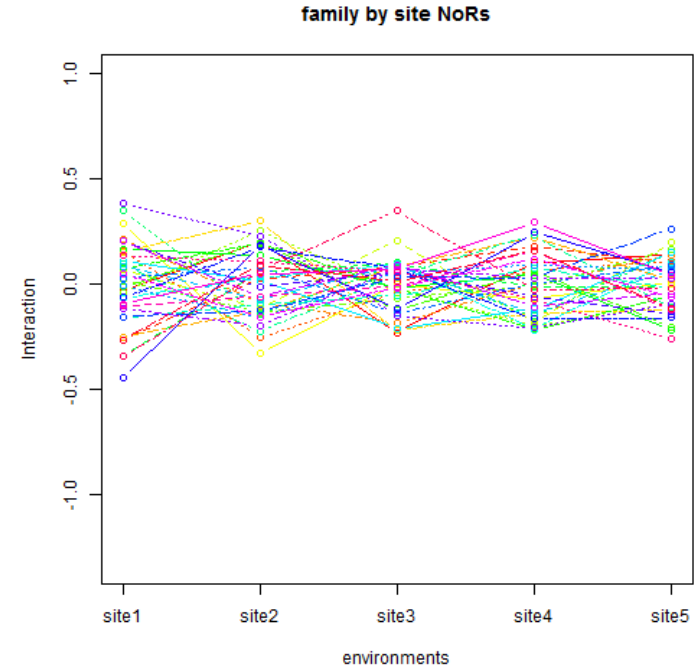
family by site NoRs
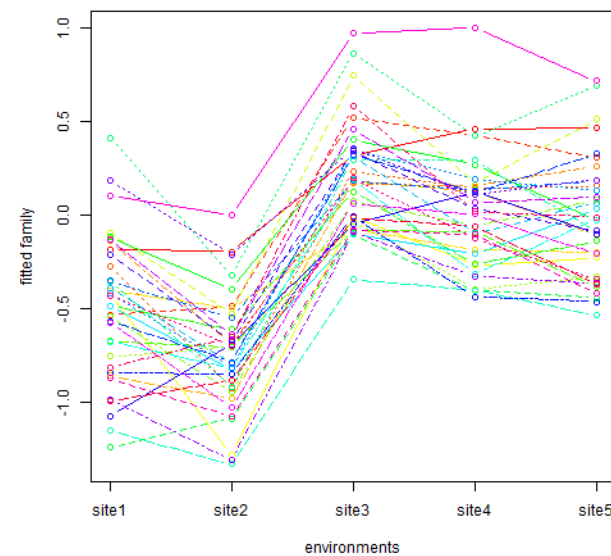
$\sigma^2{}_f = 0.07581$

$\sigma^2{}_i = 0.03927$

$\sigma^2{}_e = 0.29903$

how families contribute differently to G x E?

σ^2_f = 0.1645

σ^2_i = 0.0048

σ^2_e = 0.2905
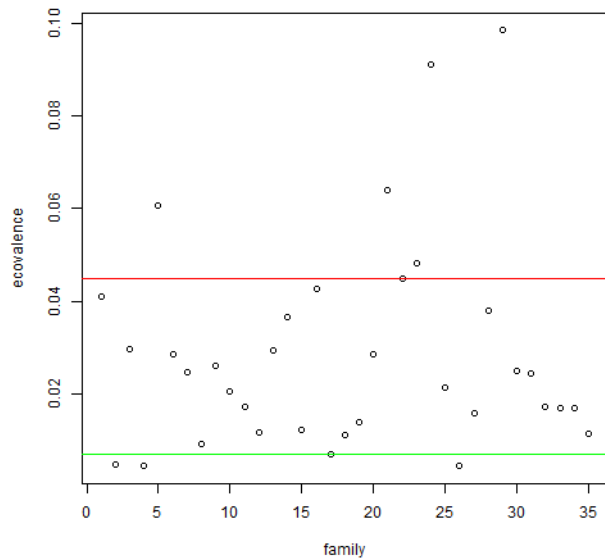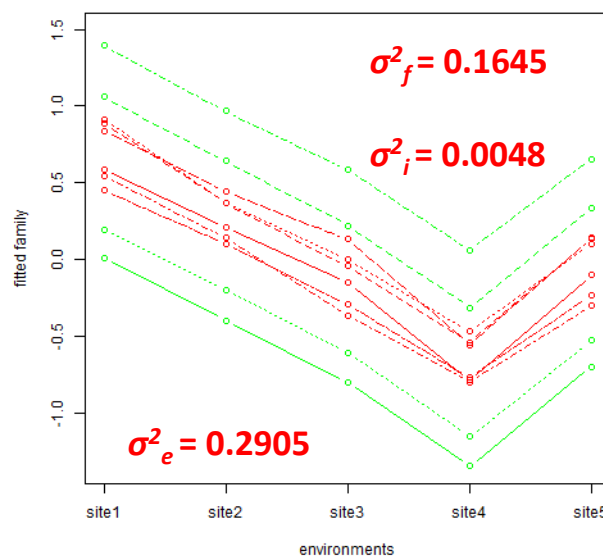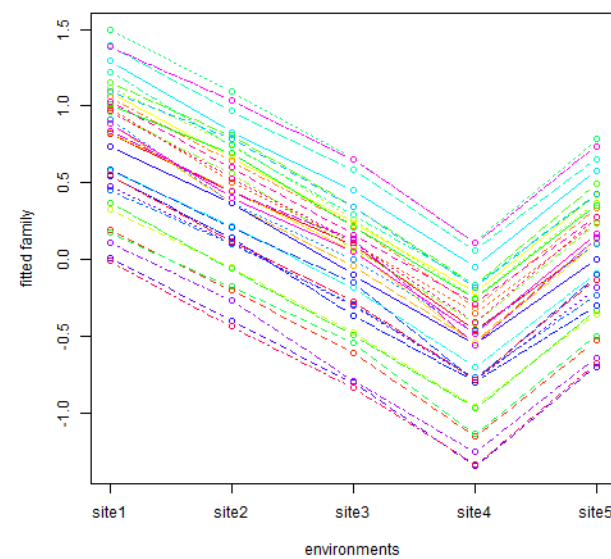
🅡 toy_examples_gbye_plots.R ×   🅡 first_toy_example.R ×   🅡 simulate_distributions.R* ×   🅡 map_france.R ×   🅡 corB_toy_example.R ×   🅡 ecovalences.R ×

