Basic concepts and definitions in multi-environment data: G, E, and GxE

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Contents

- The basic concepts: introduction and definitions
  - Phenotype, genotype, and environment
  - Reaction norms
  - Terminology: plasticity, environmental sensitivity, adaptability
- Concepts of stability in plant breeding

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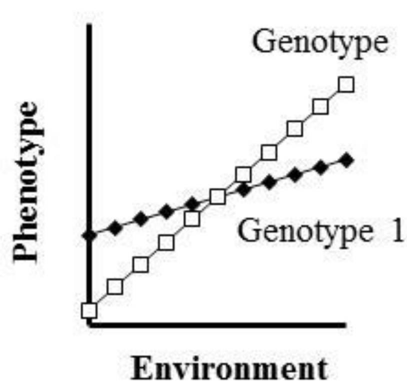
Learning outcomes

- To understand and apply the basic concepts of GxE and the different terminology in different disciplines
- To understand and apply the different concepts of stability in plant breeding

Some basic definitions...

- Phenotype...
- Genotype...
- Environment...
- and GxE!



What's the phenotype?

$$P(t) = \int_0^t f(G,E)dt$$

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The phenotype, the outcome of...

$$P(t) = \int_0^t f(G,E)dt$$

- "Genotype":
  - DNA constitution of the organism
    - Alleles present and their intra and inter-loci combinations
    - ... but much more than that!
- "Environment":
  - External stimuli provided by the surrounding where the organism develops / lives:
    - Temperature / light / humidity / nutrients / management / etc
- "Development":
  - Time span when the life cycle of the organism occurs
    - Conditions both the "genotype" and the "environment"

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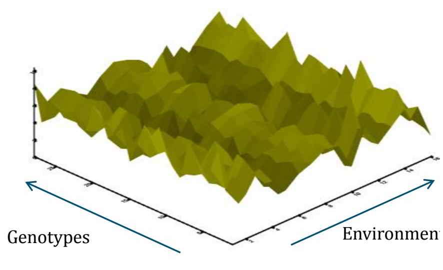
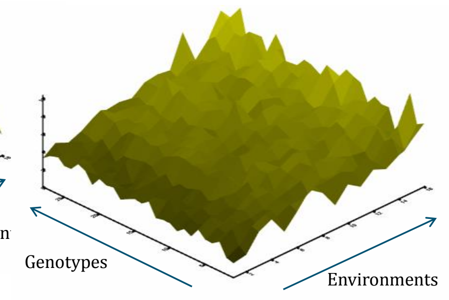
Phenotype a high-dimensional problem...





- G-E landscape: complex outcome of multiple "genotypic" and "environmental" factors interacting with each other...
  - Genotypic dimension: population or sample of a population.
  - Environmental dimension: Target Population of Environments (TPE), set of conditions that the genotypes or the population under study are likely to experience.

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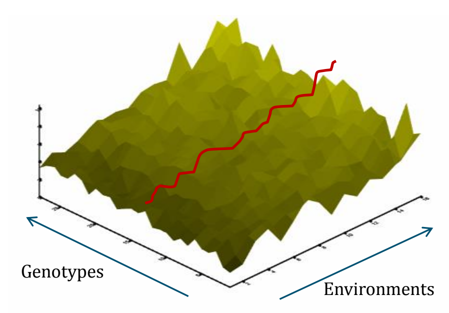
Individual genotype response:
A "slice" from this landscape...



- The red line is the "path" that represents the phenotype of a particular genotype across the environmental gradient...
- That path related with the reaction norm of that particular genotype.

