

Modelling and evaluating breeding progress in rye for hybrid and population varieties

Friedrich Laidig
Biostatistics Unit
University of Hohenheim
Germany

Joint work with:

Hans-Peter Piepho, Hohenheim University

Dirk Rentel, Thomas Drobek and Uwe Meyer, Bundessortenamt, Germany

Alexandra Hüsken, Max-Rubner Institut, Germany

Models used in this study based on approaches described in

Piepho et al. (2014)

Laidig et al. (2016)



Questions

- Contribution of plant breeding to yield increases (genetic trend)?
- Contribution of improved agronomic practices and environmental factors to yield increases (non-genetic trend)?
- Effect of variety age on yield progress?
- Gap between trial and on-farm yields?



Overview

- 1. Basic mixed model
- 2. Genetic and non-genetic trends
- 3. Effect of variety age
- 4. Trial vs on-farm yield progress
- 5. Conclusions

Rye production

Cereal with

- high winter hardiness,
- high tolerance to other abiotic and biotic stress factors,
- suitable for nutrient-poor, sandy soils,
- out yield wheat and triticale under these poor conditions,
- rye bread has a high dietary value.

Country	Production	Acreage	Grain yield	
	(1000 t)	(1000 ha)	(t ha ⁻¹)	
Germany	3,174	571	5.56	
Russian Federation	2,541	1,250	2.03	
Poland	2,200	761	2.89	
Belarus	651	241	2.70	
Denmark	577	100	5.80	
China	525	164	3.21	
Ukraine	392	144	2.73	
Canada	382	131	2.92	
USA	342	168	2.04	
Spain	316	157	2.01	
WORLD	12,944	4,403	2.94	

Source: FAO (2018)

Data

- Official VCU (value for cultivation and use) trials in Germany
- Regular trial period three years
- Only released hybrid and population varieties included
- Intensities:
 - Intensity 1 no crop protection and growth regulators
 - Intensity 2 fungicides, equal or higher nitrogen fertilization rates
- Split-plot design:
 - Intensity on main plots (RCBD)
 - Variety on sub-plots (completely randomized)
 - Hybrid and population varieties randomized together

Data (cont.)

- Investigated years 1985 2016
- Traits
 - Grain yield (dt ha⁻¹)
 - Ear density (ears m⁻²)
 - Single ear weight (g ear⁻¹)
- On-farm data

National averages for grain yield (1985-2016) from harvest survey comprising all types of varieties

Basic information (VCU trials)

	Hybrid varieties	Population varieties			
Total # varieties	68	23			
Standards	18	10			
First trial year	1982	1955			
Years in trial	7	9			
Observations	6500	3600			
Trials	1300				
Locations	105				
% GxYxL combinations	2.45	2.56			

Basic model for long-term MET data

$$y_{ijk} = \mu + G_i + L_j + Y_k + (LY)_{jk} + (GL)_{ij} + (GY)_{ik} + (GLY)_{ijk}$$

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y_{ijk} = mean yield of the i-th genotype in the j-th location and k-th year \mu = general mean = main effect of the i-th genotype (variety) = main effect of the j-th location, = main effect of the k-th year (LY)_{jk} = jk-th location \times year interaction (GL)_{ij} = ij-th genotype \times location interaction (GY)_{ik} = ik-th genotype \times year interaction (GLY)_{ijk} = residual comprising both genotype \times location \times year interaction and error of the mean
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⇒ Separate analysis for hybrid and population varieties

Graphical representation

Take G_i and Y_k as fixed (can't take random because of time trend) and the other effects as random i. i. d. normal with constant variance

Adjusted means for G_i assess genetic trend \Rightarrow Plotted against year in which variety entered trial (first trial year)

Adjusted means for Y_k assess non-genetic trend \Rightarrow Plotted against harvest year (Two-step approach; *Mackay et al., 2011; Rijk et al. 2012*)