◁ ⇨ | 🔲 ☐ Source on Save | 🔍 ⚡ ▾ | ⊞   ⇒ Run | ⮌ | ⇨ Source ▾

```
124    lines(fam_set$site, fam_set$inter, type="b", lwd=1.5,
125          lty=linetype[i], col=colores[i])
126  }
127  dev.off()
128
129  # calculates ecovalences from interaction blups
130  aggdata$sq_inter <- aggdata$inter^2
131  aggdata_inter <- data.frame(aggregate(aggdata$sq_inter, by=list(aggdata$fam),FUN=sum))
132  names(aggdata_inter) <- c("fam","sq_inter")
133  total_sq_inter <- sum(aggdata_inter$sq_inter)
134  aggdata_inter$ecoval <- aggdata_inter$sq_inter/total_sq_inter
135
136  # rank in ascending order families by their ecovalence
137  rank <- aggdata_inter$fam[order(aggdata_inter$ecoval)]
138  upper_rank <- 4
139  upper_threshold <- aggdata_inter$ecoval[rank[upper_rank]]
140  lower_rank <- num_fam-upper_rank-1
141  lower_threshold <- aggdata_inter$ecoval[rank[lower_rank]]
142
143  heading <- "ecovalences per family"
144  tiff(filename="ecovalences_by_family.tif",width=500,height=500,compression = c("none"))
```

136:22   (Top Level) ◆   R Script ◆

```
> summary(two_way)
Linear Mixed Model with pedigree and spatial effects fit by AI-REMLF90 ver. 1.110
  Data: data_toy
  AIC  BIC logLik
 5981 5999  -2987


Variance components:
            Estimated variances      S.E.
factor(fam)            0.215030 0.051402
factor(inter)          0.001255 0.000000
Residual               0.306700 0.007332


Fixed effects:
                value   s.e.
factor(site).1 -0.025904 0.0813
factor(site).2  0.762004 0.0813
```

Alternatives to univariate analyses for G x E and type B correlations

Univariate two-way analysis are:

- prone to biased type B correlations due to unbalanced-ness in data and heterogeneous variances across environments

- frequently producing correlation estimates out of the theoretical parametrical space

