Selection of genotypes for resistance and tolerance to pathogens:

A bivariate statistical analysis of yield and disease response.

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\triangleright Background to the agricultural research problem

- I linear mixed model formulation
- \blacktriangleright Interpretation of results

Phenotyping for the effect of disease on genotypes in a plant breeding program requires measurement of

- \triangleright growth of the pathogen in the plant
- \triangleright subsequent effect of the pathogen on grain production in the plant

A bivariate statistical analysis of yield and disease **Definitions**

Resistance

- \blacktriangleright The ability of the host to prevent pathogen entry and control pathogen spread.
- \blacktriangleright In this application, the ability of the plant to reduce pathogen burden and hence suppress disease expression.

Tolerance

- \blacktriangleright The ability of the host to limit the impact of pathogen burden on host health.
- \blacktriangleright In this application, the ability of the plant to produce grain in the presence of disease.

Uncoupling resistance and tolerance is a challenge, but is desireable for a number of reasons (Kause and Odegard, 2012).

- \blacktriangleright Each have a different impact on the relationship between the host and the pathogen.
- \blacktriangleright In plants (and animals) they are weakly genetically correlated, so are dfferent traits
- \triangleright Plant breeders should exploit both traits to provide a responsible solution to sustainable farming practices and increased food production.

Host: Wheat Pathogen: Fusarium pseudograminearum

- \blacktriangleright Experiments to test the resistance and tolerance of genotypes involve a disease treatment with 2 levels: an untreated control (nil) and an imposed disease level (plus).
- \triangleright The experimental design typically consists of replicated field trials in a strip-plot arrangement of the disease treatment, where genotypes are grown under these two conditions in paired plots.
- \triangleright Aim: To select genotypes possessing combined traits of resistance and tolerance to disease.

A bivariate statistical analysis of yield and disease Experimental design

Field trial planted as a rectangular array of plots in 25 columns by 44 rows, grown at Narrabri, NSW in 2014

A bivariate statistical analysis of yield and disease Experimental design

Treatment allocation for a subset of plots: 25 columns by 4 rows

Inoculum strips (nil,plus)

Genotype mainplots

A bivariate statistical analysis of yield and disease Experimental design

Measurements

- \blacktriangleright Yield of grain (t/ha).
- \triangleright Disease level of stem browning (cm).

Issues surrounding the methodology

- \triangleright A baseline treatment of nil disease aims to estimate yield potential.
- \triangleright Achieving this baseline is difficult in practice due to background levels of disease in the field.
- \blacktriangleright The severity of disease expression will change with environmental conditions.

The form of the linear mixed model for a single trait $(i=Y, D)$ is

$$
\mathbf{y}_j = \mathbf{X}_j \boldsymbol{\tau}_j + \mathbf{Z}_{g_j} \mathbf{u}_{g_j} + \mathbf{Z}_{s_j} \mathbf{u}_{s_j} + \mathbf{e}_j
$$

 $\mathsf{y}_{j}^{(n\times1)}$ is the vecter of responses measured on n plots, $\bm{\tau}^{(t\times1)}_j$ is a vector of fixed effects for inoculum with design matrix $\bm{\mathsf{X}}^{(n\times t)}_j$, $\mathbf{u}_{g_j}^{(tm\times1)}$ is a vector of random effects for genotype, partitioned for inoculum level, with design matrix $\mathsf{Z}_{j}^{(n \times m)}$, $\mathsf{u}_{\mathsf{s}_j}^{(\mathsf{s} \times 1)}$ is a vector of random effects for structural terms, with design matrix $\mathsf{Z}_{s_{j}}^{(n\times s)}$, and $\mathbf{u}_{s_j} = (\mathbf{u}_{r_j}', \mathbf{u}_{b_j}', \mathbf{u}_{ip_j}', \mathbf{u}_{gp_j}')'$ and ${\bf e}_j^{(n\times 1)}$ is the vector of residual errors.

The variance of the random inoculum by genotype effects, $\mathbf{u}_{\mathcal{g}_j}$, is

$$
\mathsf{var}(\mathbf{u}_{g_j}) = \begin{bmatrix} \sigma_{g_{n_j}}^2 & \sigma_{g_{n_p_j}} \\ \sigma_{g_{n_p_j}} & \sigma_{g_{n_j}}^2 \end{bmatrix} \otimes \mathsf{I}_m
$$

The random effects for structural terms and residual errors are assumed to be independent and identically distributed normal variates with mean zero and variance structures, var $(\mathbf{u}_{s_{j_i}}) = \sigma_{s_{j_i}}^2 \mathbf{l}_{n_{s_i}}$ and var $(\mathbf{e}) = \sigma_j^2 \mathbf{l}_{n_i}$ (where n_{s_i} is the length of $\mathbf{u}_{s_{j_i}})$.