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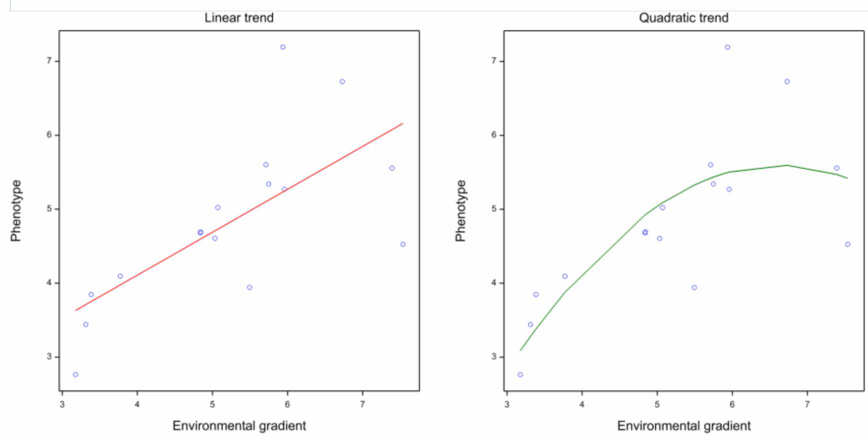
Reaction norms



- Reaction norm: Genotype-specific functional relationship between phenotypic response and environmental gradient(s).
  - Which factor(s) drive the environmental gradient?
  - Here gradient expressed in terms of environmental means.

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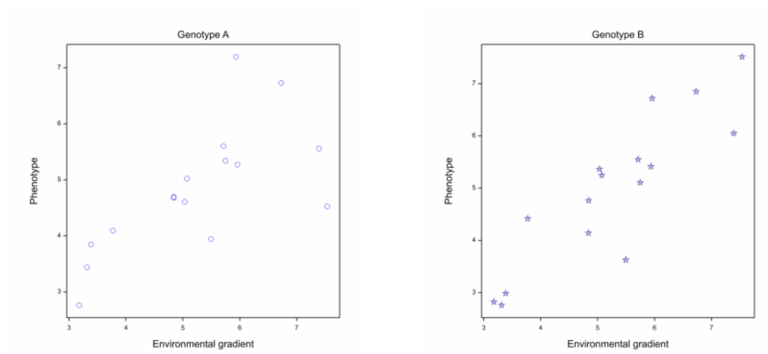
GxE and reaction norms



- Genotypes can react differently to the same environmental gradient.
  - Reaction norms change from genotype to genotype...
  - With different reaction norms → G x E!

- Which factor(s) drive the environmental gradient?
  - Important component in GxE research...
  - Why genotypes respond differently? And to what?

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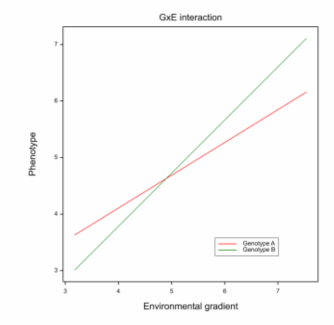
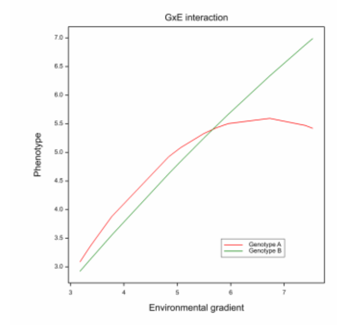
GxE occurs when reaction norms are not parallel!





- Non-parallel reaction norms reveals GxE
  - GxE: differential reaction of genotypes to environmental changes
  - Variation in adaptation / plasticity / environmental sensitivity / stability / ...

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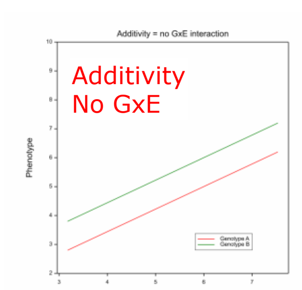
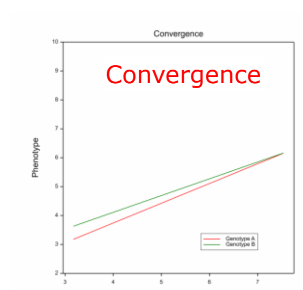
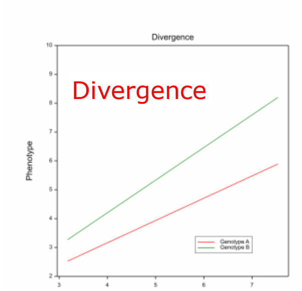
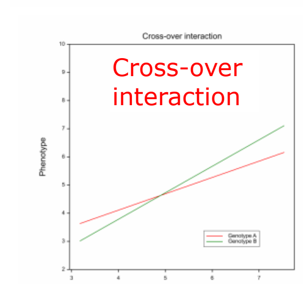
Examples of pairs of reaction norms