- unable to account for relatedness between genetic groups

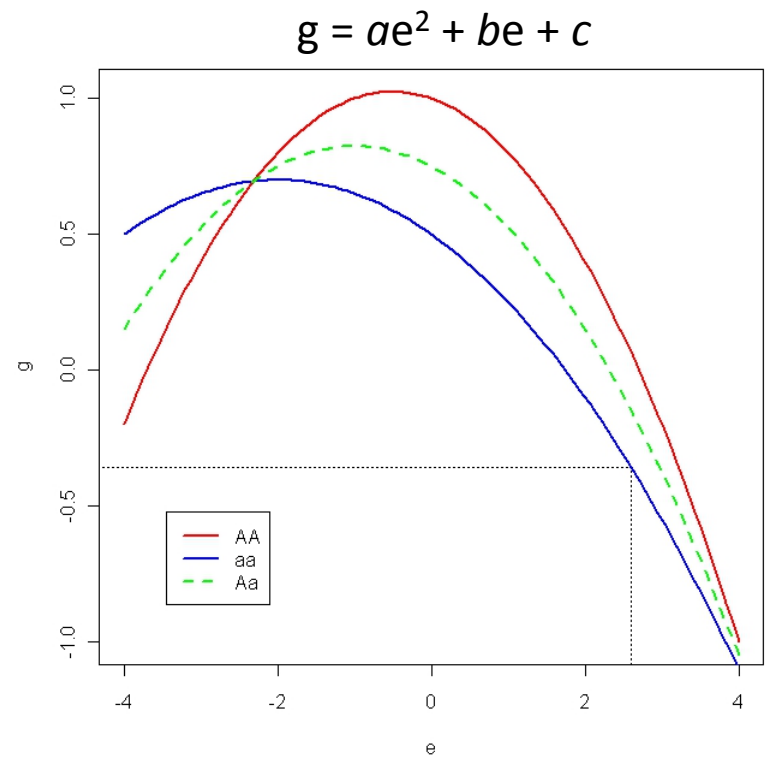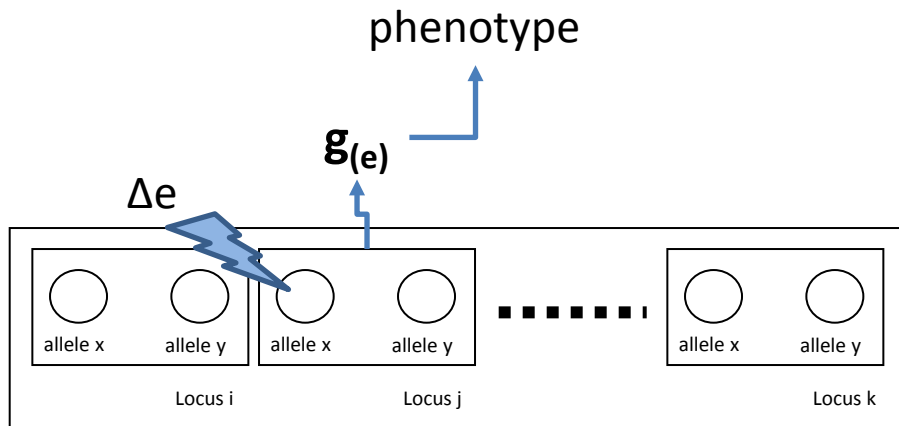Multivariate methods can estimate genetic variances (within environments) and covariances (between environments) simultaneously and properly.

- This latter feature will be ready soon in breedR via multiple trait analyses

Compared to clones, does the use of relatives across environments produce different norms of reaction?
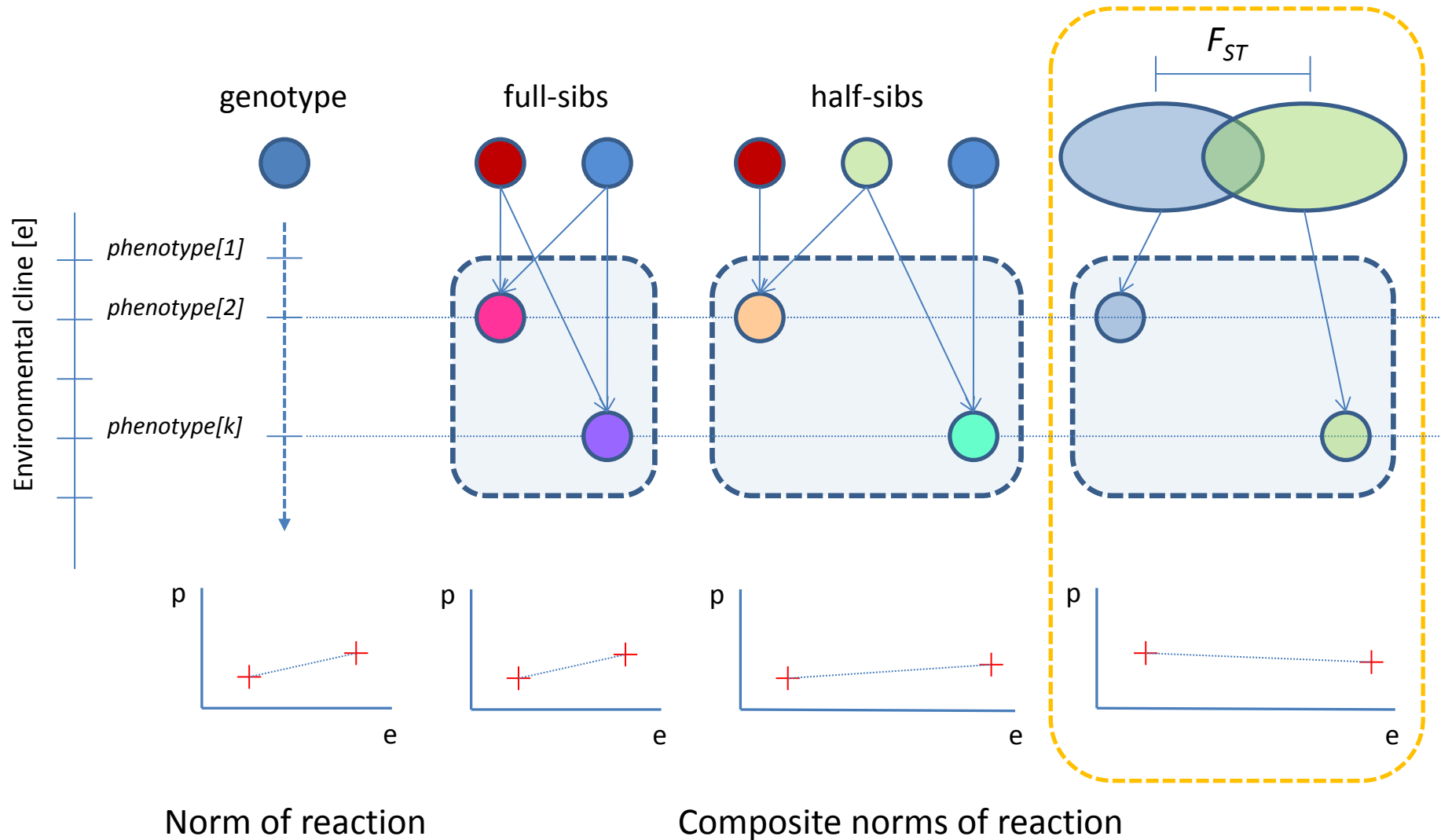
Norm of reaction

