

Breeding progress of nitrogen use efficiency of cereal crops, and winter oilseed rape in long-term variety trials

Friedrich Laidig
Biostatistics Unit
Institute of Crop Science
University of Hohenheim

Joint work with

Hans-Peter Piepho, University of Hohenheim, Stuttgart
Till Feike, Federal Research Center for Cultivated Plants, Kleinmachnow
Caroline Lichthardt, Federal Plant Variety Office (Bundessortenamt), Hannover
Antje Schierholt, Georg-August-University, Göttingen







Overview

- Background
- Trials
- Key questions
- Overall trend and breeding progress
- Genotypic, environmental and G 🛽 E variation
- Genotypic, environmental and G 🛽 E correlation
- Heritability of variety means over testing period
- Conclusions

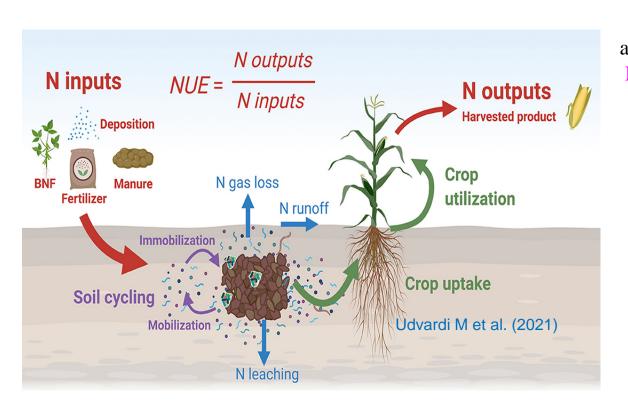


Background (1)

- Introduction of growth control chemicals and short straw (rh) genotypes allowed for higher N fertilizaten rates
- Adverse environmental impact increased with more intensive cropping systems
- About 208 kg total N per ha used in agricultural land in Germany,, output of N with the harvested crops accounts for 67% (139 kg N per ha), resulting in a considerable budget surplus of 33% (69 kg N per ha) (BMEL 2022)
- EU policy measures (Farm-to-Fork Strategy 2020): reduction of N surplus by 50% and N fertilizer use by 20% until 2030
- Increasing world population (about 10 Billion until 2050) 🗈 increasing global demand for food and non-food agricultural products
- Improved varieties with higher yield and quality with less nitrogen use are needed, i. e. higher nitrogen use efficiency (NUE)

Background (2)

Nitrogen use efficiency (NUE), a complex and dynamic process during yield building Interaction between soil, environment, plant and crop management



N inputs
available N =
N fertilization rate + Nmin)

Outputs

Grain yield, N yield (N accumulated in grain)

Nitrogen use efficiency NUE=(N) Yield/ available N



Key questions

- Was breeding progress achieved for NUE and related traits in registration trials?
- How large is the evironmental impact on variation of NUE compared to the genotypic?
- How closely linked is grain yield (GYLD) and grain protein concentration (GPC) with grain nitrogen yield (NYLD)?
- Is there a potential to improve NUE in registration trials?



Trials (1)

- Trials were treated according to crops good local agronomic practice (N, P, K, fungicides growth regulators, pesticides)
- All varieties of a trial received identical treatment, one N-level per trial
- Trial data assessed 1983 2021
 - Total N application rates (N fertilization rate kg ha⁻¹)
 - Soil mineralized N (Nmin kg ha⁻¹)
 - Soil fertility points (0 sand, 120 best soil)
 - Pre-crops (cereals, mais, foliage, legumes)
- Testing period 3 years (testing cycle)
- One to three trial series per year (S1, S2, S3 varieties in first, second and third testing year), Spring wheat (all varieties in one series)







Trials (2)

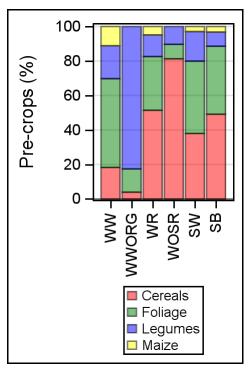
	First	Obser-	No. of	No. of	
Crop	Code	year	vations	trials	varieties
Winter wheat	WW	1983	25290	897	852
Winter wheat organic§	WWORG [§]	2013	842	69	31
Winter rye hybrid varieties	WR Hyb	1989	7712	569	244
Spring wheat	SW	1983	9546	640	155
Spring barley	SB	1983	18619	836	738
Winter oil seed rape	WOSR	1995	25655	696	797