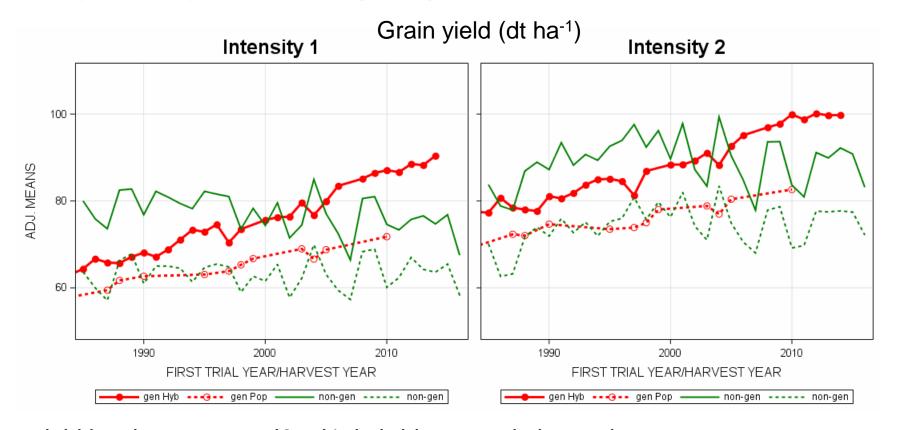
Alternative representation of genetic trend

 $G_i = C_p + H'_i$, where C_p is a categorical effect for groups of varieties with the same first trial year r_i . H'_i is the random deviation from group mean.

Adjusted means for C_p assesses genetic trend

 \Rightarrow Plotted against first trial year r_i

Graphical representation (cont.)



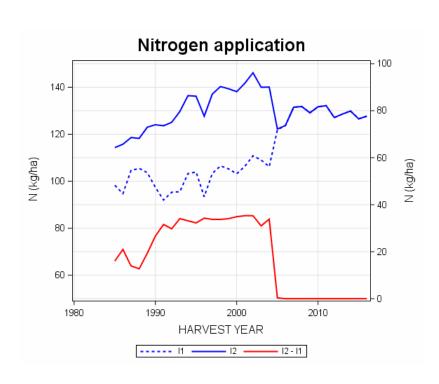
yield levels \Rightarrow 12 > 11, hybrids > population varietes

genetic trends ⇒ about linear increasing

non-genetic trends ⇒ parallel year-to-year variation

 \Rightarrow different slopes: period 1985 – 2004 and 2005 – 2016

Reason for change of non-genetic trend?



Change of nitrogen application rate

- Period p=1 1985 2004; N-rate | 12 ≠ 11
- Period $p=2\ 2005 2016$; N-rate 12 = 11
- ⇒ Focus on disease susceptibility of varieties,

Genetic trend

$$G_i = \beta r_i + H_i \qquad H_i \sim N(0, \sigma_H^2)$$

 β fixed regression coefficient for genetic trend r_i first year in trial of *i*-th variety

Non-genetic trend (two regression lines)

$$Y_{pk} = \mu_p + \gamma_p t_{pk} + Z_k$$
, where $p = 1, 2$ $Z_k \sim N(0, \sigma_Z^2)$

 γ_p fixed regression coefficient for non-genetic trend of period p

If
$$t_k$$
 is the harvest year, $t_{1k} = \begin{cases} t_k & if & t_k \leq 2004 \\ 0 & if & t_k > 2004 \end{cases}$ and
$$t_{2k} = \begin{cases} 0 & if & t_k < 2005 \\ t_k & if & t_k \geq 2005 \end{cases}$$

 $E(y_{pijk}) = \eta_{pik} = \mu_p + \beta r_i + \gamma_p t_{pk}$ fixed (regression) part of model