Composite norms of reaction

Loci with gene effects defined by functions of [e]

Allelic sensibility (or pleiotropic plasticity) : modification of the effect of a gene on one (or several) traits as function of an environmental cline [e]

phenotype

$g_{(e)}$

Δe

| allele x | allele y | allele x | allele y | | allele x | allele y |

Locus i   Locus j   Locus k

$g = ae^2 + be + c$

Loci with gene effects defined by functions of [e]

Allelic sensibility (or pleiotropic plasticity)

Genetic regulation or epistasis: modification of the effect of one (or several) gene(s) on the phenotype via epistatic interactions with another gene that responds to an environmental cline [e]

Loci with gene effects defined by functions of [e]

Allelic sensibility (or pleiotropic plasticity)

Genetic regulation or epistasis: modification of the effect of one (or several) gene(s) on the phenotype via epistatic interactions with another gene that responds to an environmental cline [e]
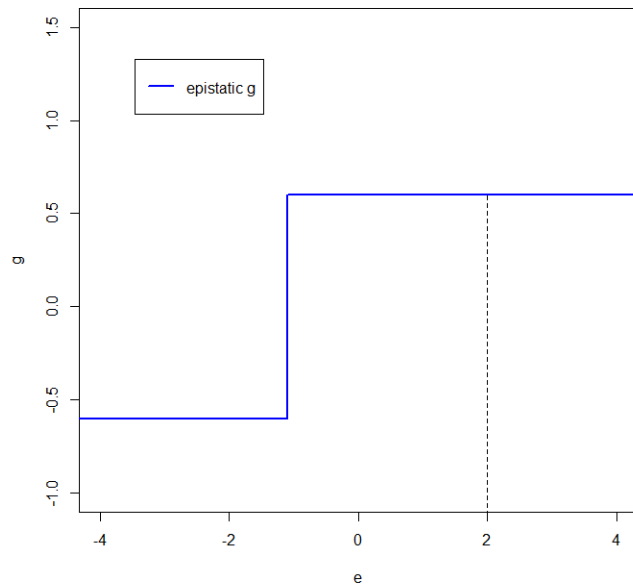
epistatic effect

Δ in shape or level of regulated gene

non-plastic gene

Loci with gene effects defined by functions of [e]

Allelic sensibility (or pleiotropic plasticity)

Genetic regulation or epistasis: modification of the effect of one (or several) gene(s) on the phenotype via epistatic interactions with another gene that responds to an environmental cline [e]
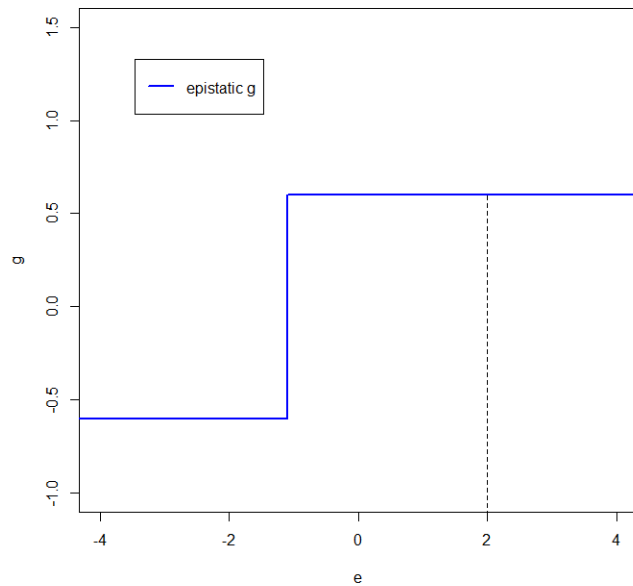
epistatic effect

