G x E interaction and Phenotypic stability
General Considerations in potato breeding

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• **Genetics:** Study of heredity and variation.

• **Breeding:** Consist of principles and methods required for favourable changing the genetic constitution of crop. Plant breeding aims to develop an improved crop variety utilized by farmers for commercial cultivation.

• **Variety:** A taxonomic subdivision of a species consisting of naturally occurring or selectively bred populations or individuals that differ from the remainder of the species in certain minor characteristics.

• **Cultivar:** A plant or grouping of plants selected for desirable characteristics that can be maintained by propagation.

• **Clone:** Clone group of identical plants derived from single plants through asexual propagation.

• Single outstanding plant selected from population form the basis of variety.
Potato

- Family Solanaceae
- Genus *Solanum*: 8 cultivated species & 2000 wild relatives
- About 235 *Solanum* species tuberize
- Basic chromosome: $x = 12$
- Ploidy level: $2x$ to $6x$
- 73% diploids, 4% triploids, 15% tetraploids, 2% pentaploids and 6% hexaploids
- Auto-tetraploid or segmental allo-tetraploid
- Highly heterozygous
- High inbreeding depression
- Tuber-bearing species: *S. tuberosum* ssp. *tuberosum* and *S. tuberosum* ssp. *Andigena*
- Seven primitive cultivated species:
  - *S. ajanhuiri*, *S. goniocalyx*, *S. phureja* & *S. stenototum* (diploids)
  - *S. chaucha* and *S. juzepczukii* (triploid);
  - *S. curtilobum* (pentaploid)
• Potato originated in high Andean region of South America
• Till 16th century it was unknown to rest of the world.
• Potato moved from South America to Spain (1570) and UK (1590).
• Potato’s global voyage began in the 17th century from Europe.
• In India & Sri Lanka, potatoes were introduced in early 17th century.
• Potatoes, became one of the most important world crops in a span of 300 years
Potato Breeding

- Potato selection started as soon as potato cultivation started.
- **1807:** First hybridization by Knight, Potato a major crop in England & degeneration-problem.
- **1843-1847:** Acceleration of potato breeding was due to severe late blight epidemic in Ireland.
- **1900:** Potato breeding gained impetus with rediscovery of Mendel’s law of inheritance.
- **Early 1900’s:** Germplasm collection (Russia, Germany, UK and USA), Male fertility-parent
- **Late 1900’s:** Base broadening, pre-breed, and sexual polyploidization (USA, Europe and CIP), Breeding for target traits.
- Cultivated potato proved to be difficult species for genetical research because of its complex inheritance.
In Andes of South America, potato was adapted to short days, tropical highlands (2,000 and 4,000 m).

Its equatorial origin makes potato essentially short-day dependent for tuberization.

In Europe, tuber formation was inhibited under long photoperiod (long days).

Long-day acclimation for tuberization to achieve higher tuber yields in Europe.

Breeding over more than 150 years led to plants tolerating long day condition.

The mutations in tuber formation regulator allow potatoes to escape the original short day regulation mechanism suited to the Andes, so potatoes can be grown in Europe & other northern latitudes of world.

Mutations in the tuber formation regulator gene which occur in different combinations in modern potato cultivars, giving rise to early, medium and late varieties, depending on the combination of the gene variants present in the tetraploid crop (Kloosterman et al. 2013).

Potato Breeding

• Cultivated potato is auto-tetraploid and highly heterozygous.
• Heterosis is observed on crossing diverse parents.
• Breeding of potato involves hybridization between identified parents and selection of superior clones from the progeny.
• The genetic constitution of the genotype obtained following hybridization is fixed in seedling stage.
• Due to vegetative propagation the genetic constitution of potato genotype with all its intra- and inter-locus interactions responsible for its phenotypic expression are maintained in the clonal generations.
• Hence, a clone if perceived desirable can be multiplied for commercial cultivation even though initially it may be present as a single plant.
• More than 50 traits should be combined in a modern potato variety (Ross, 1986).
• An ideal potato variety affects not only yield and quality but also production cost, environmental issues, post harvest and yield of future crops (Struik and Wiersema, 1999, Collard and Mackill, 2008).
• It can take 10 to 15 years to release a variety.
Old variety (A)---- New potato variety (B)