[§] Winter wheat under organic testing regimen

Trials (3)



Pre-crops

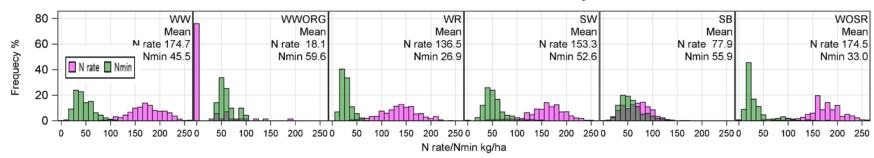


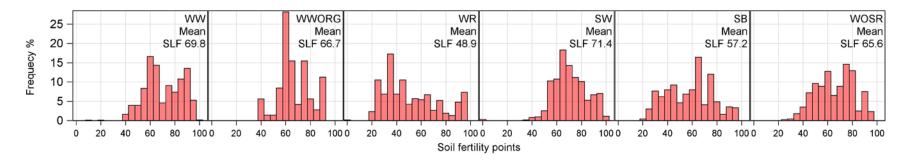
WW Winter wheat; WWORG Winter wheat organic; WR Winter rye, Hyb hybrid varieties; SW spring wheat;

Trials (4)



N fertilization rates, Nmin and soil fertilty





WW Winter wheat;; WR Winter rye, Hyb hybrid varieties; SW spring wheat; SB Spring barley; WOSR Winter oil seed rape; ORG organic SLF Soil fertility points

Trials (5)

Prediction of Nmin by BLUP from data 2019 – 2021 using a backward model selection procedure

$$y_{jkl} = \mu + (CP)_{im} + \delta_m a_{jkl} + \eta_i c_{jkl} + L_j + Y_k + (LYT)_{jkl}$$
 (1)

observed Nmin per location j, year k and trial l y_{ikl} $(CP)_{im}$ trial categorical effect for crop i and pre-crop m covariable soil fertility points a_{jkl} covariable N rate c_{jkl} random effect location Y_k random effect year $(LYT)_{jkl}$ random effect residual error

Coefficient of determination $R^2=41.5\%$

Overall trend and breeding progress (1)

Basic model

$$y_{ijkl} = \mu + G_i + Y_k + L_j + LYT_{jkl} + (GL)_{ij} + (GY)_{ik} + \epsilon_{ijkl}$$
 (2)

 y_{ijkl} variety 2 location 2 year 2 trial G_i genotype L_i location

 Y_k year

 LYT_{jkl} trial within location and year

 $(GL)_{ij}$ G \square L interaction

 $(GY)_{ik}$ G \square Y interaction

 ϵ_{ijkl} residual error

NUE and related traits

- Grain yield (GYLD) dt ha⁻¹
- Grain protein concentration (GPC) %
- N yield (NYLD) kg N ha⁻¹ (derived from GYLD and N concentration

converted from GPC)

- NUE of
 - N yield (NYLD_{NUE}) kg N in grain per kg available N (N fertilization rate +Nmin)
 - grain yield (GYLD_{NUE}) kg grain per kg available N

Overall trend and breeding progress (2)

Overall model

Let genotypes be confounded with years, then effects G_i and $(GL)_{ij}$ not nested within years are dropped in the basic model

$$y_{ijkl} = \mu + Y_k + L_j + (LYT)_{jkl} + (GY)_{ik} + \epsilon_{ijkl}$$

Overall model

$$y_{ijkl} = \mu + \alpha_1 t_k + \alpha_2 t_k^2 + Y_k' + L_j + (LYT)_{jkl} + (GY)_{ik} + \epsilon_{ijkl}$$
(3)

$$E(y_{ijkl}) = \mu + \alpha_1 t_k + \alpha_2 t_k^2.$$

Overall trend function

Overall breeding progress

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y_{ijkl} variety 2 location 2 year 2 trial observation
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 Y_k location year