Δ in shape or level of regulated gene

plasticity gene

How to build **composite NoRs**?
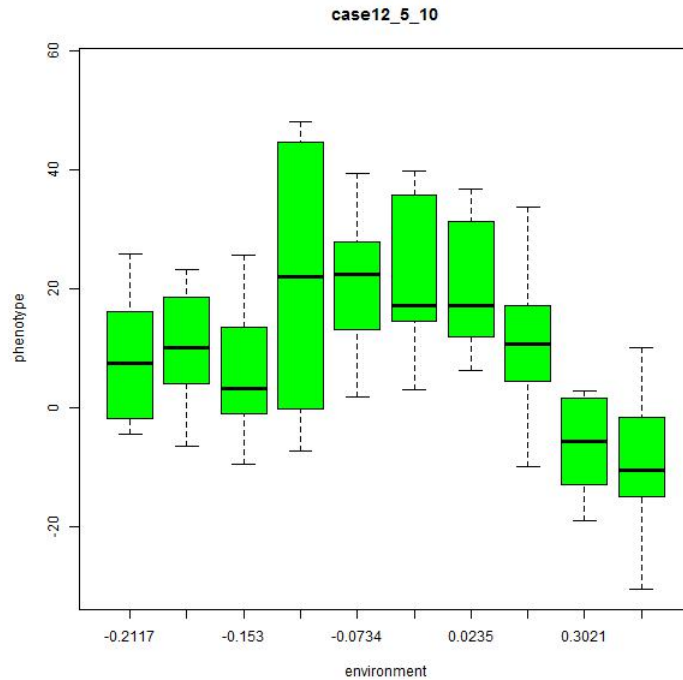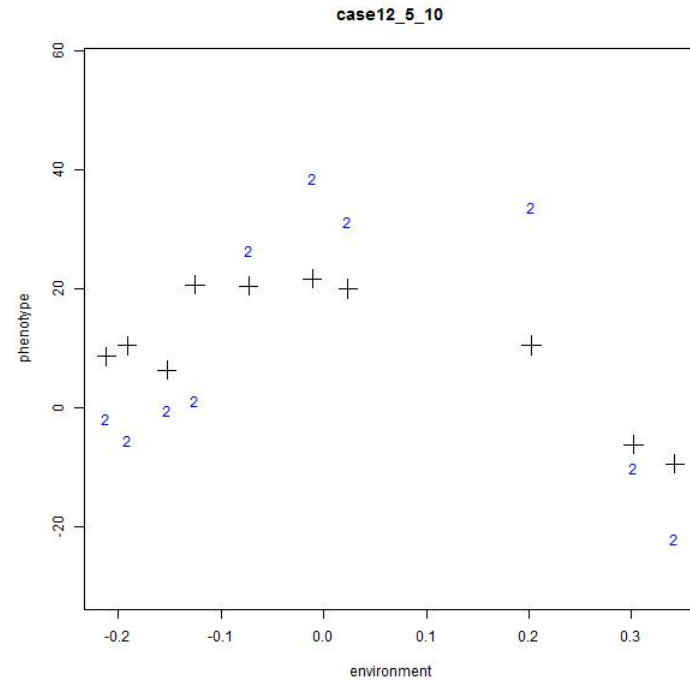
Iteration over *n* (10) offspring
→ *n* composite NoRs

One family: 10 sibs, one per
environment

Cases in following comparisons:
- same underlying gene effect functions, gene pool and
  environmental effects distribution
- same population size, family sizes

How to build **composite NoRs**?
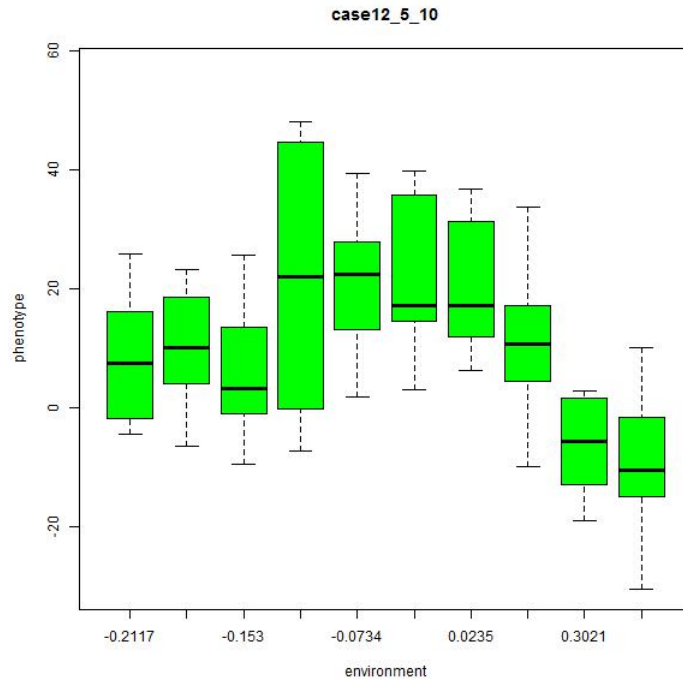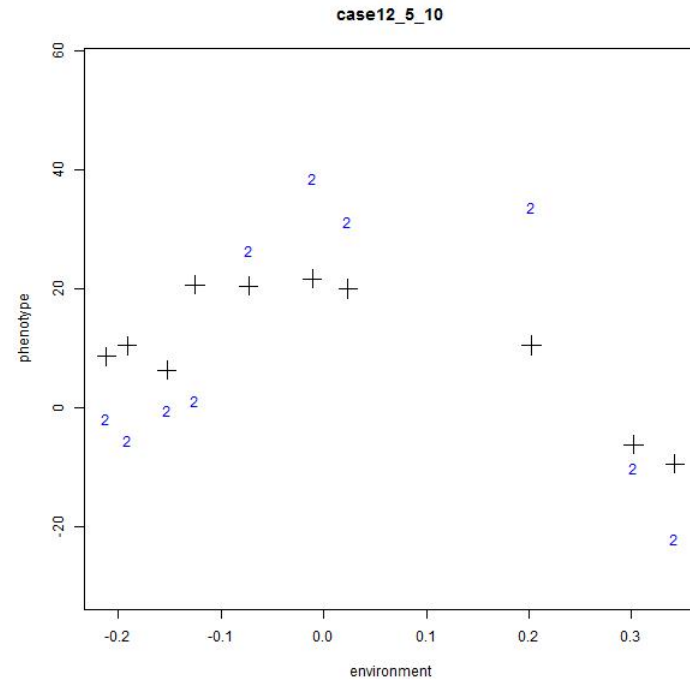
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- same underlying gene effect functions, gene pool and
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What are the main factors affecting the distribution of composite NoRs over given environmental cline?