Results

I2 < I1	12 > 11
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		Trends						
			genetic	(r _i)	non-genetic (t _{nk})			
Traits	Int.	Туре			Slope ₁	Slope γ_2 §		
Yield	2	Hyb	0.77***	ns	0.55**	0.28 ^{ns} *		
(dt ha ⁻¹)	2	Pop	0.24***	*	0.64***	0.41 ^{ns} **		
	1	Hyb	0.87***	ns	-0.14 ^{ns}	0.00ns ns		
	1	Pop	0.30***	ns	0.06 ^{ns}	0.17 ^{ns} ns		
Ear density	2	Hyb	2.49***	ns	2.10 ^{ns}	0.91 ns ns		
(ears m ⁻²)	2	Pop	0.87*	ns	0.87 ^{ns}	-0.14 ^{ns} ns		
	1	Hyb	3.02***	*	0.36 ^{ns}	1.59 ^{ns} ns		
	1	Pop	0.65 ^{ns}	ns	-0.06 ^{ns}	1.36 ^{ns} ns		
Ear weight	2	Hyb	0.007***	ns	0.007 ^{ns}	0.005 ^{ns} ns		
(g ear ⁻¹)	2	Pop	0.002*	ns	0.010*	0.009 ^{ns} *		
	1	Hyb	0.009***	**	-0.001 ^{ns}	-0.003 ^{ns} ns		
	1	Pop	0.005***	ns	0.003 ^{ns}	0.001 ns ns		

Change of agronomic conditions 1985 - 2016
VCU trials
Sowing rate -43*** kernels m-2 (15%)
Sowing date 3* days earlier
Harvesting date 1ns days earlier
Daily air temperature +0.9*** °C

- & Test of deviation from linear genetic trend
- § Test of deviation from unique non-gen trend Significance levels
- * 5%
- ** 1%
- *** 0.1%

Extended regression model

- Disease susceptibility may increase with time for a number of years
- Inefficient maintenance breeding may lower performance, etc.
- This is expected to have an effect on time trends for yield etc.
- Use age at testing as another covariate in the model

 $\Rightarrow a_{ik} = t_k - r_i$ age at testing for the *i*-th variety in the *k*-th harvest year

 $\eta_{pik} = \mu_p + \beta r_i + \gamma_p t_{pk} + \delta a_{ik}$ extended regression model

 δ fixed regression coefficient for age covariate a_{ik} and of negative value for yield

Extended regression model (cont.)

Problem: Model over-parameterized (multi-collinearity)

$$\eta_{pik} = \mu_p + \beta r_i + \gamma_p t_{pk} + \delta(t_k - r_i)$$

Can be reparametrized as:

$$\eta_{pik} = \mu_p + \tilde{\beta} r_i + \tilde{\gamma}_p \ t_{pk}$$
, where $\tilde{\beta} = \beta - \delta$ and $\tilde{\gamma}_p = \gamma_p + \delta$

- \Rightarrow Regression on r_i and t_k may be biased due to age effects!
- ⇒ Can't separate out trend due to age effect

True genetic trend: $\beta = \tilde{\beta} + \delta$

True non-genetic trend: $\gamma_p = \tilde{\gamma}_p - \delta$

If age effect negative: $\delta < 0$:

 $\beta < \widetilde{\beta} \Rightarrow \text{genetic} \text{ trend}$ over-estimated $\gamma_p > \widetilde{\gamma}_p \Rightarrow \text{non-genetic} \text{ trend under-estimated}$

How to estimate age effect δ ?

⇒ Compare the two intensities

Intensity 1:
$$\eta_{pik1}=\mu_{p1}+\tilde{\beta}_1r_i+\tilde{\gamma}_{p1}\;t_{pk}$$
, where $p=1,2$
Intensity 2: $\eta_{pik2}=\mu_{p2}+\tilde{\beta}_2r_i+\tilde{\gamma}_{p2}\;t_{pk}$

Intensity 1

Intensity 2

Assumptions:

$$egin{array}{ll} eta_1 &= eta - \delta_1 \quad ext{and} \quad ar{eta}_2 = eta - \delta_2 \ ar{\gamma}_{p1} &= \gamma_p + \delta_1 \quad ext{and} \quad ar{\gamma}_{p2} = \gamma_p + \delta_2 \end{array}$$

- (1) genetic trends identical in I1 and I2
- (2) non-genetic trends identical in I1 and I2

Difference of response for both intensities under assumptions (1), (2)

$$\eta_{pik2} - \eta_{pik1} = (\mu_{p2} - \mu_{p1}) + (\delta_1 - \delta_2)r_i - (\delta_1 - \delta_2)t_{pk}$$
$$= (\mu_{p2} - \mu_{p1}) - (\delta_1 - \delta_2)a_{ik}$$

 \Rightarrow regression on a_{ik} estimates $\bar{\delta} = -(\delta_1 - \delta_2)$

How to estimate age effect δ (cont.)?