 t_k harvest year

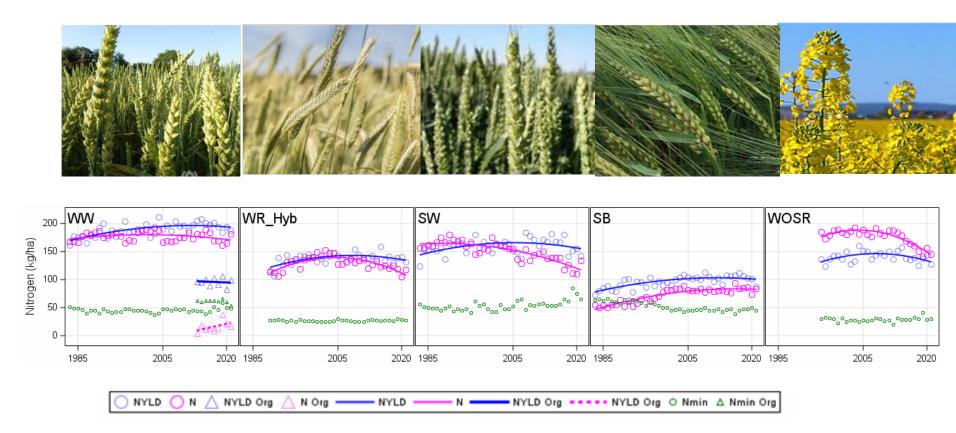
 Y_k deviation from overall trend, t_k harvest year

 LYT_{jkl} trial within location and year

 $(GY)_{ik}$ G \mathbb{Z} Y interaction

 ϵ_{ijkl} residual error

Overall breeding progress (1995 - 2021) (1)



WW Winter wheat;; WR Winter rye, Hyb hybrid varieties; SW spring wheat; SB Spring barley; WOSR Winter oil seed rape; SLF Soil fertility points

NYLD nitrogen yield; Nmin soil mineralized nitrogen; Org organic wheat;

Overall breeding progress (1995-2021) (4)

		N yield	l ko l	-1 na	N kg ha ⁻¹					
Crop	1995	2021		%	sig	1995	2021		%	sig
Winter wheat	187.4	194.0	6.6	3.5	ns	180.3	170.0	-10.3	-5.7	ns
Winter rye Hyb	134.1	135.1	1.1	0.8	ns	130.4	107.8	-22.6	-17.4	***
Spring wheat	160.9	155.0	-5.9	-3.6	ns	164.6	111.2	-53.4	-32.4	***
Spring barley	94.3	102.3	8.0	8.5	*	67.2	78.5	11.3	16.8	**
Winter oil seed rape	131.4	131.6	0.1	0.1	ns	176.9	143.5	-33.4	-18.9	***
	Gra	ain pro	tein c	onc. %	G	Frain y	ield dt	ha ⁻¹		
	1995	2021	Diff	%	sig	1995	2021		%	sig
Winter wheat	13.1	12.5	-0.6	-4.4	**	95.4	103.3	7.9	8.3	**
Winter rye Hyb	10.5	9.3	-1.2	-11.2	***	84.9	96.6	11.6	13.7	**
Spring wheat	14.0	13.9	0.0	-0.2	ns	76.8	74.4	-2.3	-3.0	ns
Spring barley	10.8	10.3	-0.5	-4.5	ns	64.0	72.4	8.4	13.2	**
Winter oil seed rape	18.8	17.4	-1.4	-7.6	**	44.8	48.6	3.8	8.5	*
	NUI	E of N	yield	kg kg	-1	NUE of Grain yield kg kg				
	1995	2021	Diff	%	sig	1995	2021		%	sig
Winter wheat	0.85	0.91	0.06	7.3	*	43.0	48.3	5.2	12.2	***
Winter rye Hyb	0.89	1.00	0.11	11.9	ns	56.4	71.6	15.2	27.0	***
Spring wheat	0.76	0.88	0.12	16.0	*	36.2	42.4	6.2	17.1	*
Spring barley	0.76	0.83	0.07	8.7	ns	51.9	59.0	7.2	13.9	*
Winter oil seed rape	0.66	0.77	0.12	17.9	***	20.9	27.3	6.4	30.8	***