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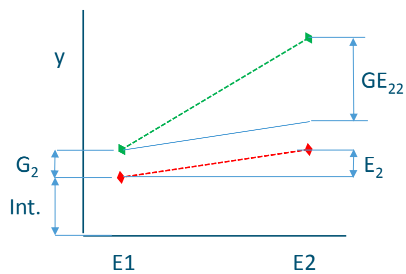
G x E considered as interaction

Different genotypes respond differently to a change in the environment



Model: $y_{ij} = int + G_i + E_j + GE_{ij}$

$y_{11} = int$
$y_{12} = int + E_2$
$y_{21} = int + G_2$
$y_{22} = int + G_2 + E_2 + GE_{22}$

$GE = 0 \rightarrow$ no GxE-interaction

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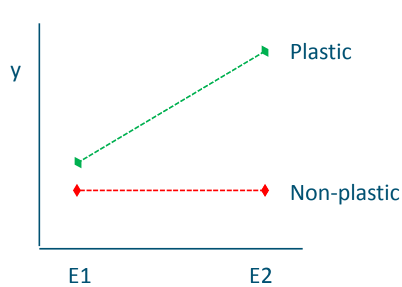
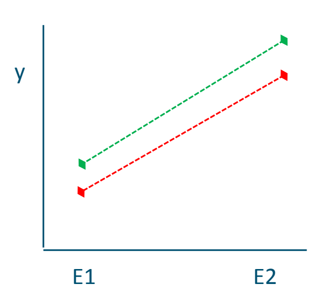
G x E and (phenotypic) Plasticity

A genotype changes its phenotype when the environment changes



Plasticity does not necessarily imply GxE-interaction!



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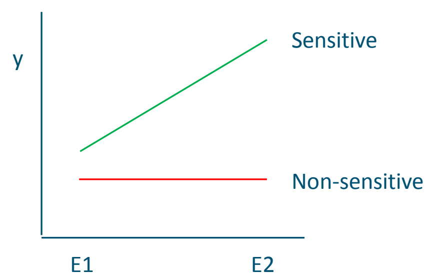
G x E and environmental sensitivity

- Refers to the slope of the reaction norm
- Measures degree of plasticity



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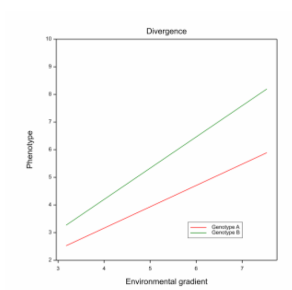
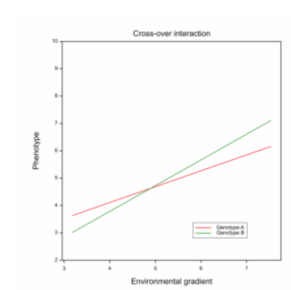
General versus specific adaptation





- Adapted genotype → a genotype whose reaction norm is above certain standard or reference genotype.
  - General or wide adaptation: superior across the entire TPE
  - Specific or narrow adaptation: superior but only over a range of the TPE

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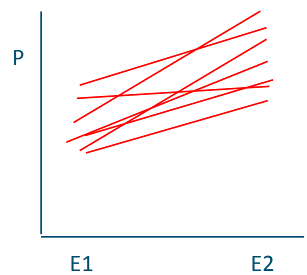
G x E, adaptation, plasticity and environmental sensitivity

- Non-parallel reaction norms
- Genetic variation in adaptation
- Genetic variation in plasticity
- Genetic variation in environmental sensitivity

} G x E



With many genotypes, ranking differs between environments.

