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
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?

\[ P(t) = \int_{0}^{t} f(G, E)dt \]

The phenotype, the outcome of...

- "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”
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.

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.
**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.

**GxE and reaction norms**

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

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

Examples of pairs of reaction norms

- Additivity
  - No GxE
- Convergence
- Divergence
- Cross-over interaction
**G x E considered as interaction**

Different genotypes respond differently to a change in the environment.

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

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

$GE = 0 \rightarrow \text{no GxE-interaction}$

**G x E and (phenotypic) Plasticity**

A genotype changes its phenotype when the environment changes.

Plasticity does not necessarily imply GxE-interaction!
G x E and environmental sensitivity

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

![Diagram showing sensitive vs. non-sensitive reaction norms]

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
**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

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
**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)
- \( r_g < 1 \) → G x E

\[
\text{Model: } y_{ijk} = \mu_j + G_{ij} + \epsilon_{ijk}
\]
\[
r_g = \text{corr}(G_{ij}, G_{ij}')
\]

**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.
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

Concepts of stability
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

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
Key differences in stability concepts

- Slope of the reaction norm
- Variability around reaction norm

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)
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: \( \text{var}(\mu_{i.}) \) across environments

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: \( \sigma^2 \times \sigma_{G_i \times E} \)

Does not penalize genotypes for variation due to a predictable response to the environment (\( \sigma^2_E \))
Dynamic versus static stability in figures

- Not static stable \( b = 1.5 \)
- Static stable \( b = 1.0 \)

Finlay-Wilkinson regression & stability measures

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

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

- \( \mu \) = overall mean
- \( G_i \) = overall value of genotype i
- \( E_j \) = overall value of environment j
- \( \beta_i \) = (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
Finlay-Wilkinson Regression

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

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

\[
GE_{ij} = \beta_i E_j + \delta_{ij}
\]

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

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

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 $\sim 0$
- $\beta \approx -1$

Dynamic stable, $b=1$

Static stable, $b=0$
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 \( \sim 1 \)
- \( \beta \approx 0 \) and \( \text{var}(\delta) \) is small
- \( \text{GE} \approx 0 \)

![Dynamic stable, b=1](dynamic_stability.png)

![Static stable, b=0](static_stability.png)

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
- \( \beta \) can take any value, but \( \text{var}(\delta) \) is small
- Stable genotype has low residual variance or high \( R^2 \)
- Dynamic stability measure
- Eberhart and Russell (1966)
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)

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
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

Summary

Difference in slope of reaction norm

Difference in residual variance

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

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