Cosiderable progress for NUE achieved in registration trials despite N fertilizer reduction

ns not significant

* signifcant a 5%-level

** signifcant a 5%-level

*** signifcant a 5%-level

Genotypic, environmental and G E variation (1)

Basic model

$$y_{ijkl} = \mu + G_i + Y_k + L_j + LYT_{jkl} + (GL)_{ij} + (GY)_{ik} + \epsilon_{ijkl}$$

Extended model

$$y_{ijkl} = \mu + \beta r_i + G'_i + \gamma_1 t_k + \gamma_2 t_k^2 + Y'_k + L_j + LYT_{jkl} + (GL)_{ij} + (GY)_{ik} + \epsilon_{ijkl}$$
(4) genetic trend non-genetic trend
$$r_i \text{ first trial year of variety i} t_k \text{ harvest year k}$$

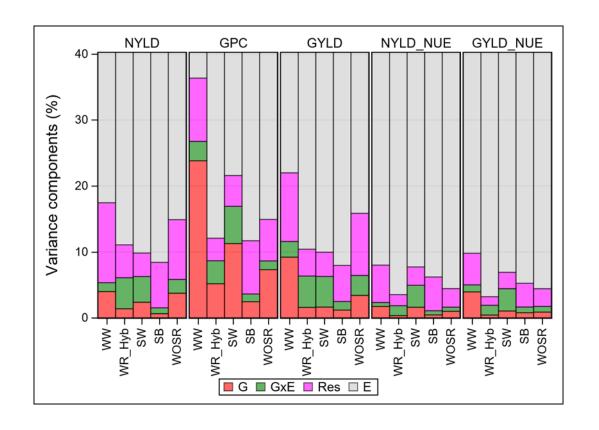
Variance components

Genotypic
$$\sigma_{G'}^2$$

Environmental $\sigma_E^2 = \sigma_L^2 + \sigma_{Y'}^2 + \sigma_{LTY'}^2$
G \boxtimes E $\sigma_{G'E}^2 = \sigma_{G'L}^2 + \sigma_{G'Y'}^2$
Residual σ_{ϵ}^2
Marginal $\sigma_M^2 = \sigma_{G'}^2 + \sigma_E^2 + \sigma_{G'E}^2 + \sigma_{\epsilon}^2$

Genotypic, environmental and G 🛽 E variation

Genotypic, environmental and G 2 E variation as per cent of total variation



Environmental variation is extremely dominating over genotypic variation

WW Winter wheat;; WR Winter rye, Hyb hybrid varieties; SW spring wheat; SB Spring barley; WOSR Winter oil seed rape; NYLD Nitrogen yield in grain; GPC Grain protein concentration; GYLD Grain yield; $NYLD_NUE$ ($GYLD_{NUE}$) Nitrogen fertilizer use efficiency of nitrogen yield; $GYLD_NUE$ ($GYLD_{NUE}$) Nitrogen fertilizer use efficiency of grain yield; G Genotype; G Genotype G Genotype G environment; G Environment;

Genotypic, environmental, and G E correlation (1)

Decomposition of the correlation between two traits (U, V) due to the random effects of the extended model

$$y_{ijkl} = \mu + \beta r_i + G'_i + \gamma_1 t_k + \gamma_2 t_k^2 + Y'_k + L_j + LYT_{jkl} + (GL)_{ij} + (GY)_{ik} + \epsilon_{ijkl}$$
 (4) by a univariate approach (Piepho et al. 2014)

- 1. Computing variance components of random effects according to the extended model for trait U and V and for the difference U V between both traits.
- 2. Computing covariances between the random effects of trait U and V from variance components by using the equation $var(U-V) = var(U) + var(V) \cdot 2cov(U,V) \cdot$
- 3. $r_{UV} = cov(U, V) / \sqrt{var(U)var(V)}$

Genotypic, environmental, and G 🗈 E correlation (2)