Correlation of the ranks between environments ≠ 1

Variance among genotypes may differ between environments

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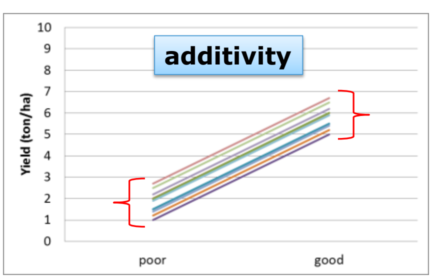
GxE and heterogeneity of variation



- Additivity: constant variance across environments.
- If GxE: variability changes from environment to environment
  - typically low variance in poor environments, high in good environments.
- No effect on ranking of genotypes, therefore no consequences for selection

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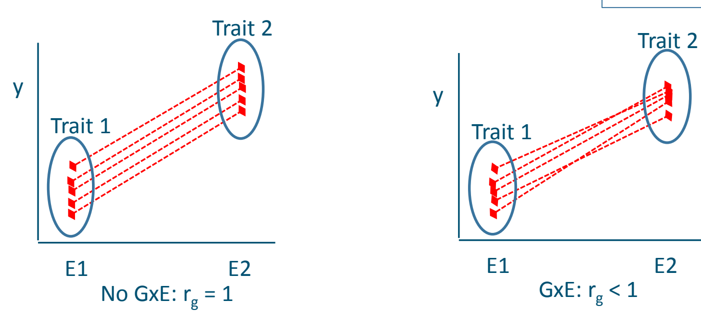
G x E and reranking

- Treat the trait in each environment as a genetically distinct trait
- Genetic correlation between trait in different environments is a measure of G x E (Falconer, 1952)
- $r_g < 1 \rightarrow$ G x E

Model: $y_{ijk} = \mu_j + G_{ij} + \varepsilon_{ijk}$

$r_g = corr(G_{ij}, G_{ij'})$



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Typical research questions regarding GxE in plant breeding

- Related with the genotypes:
  - Adaptation: are particular genotypes adapted to certain environmental range?
  - Adaptability / sensitivity: are particular genotypes able to be adapted to improvements in the environment?
  - Stability: is the performance of particular genotypes consistent?
- Related with the environments:
  - Grouping of trials into mega-environments: finding structure in the TPE.
  - Given a structure of the TPE optimize the choice of trials to represent the TPE.

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Summary

- G x E = Different genotypes respond differently to a change in the environment
- G x E may result in heterogeneity of variance and reranking
- Reaction norm is an important concept
- Non-parallel reactions norms = G x E = genetic variation in environmental sensitivity/plasticity/adaptability

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Concepts of stability

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Different concepts of stability

- Stability is a measure of variability in performance across environments
- Constant performance is better than no performance (food security)
- Predictable response to improvement of environment is desirable,
  - E.g. fertilizer
- Different definitions needed

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Stability and predictability

- Desirable:
  - Low sensitivity to unpredictable changes in E
    - E.g. Temporal fluctuation in E, such as the weather
  - High sensitivity to predictable changes in E
    - E.g. Good response to fertilizer

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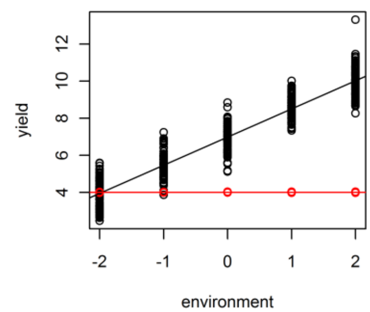
Key differences in stability concepts

- Slope of the reaction norm
- Variability around reaction norm



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Definitions of stability

- Static and dynamic stability (Becker and Leon, 1988)
- Type 1 to 4 (Lin et al., 1986; Lin and Binns, 1988)
- Macro-environmental, micro-environmental sensitivity and uniformity (Falconer and Mackay, 1996; Mulder et al. 2013)

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Static stability

- = "Biological concept of stability"
- Measures the overall variability of a genotype (or a "line") over environments