The form of the linear mixed model for both traits $(j=Y,D)$ is

$$
\textbf{y} = (I_2 \otimes \textbf{X})\boldsymbol{\tau} + (I_2 \otimes \textbf{Z}_g)\textbf{u}_g + (I_2 \otimes \textbf{Z}_s)\textbf{u}_s + \textbf{e}
$$

where

$$
\mathbf{y} = (\mathbf{y}'_Y, \mathbf{y}'_D)', \quad \boldsymbol{\tau} = (\boldsymbol{\tau}'_Y, \boldsymbol{\tau}'_D)', \quad \mathbf{u}_g = (\mathbf{u}'_{g_Y}, \mathbf{u}'_{g_D})', \quad \mathbf{u}_s = (\mathbf{u}'_{s_Y}, \mathbf{u}'_{s_D})' \text{ and}
$$

$$
\mathbf{e} = (\mathbf{e}'_Y, \mathbf{e}'_D)'
$$

The variance of the random inoculum by genotype effects, \mathbf{u}_{g} , for both traits(Y,D) is

$$
\text{var}(\mathbf{u}_{g}) = \begin{bmatrix} \sigma_{g_{\gamma_{n}}}^{2} & \sigma_{g_{\gamma_{p}}}^{2} \\ \sigma_{g_{\gamma_{n}p_{n}}} & \sigma_{g_{\gamma_{p}}p_{n}}^{2} & \sigma_{g_{D_{n}}}^{2} \\ \sigma_{g_{\gamma_{n}D_{n}}} & \sigma_{g_{\gamma_{p}D_{n}}} & \sigma_{g_{D_{n}}}^{2} & \sigma_{g_{D_{p}}}^{2} \end{bmatrix} \otimes I_{m}
$$

Additionally, the variance of the random structural effects and the residual errors, e , for both traits (Y, D) are

$$
\text{var}(\mathbf{u}_{s_i}) = \begin{bmatrix} \sigma_{s_{Y_i}}^2 & \\ \sigma_{s_{YD_i}} & \sigma_{s_{D_i}}^2 \end{bmatrix} \otimes I_{n_{s_i}}
$$

$$
\mathsf{var}(\mathbf{e}) = \begin{bmatrix} \sigma_Y^2 \\ \sigma_{YD} & \sigma_D^2 \end{bmatrix} \otimes \mathsf{I}_n
$$

We fit the linear mixed model in ASReml-R (Butler et al., 2013).

- \blacktriangleright Estimate the variance components using Residual maximum likelihood (REML) (Patterson and Thompson, 1977).
- \triangleright Produce Best Linear Unbiassed Predictors of the random genotype by inoculum effects.
- \triangleright Use the inherent regression structure in the bivariate analysis to interpret the results, relating this back to tolerance and resistance in the plant-pathogen context.

Trait by Inoculum means and genetic variances estimated from the model.

Results Genotype predictions (BLUPs)

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We focus on the genotype blups, and use the regression structure inherent in the bivariate model to interpret the results.

For Yield, plus vs nil blups

$$
\mathbf{u}_{g_{Y_p}} = \beta_Y \mathbf{u}_{g_{Y_n}} + \epsilon_Y, \quad \beta_Y = \frac{\sigma_{g_{Y_{np}}}}{\sigma_{g_{Y_n}}^2}.
$$

Define yield responsiveness as ϵ_Y , where responsiveness has zero covariance with yield potential, $\mathbf{u}_{\mathcal{G}\mathsf{y}_n}$

Yield responsiveness, ϵ_Y

Genotypes with high yield potential and responsiveness under disease pressure

Yield−nil

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Again, we use the regression structure inherent in the bivariate model to interpret the results.

For Plus disease plots, yield vs disease blups

$$
\mathbf{u}_{g_{Y_p}} = \beta_P \mathbf{u}_{g_{D_p}} + \epsilon_P, \quad \beta_P = \frac{\sigma_{g_{Y_p D_p}}}{\sigma_{g_{D_p}}^2}.
$$

Define yield advantage under disease as ϵ_P , where yield advantage has zero covariance with disease severity under inoculation, $\mathbf{u}_{\mathcal{S}_{D_p}}$.

Combined selection for tolerance and resistance

Yield advantage under disease, ϵ_D

- \triangleright We have extended this model to an analysis across multiple trials (environments).
- \triangleright We have included a genetic covariance relationship through the pedigree of the genotypes.
- \blacktriangleright This will be extended to a genomic relationship matrix as marker data is available next year.

The National Crown Rot Initiative team

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