h²[e]=0.2 ← Depends on heritabilities at each environment [e] → h²[e]=0.6
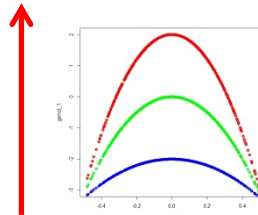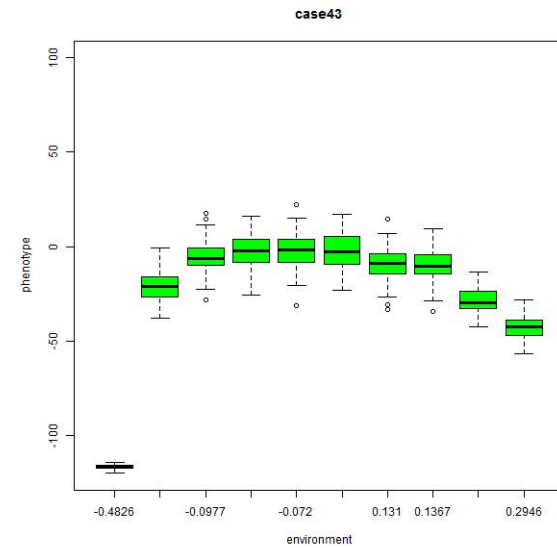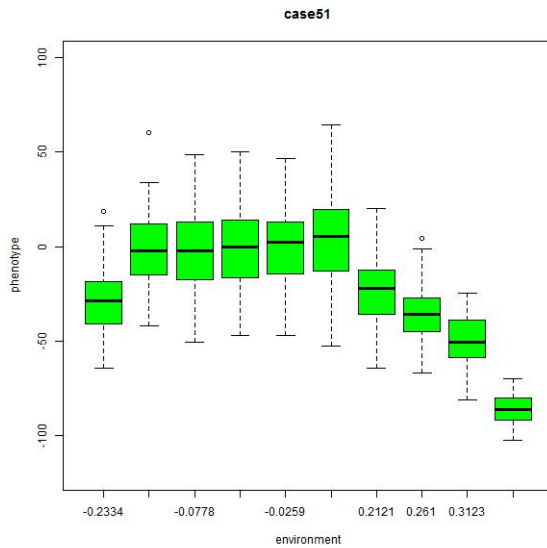
Depends on underlying gene effects function [e]
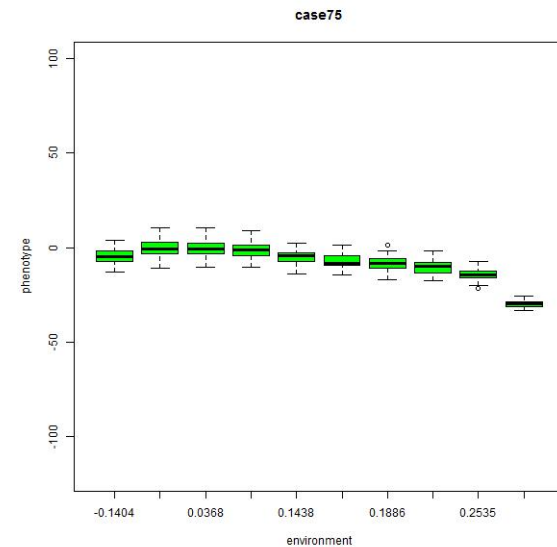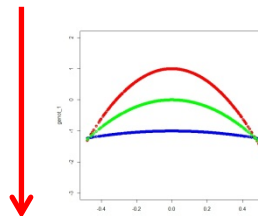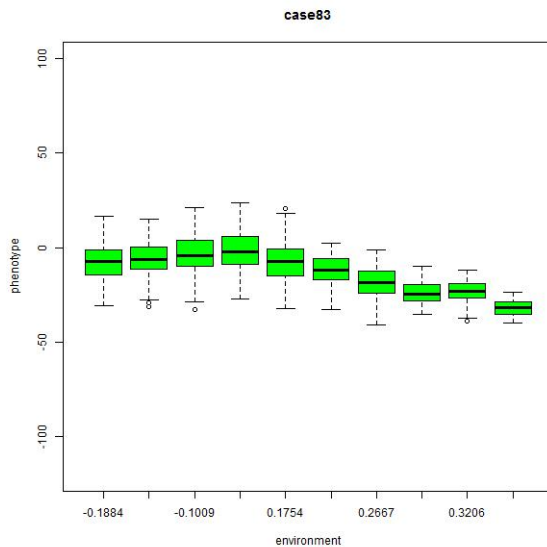
Composite **clonal NoRs** versus composite **fullsib NoRs**: weak plasticity functions [e]
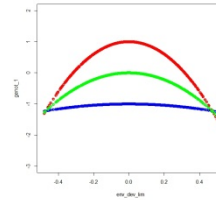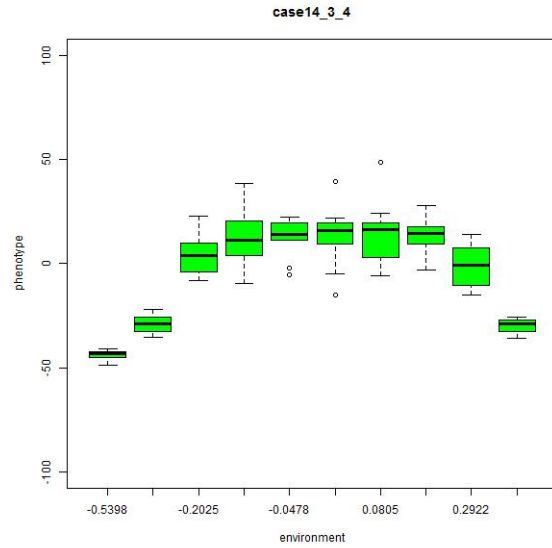
Clones