⇒ Compare the two intensities

Intensity 1:
$$\eta_{pik1}=\mu_{p1}+\tilde{\beta}_1r_i+\tilde{\gamma}_{p1}\;t_{pk}$$
, where $p=1,2$ Intensity 2: $\eta_{pik2}=\mu_{p2}+\tilde{\beta}_2r_i+\tilde{\gamma}_{p2}\;t_{pk}$

Intensity 1 Intensity 2 Assumptions:
$$\tilde{\beta}_1 = \beta - \delta_1$$
 and $\tilde{\beta}_2 = \beta - \delta_2$ (1) genetic trends indentical $\tilde{\gamma}_{p1} = \gamma_p + \delta_1$ and $\tilde{\gamma}_{p2} = \gamma_p + \delta_2$ (2) non-genetic trends identical $\tilde{\gamma}_{p1} = \gamma_{p1} + \delta_1$ and $\tilde{\gamma}_{p2} = \gamma_{p2} + \delta_2$ (3) non-genetic trends not identical

- (3) non-genetic trends <u>not</u> identical in I1 and I2

Difference of response for both intensities under assumptions (1), (3)

$$\eta_{pik2} - \eta_{pik1} = (\mu_{p2} - \mu_{p1}) + (\delta_1 - \delta_2)r_i + \left[\left(\gamma_{p2} - \gamma_{p1} \right) - (\delta_1 - \delta_2) \right] t_{pk} \\
= (\mu_{p2} - \mu_{p1}) + \left(\gamma_{p2} - \gamma_{p1} \right) t_{pk} - (\delta_1 - \delta_2) a_{ik}$$

 \Rightarrow joint regression on t_{pk} and a_{ik} estimates $\delta = -(\delta_1 - \delta_2)$

Graphical representation

Consider basic model of differences of I2 – I1

$$y_{p_{1}ijk_{2}} - y_{p_{1}jk_{1}} =$$

$$= (\mu_{p_{2}} - \mu_{p_{1}}) + G_{i} + L_{j} + Y_{p_{k}} + (LY)_{jk} + (GL)_{ij} + (GY)_{ik} + (GLY)_{ijk}$$

Representation of age effects:

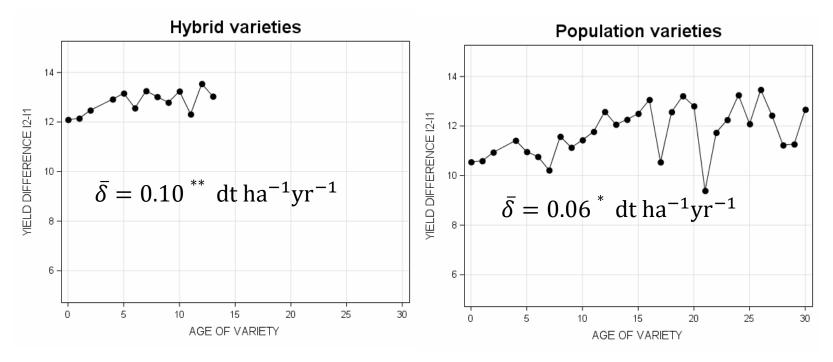
Take Y_{pk} be as fixed effect and

 $(GY)_{ik} = D_q + (ZH)_{ik}$ where D_q is a categorical fixed effect for the q-th age class, and the other effects are random.

Jointly estimate adjusted means for Y_{pk} and D_q Adjusted age means for D_q visualizes age trend $\bar{\delta} \Rightarrow$ Plotted against age

Graphical representation (cont.)