- Existing variety (A) lacks some economic characters
- New potato variety (B) developed to replace the existing variety.
- On adoption, new variety (B) become existing variety (A).
- Target is to develop another new variety to replace the existing variety (A).
- Development of new variety put new challenge to breeder
- Consumer demand or climate change also put new targets
Potato breeding methodology

Parental preference

Selection of parents

Selection parameters

Phenotypic performance, adaptation, genetic divergence, combining ability, heterosis, progeny tests

Hybridization

1) Establishing parents
2) Pollen fertility estimation (2% Aceto-carmine)
3) Emasculation
4) Pollen collection & pollination
5) Berry, TPS extraction, storage

Assessment of segregating population

Evaluation of clones ($F_1C_1$-$F_1C_7$)

Seedling stage: Good vigour, desirable tuber colour, shape, eye depth, no-cracking, irregularity

Initial evaluations ($F_1C_1$-$F_1C_3$): Un-replicated trials

Advanced evaluations ($F_1C_4$-$F_1C_7$): Replicated trials

DUS, DNA fingerprinting

Multi-location & on-farm trials under AICRP (P)

AICRP (P): 25 (18+7)

Multi-location trials: 2 years

On-farm trials: 1-2 years

Release & notification of variety

10-15 years of concerted efforts
Adaptation refers to changes in structure or function of an individual or population which lead to better survival or greater fitness in the given environment.

Features of adaptations

1. It is the process of adjustment of living organism to the changing environment.

2. It favours those characters which are advantageous for survival and through which an individual acquires adaptive or fitness to the given environment.

3. In the process of adaptation survival is the main concern.

4. Natural selection play an important role in the process of adaptation
Adaptability

Adaptability is the capacity of a genotype or population for genetic changes in adaptation

Features of adaptability

1. Adaptable genotypes produce narrow range of phenotypes in different environments.
2. Adaptability leads to stable performance of a genotype over a wide range of environments.
3. General genotypic and general population adaptations are the examples of wide adaptability.
4. Varietal adaptability of is the result of genetic and physiological homeostasis.
5. Productivity is the main concern in varietal adaptability.

Genetic homeostasis is the ability of genotype to withstands environmental fluctuations (Lerner, 1954). Thus variability in the performance over a wide range of environments can be used a criterion for measure of phenotypic stability.

Physiological homeostasis refers to physiological or developmental capacity of a genotype to the environment fluctuations. The internal self regulatory mechanisms enable the individual to adjust to the fluctuating environment by resisting such changes. It is generally higher in heterozygous genotypes than in homozygous one.
G X E Interaction

Genotype: The genotypic effects are heritable and therefore, stable.

Environment: External conditions that affects expression of gene of an individual or genotype.

Genotype x Environment: Environment and interactions effects are non-heritable and can-not be fixed.

The phenotypic value (P) measured on suitable scale is not equal to genotypic value (G) when the genotype is grown under more than one environment (E). That is,

\[ P \neq G + E \]

But,

\[ P = G + E + (G \times E) \]

• G x E interaction underlines the very success of a scientific crop improvement programme related to stability of genotypes/varieties.

• It also influences the adoptive evaluation of improved strains before being released for commercial cultivation.
Phenotypic stability

• Phenotypically stable genotypes are of great importance, because the environmental conditions vary from season to season and year to year.

• Stability in performance is one of the most desirable properties of a genotype to be released as a variety for wide adaptations.

• Wide adaptation to the particular environment and consistent performance of recommended varieties are very important for successful cultivation of potatoes.

• Allard and Bradshaw (1964) suggested that, while developing cultivars with specific adaptations to predictable specific environments, plant breeder should aim to produce cultivars that are adapted to withstand unpredictable transient environmental variations.

• It is important to develop potato genotypes having predictable performance for trait of interest with minimal genotype x environmental interactions (GEI) Lin et al 1986 and Tai 2007.