General model: $\mu_{ij} = \mu + G_i + E_j + GE_{ij}$

Static (in)stability: $\mathrm{var}(\mu_{i.})$ across environments

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Dynamic stability

- "Agronomic concept of stability"
- Does not include the predictable variability in performance across environments

General model: $\mu_{ij} = \mu + G_i + E_j + GE_{ij}$

Dynamic (in)stability: $\sigma^2_{G_i \times E}$

Does not penalize genotypes for variation due to a predictable response to the environment (σ^2_E)

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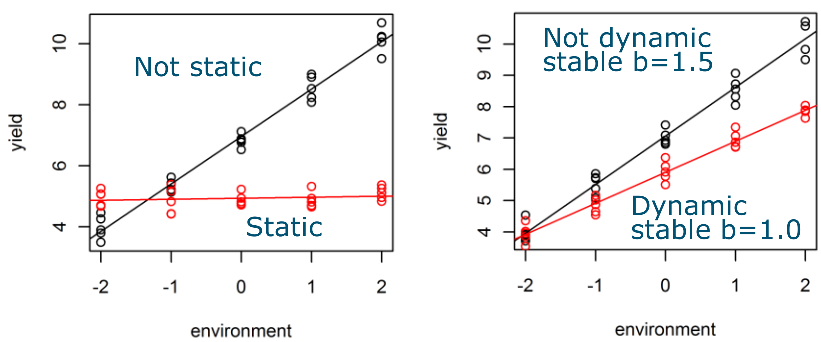
Dynamic versus static stability in figures



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Finlay-Wilkinson regression & stability measures

- FW-regression = Linear reaction-norm model
  - For the average performance μ_{ij} of line i in environment (j)

$$\mu_{ij} = \mu + G_i + E_j(1+\beta_i) + \delta_{ij}$$

μ = overall mean
G_i = overall value of genotype i
E_j = overall value of environment j
β_i = (linear) **sensitivity** of genotype i to environment
$\beta > 0$: above average sensitive
$\beta < 0$: below average sensitive

E_j is the average performance in environment j = measure of "quality" of environment

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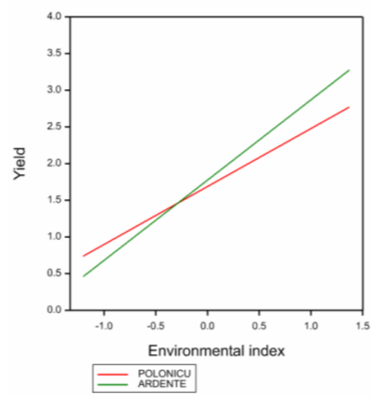
Finlay-Wilkinson Regression

$$\mu_{ij} = \mu + G_i + E_j(1+\beta_i) + \delta_{ij}$$

$$\mu_{ij} = \mu + G_i + E_j + \beta_i E_j + \delta_{ij}$$

$$GE_{ij} = \beta_i E_j + \delta_{ij}$$



FW-regression tries to capture GxE-interaction as a linear function of the environment

Idea:
- Some genotypes are generally more responsive to environmental change (β>0)
- Other genotypes are generally less responsive to environmental change (β<0)

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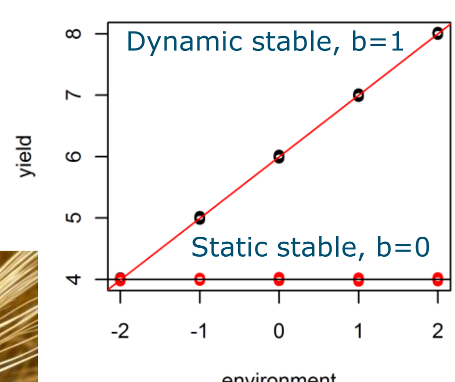
Type 1 stability = static stability