Grain yield: age trends for I2 – I1: $\bar{\delta} = -(\delta_1 - \delta_2)$



If $\delta_2 = 0$ then grain yield for I1

- ⇒ hybrid variety decreasing by 0.10 dt ha⁻¹ yr⁻¹
- ⇒ population variety decreasing by 0.06 dt ha⁻¹ yr⁻¹

Results(cont.)

Age effect $\bar{\delta}=-(\delta_1-\delta_2)$, $\delta_2=0$ not realistic, no full disease control \Rightarrow assume $\delta_2=\frac{1}{3}\delta_1$

Yield	Int.		Hybrids	Population verities
Age	12-11	$ar{\delta}$	0.10	0.06
effect I1	δ_1	-0.15	-0.09	
	12	δ_2	-0.05	-0.03
True	I1	$\beta_1 = \tilde{\beta}_1 + \delta_1$	0.87-0.15=0.72	0.30-0.09=0.21
genetic trend	12	$\beta_2 = \tilde{\beta}_2 + \delta_2$	0.77-0.05=0.72	0.24-0.03=0.21
True	I1, <i>p</i> =1	$\gamma = \tilde{\gamma} - \delta$	-0.14-(-0.15) =0.29	0.06-(-0.09) =0.15
non- genetic trend	I1, <i>p</i> =2	$\gamma_{p1} = \tilde{\gamma}_{p1} - \delta_1$	0.00-(-0.15) =0.15	0.17-(-0.09) = 0.26
	I2, <i>p</i> =1	$\gamma_{p2} = \tilde{\gamma}_{p2} - \delta_2$	0.55-(-0.05) = 0.60	0.64-(-0.03) = 0.67
	12, <i>p</i> =2		0.28-(-0.05) =0.33	0.41-(-0.03) =0.44

Reduced basic model for long-term MET data

```
y_{ijk} = \mu + L_i + Y_k + (LY)_{ik} + (GL)_{ij} + (GY)_{ik} + (GLY)_{ijk}
            = mean yield of the i-th genotype in the j-th location and k-th year
y_{ijk}
            = overall mean
\mu
            = main effect of the i-th location
            = main effect of the k-th year, (confounded with genotype effect), fixed
Y_k
(LY)_{ik}
            = ik-th location \times year interaction
            = ij-th genotype \times location interaction
(GL)_{ij}
            = ik-th genotype \times year interaction
(GY)_{ik}
            = residual comprising both genotype \times location \times year interaction
(GLY)_{ijk}
               and error of the mean
```

Overall trend

$$\begin{aligned} Y_{pk} &= \mu_p + \varphi_p \ t_{pk} + U_k, \ \text{where} \ p = 1,2; & U_k \sim N(0, \sigma_U^2) \\ \text{When} \ t_k \ \text{is the harvest year,} \ t_{1k} &= \begin{cases} t_k \ if & t_k \leq 2004 \\ 0 \ if & t_k > 2004 \end{cases} \ \text{and} \\ t_{2k} &= \begin{cases} 0 \ if & t_k < 2005 \\ t_k \ if & t_k \geq 2005 \end{cases} \end{aligned}$$

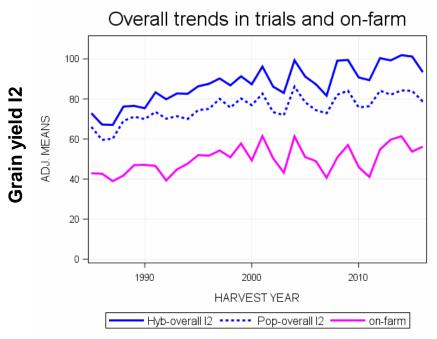
 φ_p fixed regression coefficient for overall trend of period p

 $E(y_{pijk}) = \eta_{pik} = \mu_p + \varphi_p t_{pk}$ fixed part of reduced model

Graphical representation of overall trend

Adjusted means for Y_k visualizes overall trend \Rightarrow Plotted against harvest year

Yield gap



Questions

- 1. Why plateauing of on-farm yields after year 2000?
- 2. Why large yield gap?