• GEI are extremely important in the development and evaluation of plant varieties because they reduce the genotypic stability values under diverse environments (Habert et al 1995).
Experimentation

1. All post breeding test analysis are carried out from the data collected from multi-environment data trials (including macro environments - climate, weather, photoperiod, altitude, latitude, soil and micro environment - agronomic practices, like sowing time, spacing, fertilizer schedule, irrigation).

2. Experimentation should preferable be carried out separately for early, medium and late varieties as comparison of early varieties with late ones is often erroneous under multi-environmental trials. Same is the case with tall and dwarf varieties.

3. Choice of judicious sowing time is the common sense and good judgment of experimenter. A somehow loose criterion may be that early varieties may be fare well under late sowing and vice-versa.

4. Trials to be conducted under rainfed and irrigated conditions should be well defined with regard to choice of varieties, sowing time, spacing etc.
Data collection

The data is collected for different characters plot of suitable size from multi-environment trials of the genotypes grown in RBD with 3 replication at different locations over seasons.

Data analysis

The data obtained from the multi-environmental site can be evaluated through suitable statistical software like SPAR-1, INDOSTAT, OP Stat, SAS, Genstat (GGE biplot).
1. The performance of genotype mainly depends on environmental interaction.

2. Estimation of phenotypic stability involves regression analysis.

3. An evaluation of genotypes x environmental interaction provides an idea of buffering capacity of the population under study. The low magnitude of GXE interactions indicates consistence performance of a population over variable environments.

4. The stability analysis is done from the data of replicated trials conducted over several locations or for several years on the same location or both.

5. The stability analysis consist of the following steps:
   - Location or environments wise analysis of variance
   - Pooled analysis of variance for all the location/environments.

If GXE interactions are found significant, the stability analysis can be done using the appropriate model-
Measurement of G x E interaction

- **Comstock and Robinson (1952):** measured the G x E interaction in terms of only one parameter, i.e. means of genotypes over location and years.
- **Finally and Wilkinson (1963):** Based on two parameter of stability-means and regression coefficients associated with each genotypes.
- **Eberhart and Russell (1966):** Three stability parameters Mean, regression coefficients and deviation from linearity (non-linear sensitivity) to describe varietals performance over time and space.
- **Perkins and Jinks (1968):** refined the Eberhart and Russell model and estimated regression of G x E interactions (rather than genotypic means) on environmental index, but stability parameters remained as above.
- **Hanson (1970):** Complete measure of stability obtained by combining the contribution of ith genotype to the G x E variance with its response to environmental index.
- **Freeman and Perkins (1971):** Improved the Eberhart and Russell model with respect to making environmental index really independent variable.
- **Additive main effects and multiplicative interaction (AMMI) analysis (Gauch and Zobel 1997)**
- **Genotype main effect and genotype x environment interaction (GGE) biplot analysis (Yan et al. 2000).**
Eberhart and Russel Model

1. The total variance is first divided into two components - genotypes and environment + interaction (E+GxE).
2. The second component (E+GxE) is further sub-divided into three components viz. a) environments linear, b) genotype x environment (linear) and c) pooled deviations.
3. The SS due to pooled deviation are further divided in to SS due to individual genotypes.
4. The Model consist of three parameters mean yield over locations or seasons, b) regression coefficient and c) deviation from regression.

ANOVA table for stability as per Eberhart and Russell (1966)

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>d.f</th>
</tr>
</thead>
<tbody>
<tr>
<td>Genotypes</td>
<td>g-1</td>
</tr>
<tr>
<td>Environment (E) + Interaction (G x E)</td>
<td>g(e-1)</td>
</tr>
<tr>
<td>Environment (linear)</td>
<td>1</td>
</tr>
<tr>
<td>G X E (linear)</td>
<td>g-1</td>
</tr>
<tr>
<td>Pooled deviations</td>
<td>g(e-2)</td>
</tr>
<tr>
<td>Genotype-1</td>
<td>e-2</td>
</tr>
<tr>
<td>Genotype-2</td>
<td>e-2</td>
</tr>
<tr>
<td>Pooled error</td>
<td>ge(r-1)</td>
</tr>
</tbody>
</table>
• Stable variety is one with a regression coefficient of unity \((b=1)\), and minimum deviation from the regression line \((s2d=0)\).