Full-sibs

Ratio $\sigma^2_{env} / \sigma^2_{ind}$
on 50 replicates
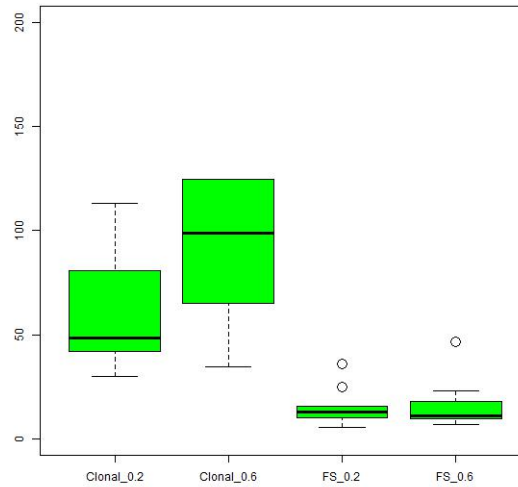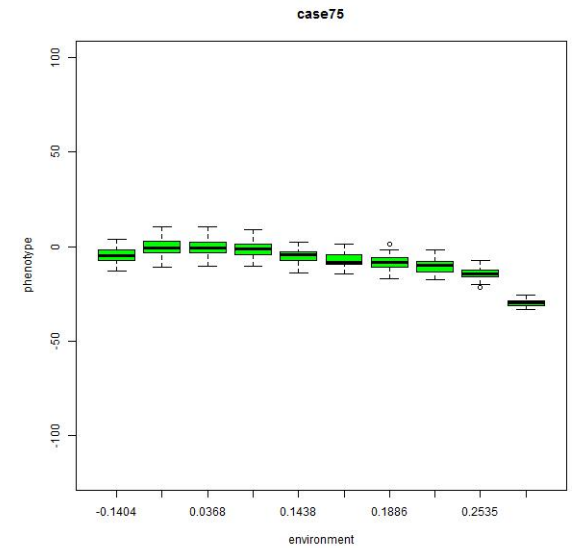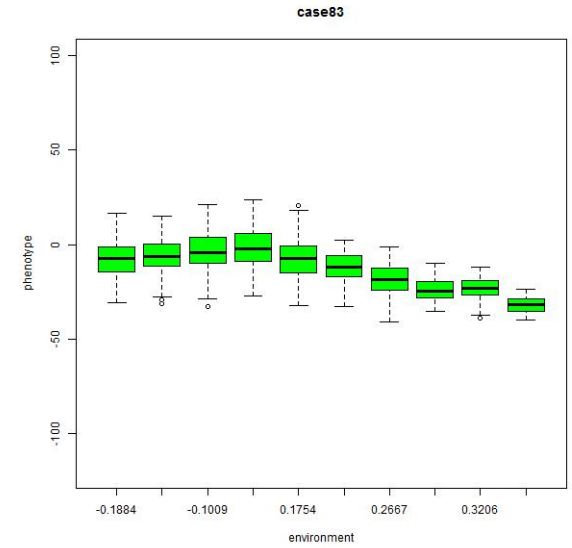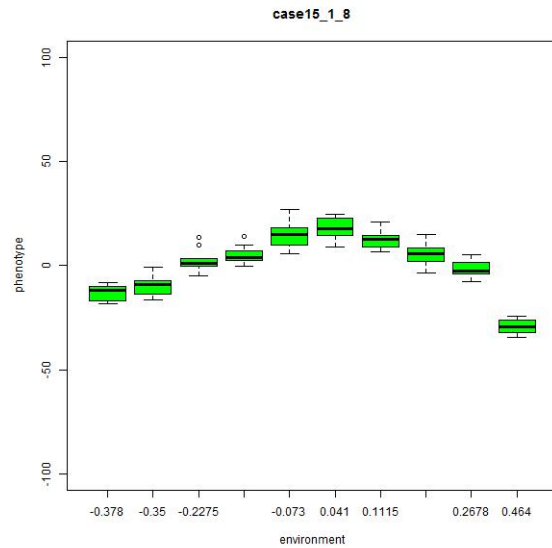
h²=0.2