Results

		Grain yield (dt/ha)								
		Trend estimates				Prediction			gap	
		overall (t_{pk})			overall			trial - on-farm		
Туре	Int.	slope\varphi_1	slope	ρ_2	§	1985	2016	diff.	1985	2016
Hyb	2	1.24	1.03	*	ns	71.1	100.2	29.1	27.3	44.5
Pop	2	0.90	0.60	ns	*	64.5	83.1	18.6	20.6	27.4
on-farm	-	0.38	-			43.8	55.7	11.9	-	-

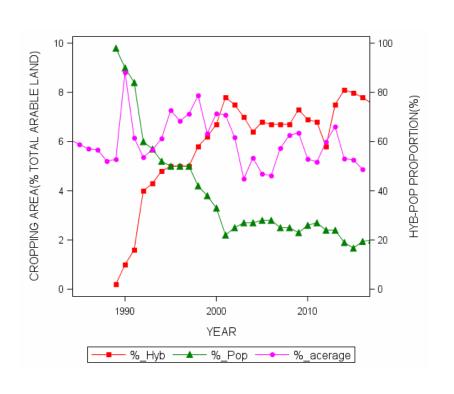
Denmark 58 dt ha⁻¹

§ Test of deviation from unique overall trend

Significance levels

- * 5%
- ** 1%
- *** 0.1%

1. Why plateauing of on-farm yields after year 2000?

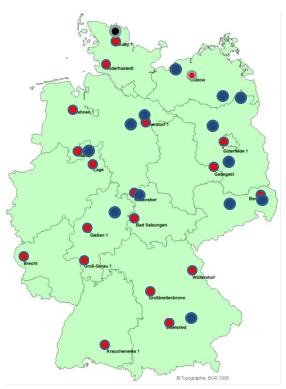


⇒ Transition to higher yielding hybrid varieties completed after year 2000

2. Why large yield gap between trials and on-farm yield?

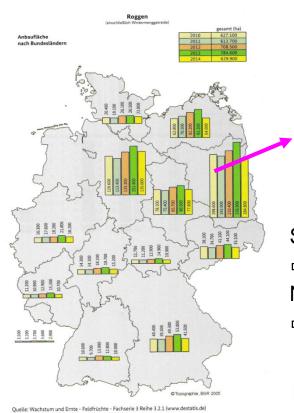
VCU trial sites 2016

Soil quality (Ackerzahl) 45 - 50



VCU 1: 1st testing year
 VCU 2: 2nd and 3rd testing year
 Słupia Wielka, 28 June 2018

On-farm cropping area by federal states 2016



30 % of national acerage Pop 39% (national average 20%)

Site conditions (soil fertility)

 \Rightarrow trials > on-farm

Not full yield potential on-farm

⇒Economic yield optimum



5. Conclusions

- Genetic trends for hybrids ∼ three times of population varieties
- Change in N rate in 2005 ⇒ two non-genetic regression functions
- Genetic and non-genetic trends ⇒ biased due to age effect
- On-farm yield level $\sim \frac{1}{2}$ of hybrids in trials
- Widening yield gap between on-farm and trials
- Gaps caused mainly by better growing conditions at trial sites and by economical factors

References

Laidig F, Piepho HP Rentel D, Drobek T, Meyer U, Huesken A (2017) Breeding progress, variation, and correlation of grain and quality traits in winter rye hybrid and population varieties and national on-farm progress in Germany over 26 years. Theor Appl Genet 130:981–998

Mackay IJ, Horwell A, Garner J, White J, McKee J, Philpott H (2011) Reanalysis of the historical series of UK variety trials to quantify the contributions of genetic and environmental factors to trends and variability in yield over time. Theor Appl Genet 122:225–238

Piepho HP, Laidig F, Drobek T, Meyer U (2014) Dissecting genetic and non-genetic sources of long-term yield in German official variety trials. Theor Appl Genet 127:1009-1018

Rijk B, van Ittersum M, Withagen J (2013) Genetic progress in Dutch crop yields. Field Crops Research 149:262–268