• Using this breeder would desire to develop a variety with high mean yield and satisfying the requirement of stability.
### Pooled analysis of variance for different characters

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f</th>
<th>Mean square</th>
<th>Total tuber yield</th>
<th>Economic tuber yield</th>
<th>Tuber number</th>
<th>Average tuber weight</th>
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<tr>
<td>Genotype1</td>
<td>33</td>
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<td>20600.75**</td>
<td>28.76**</td>
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<td>Environment1</td>
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<td>343486.00**</td>
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<td>325295.80**</td>
<td>142.59**</td>
<td>1634.55**</td>
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<td>Genotype x environment 2</td>
<td>231</td>
<td>2793.83**</td>
<td></td>
<td>2779.90**</td>
<td>2.26 **</td>
<td>34.12 *</td>
</tr>
<tr>
<td>Environment + (Genotype x environment) 3</td>
<td>238</td>
<td>12814.19**</td>
<td></td>
<td>12265.66**</td>
<td>6.38**</td>
<td>81.19**</td>
</tr>
<tr>
<td>Environment (Linear) 3</td>
<td>1</td>
<td>2404402.00**</td>
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<td>2277070.00**</td>
<td>998.14**</td>
<td>11441.84**</td>
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<tr>
<td>Genotype x environment (Linear) 3</td>
<td>33</td>
<td>10680.32**</td>
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<td>9984.91**</td>
<td>5.98**</td>
<td>76.34**</td>
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<td>Pooled Deviation 4</td>
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<td>1435.91**</td>
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<td>1532.61**</td>
<td>1.59**</td>
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<td>Pooled Error</td>
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<td>792.23</td>
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</table>

1Tested against Genotype x environment MS, 2 against pooled error MS, 3 against pooled deviation MS, 4 against pooled error MS (given separately)

*, ** Significant at P≤ 0.05 and P≤0.01, respectively
Results

- The analysis of variance showed highly significant mean squares due to genotypes and environments for all characters. Genotypes also interacted significantly with environment for all characters.

- Both linear (genotype x environment) and non-linear (pooled deviations) components of variation were highly significant for all characters indicating the presence of both predictable and non-predictable components.

- The magnitude of linear component of variation was significantly higher than the non-linear components suggesting that genotype’s performance can be predicted but with caution, and that prediction needs to be based on both regression and deviation from regression.

- Environmental index showed that environment 1 to 4 (early crop) were unfavourable, whereas environment 5-8 (main crop) were favourable.

- The temperature was higher at early planting (maximum range: 22.0-35.50C, minimum range: 4.0-25.00C) than main planting (maximum range: 17.0-34.00C, minimum range: 1.0-20.00C) due to this early season crop proved unfavourable.
<table>
<thead>
<tr>
<th>Genotypes</th>
<th>Mean</th>
<th>Total tuber yield</th>
<th>Economic tuber yield</th>
<th>Tuber number</th>
<th>Average tuber weight</th>
</tr>
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<tbody>
<tr>
<td></td>
<td></td>
<td>Mean</td>
<td>S'di</td>
<td>Mean</td>
<td>S'di</td>
</tr>
<tr>
<td>CP1362</td>
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<td>455.15</td>
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</table>

* Significant at P≤ 0.05 and P≤0.01, respectively.
Interpretation of results

- A variety with unit regression coefficient (bi=1) and deviation from regression not significantly different from zero (S2di=0) is said to be stable.
- Accessions with bi values significantly higher than 1 and non-significant deviation from regression are expected to perform better in the favourable environments.
- Accessions with bi values significantly lower than 1 and non-significant deviations from the regression are more suitable for low yielding environments.
- Those which have both bi and deviation from regression significant are unstable.
- Stable genotypes had not necessarily significantly high mean values for different characters.