FW-regression: $\mu_{ij} = \mu + G_i + E_j(1+\beta_i) + \delta_{ij}$

Little change of phenotype over environments

- Little plasticity
- Slope of reaction norm of ~0
- β ≈ -1



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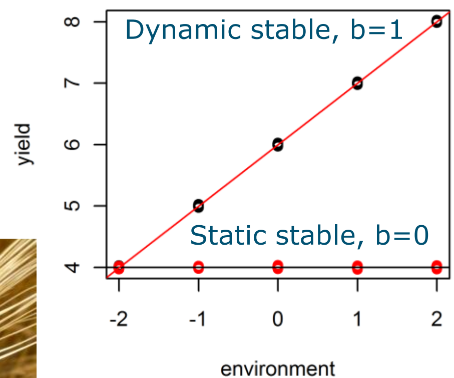
Type 2 stability = dynamic stability

FW-regression: $\mu_{ij} = \mu + G_i + E_j(1+\beta_i) + \delta_{ij}$

Expected response to environment

- Slope of reaction norm ~1
- $\beta \approx 0$ and var(δ) is small
- GE $\approx$ 0



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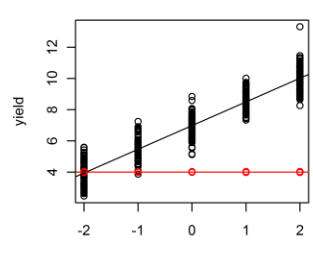
Type 3 stability

FW-regression: $\mu_{ij} = \mu + G_i + E_j(1+\beta_i) + \delta_{ij}$

Predictable change of phenotype over environments

- Linearly predictable GxE-interaction
- β can take any value, but var(δ) is small
- Stable genotype has low residual variance or high R^2
- Dynamic stability measure
- Eberhart and Russell (1966)



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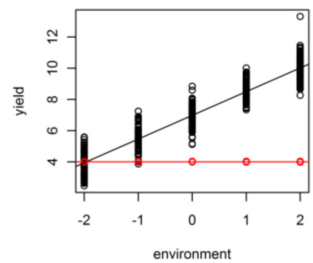
Stability type 4

FW-regression: $\mu_{ij} = \mu + G_i + E_j(1+\beta_i) + \delta_{ij}$

- Considers location vs yearly variation
- Good response to location variation
- Little response to temporal variation ("weather")
- Responsive to predictable changes, robust against unpredictable changes
- Dynamic stability
- Refinement of type 3 stability
- Lin and Binns (1988)



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Macro- and micro-environmental sensitivity

- Macro-environment: known environmental factor or the environmental mean (=Finlay-Wilkinson)
  - Differences in slope of reaction norm
  - Type 2 stability
- Micro-environment: unknown environmental factor
  - Differences in residual variance
  - Type 3/4 stability
  - Environmental canalization

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Uniformity

- = less variability
- Usually within an environment
- But can be hidden variation in reaction norm
- P = A + E; Uniformity = little variation in E
- Type 3/4 stability
- In evolution called environmental canalization
- Lectures Wednesday

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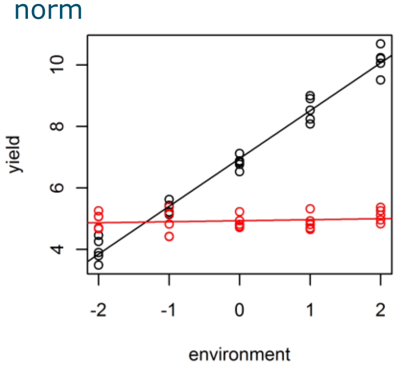
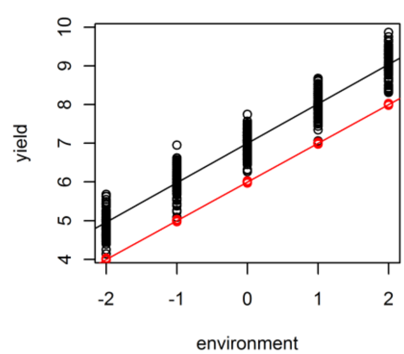
Summary

Difference in slope of reaction norm



- Type 1 and type 2 stability
- Macro-environmental sensitivity
- Plasticity
- Adaptation

Difference in residual variance



- Type 3 and type 4 stability
- Micro-environmental sensitivity
- Uniformity
- Canalization