h²=0.6

Composite **clonal NoRs** versus composite **fullsib NoRs**: strong plasticity functions [e]

Clones

Full-sibs

case16_4_6

h²=0.2

case51_1

Ratio σ²_env / σ²_ind
on 50 replicates

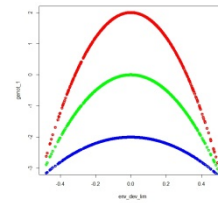### case17_4_8
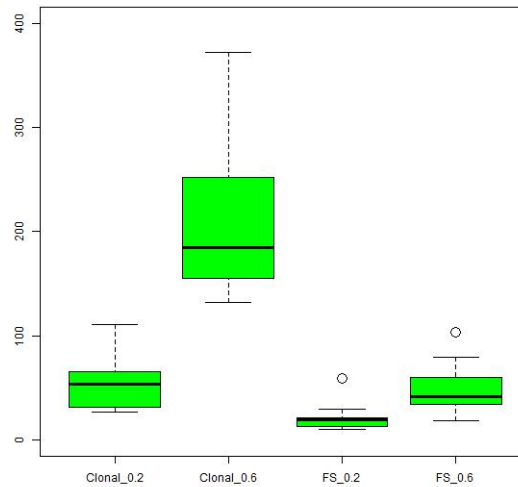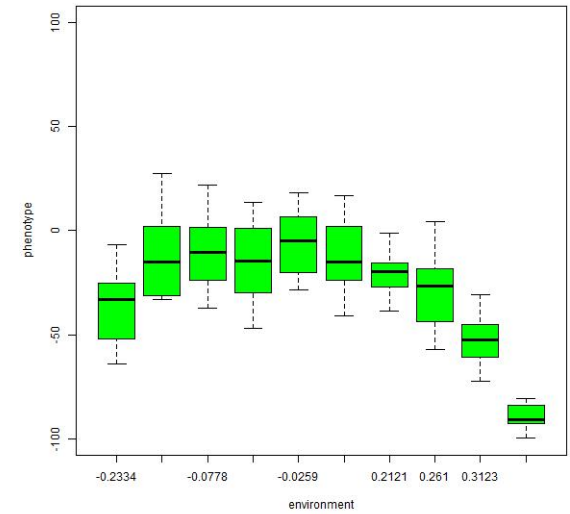
h²=0.6

case43_2
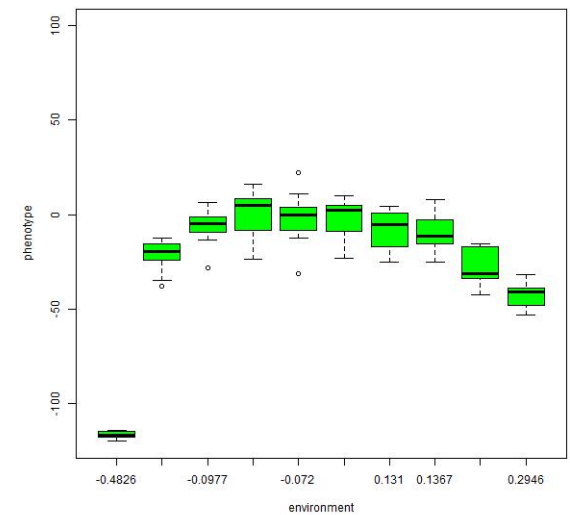
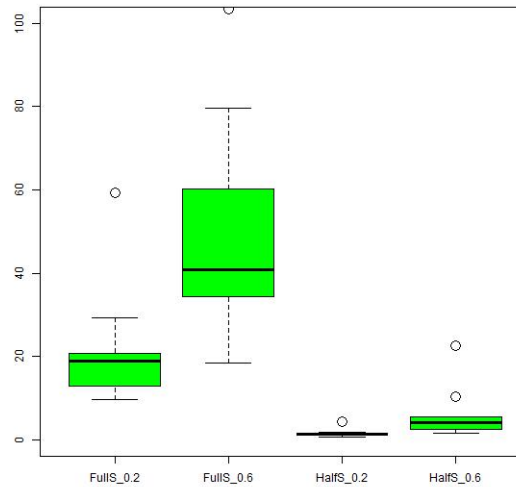# Composite **Full-sibs NoRs** versus composite **Half-sibs NoRs**: strong plasticity functions [e]