Correlation coefficients	Calculated by
Genotypic correlation	r_G variance and covariance of G_i
Environmental correlation	r_E sum of variances and covariances of L_J , Y_k and $(LYT)_{jkl}$
GPE correlation	r_{GZE} sum of variances and covariances of $(GL)_{ij}$ and $(GY)_{ik}$
Residual correlation	$r_{\mathbb{Z}}$ variance and covariance of ϵ_{ijkl}
Marginal correlation	r_M sum of variances and covariances over all individual random
	effects of the extended model

Genotypic, environmental, and G E correlation (3)

		WW	WR	WOSR	SW	SB	Mean	
			Hyb					
Observations	n	19089	4730	25524	3867	13318		
Genotypes	n_{G}	682	212	797	108	543		
	r_G	0.28	0.08	0.68	0.40	0.32	0.35	
	r_{GxE}	0.76	0.81	0.36	0.88	0.75	0.71	
NYLD GYLD	r_E	0.84	0.76	0.86	0.90	0.79	0.83	
	re	0.79	0.74	0.54	0.84	0.70	0.72	
	r_{M}	0.79	0.75	0.81	0.89	0.78	0.80	
NYLD GPC	r_G	0.33	0.68	0.62	0.66	0.45	0.55	
	r_{GxE}	0.13	0.29	-0.02	-0.20	0.20	0.08	
	r_E	0.26	0.38	0.40	0.14	0.47	0.33	
	re	0.35	0.48	0.33	0.19	0.58	0.38	
	r_{M}	0.26	0.39	0.40	0.16	0.47	0.34	
	r_G	-0.81	-0.69	-0.21	-0.42	-0.70	-0.57	
GYLD GPC	r_{GxE}	-0.52	-0.28	-0.16	-0.61	-0.45	-0.40	
	r_E	-0.31	-0.31	-0.11	-0.28	-0.15	-0.23	
	r _e	-0.25	-0.12	-0.09	-0.34	-0.10	-0.18	
	r_{M}	-0.38	-0.31	-0.11	-0.30	-0.16	-0.25	

- Nitrogen yield is stronger correlated with grain yield than with protein concentration
- Selection for higher nitrogen yield does not counteract with selection for higher grain yield and protein concentration

WW Winter wheat;; WR Winter rye, Hyb hybrid varieties; SW spring wheat; SB Spring barley; WOSR Winter oil seed rape; NYLD Nitrogen yield in grain; GPC Grain protein concentration; GYLD Grain yield; n Number of observations; n_G Number of genotypes G Genotype; \mathbb{Z} Residual; $G \mathbb{Z}E$ Genotype \mathbb{Z} environment; E Environment; E Environment

Genotypic, environmental, and G E correlation (4)

		WW	WR Hyb	SW	SB	WOSR	Mean
Observations Genotypes	n n_G	19089 682	4730 212	3867 108	13318 543	21564 797	
and any the	r_G	1.00	1.01	1.00	1.00	1.00	1.00
NYLD	r_{GxE}	0.98	1.00	0.98	0.99	0.93	0.98
with	r_E	0.59	0.42	0.68	0.83	0.33	0.57
$NYLD_{NUE}$	r _e	0.98	0.89	0.98	0.99	0.92	0.95
	r_{M}	0.63	0.44	0.70	0.84	0.37	0.60
	r_G	1.00	0.99	1.00	1.00	1.00	1.00
GYLD	r_{GXE}	0.97	0.96	0.99	0.99	0.96	0.97
with	r_E	0.61	0.41	0.71	0.80	0.30	0.57
$GYLD_{NUE}$	<i>r</i> e	0.98	0.93	0.98	0.99	0.92	0.96
	r_M	0.65	0.44	0.73	0.81	0.35	0.60

Rank of genotypic values for varieties of grain and nitrogen yield is the same as rank of NUE

(Laidig et al. 2024)

WW Winter wheat;; WR Winter rye, Hyb hybrid varieties; SW spring wheat; SB Spring barley; WOSR Winter oil seed rape; NYLD Nitrogen yield in grain; GYLD Grain yield; $NYLD_NUE$ ($GYLD_{NUE}$) Nitrogen fertilizer use efficiency of nitrogen yield; $GYLD_NUE$ ($GYLD_{NUE}$) Nitrogen fertilizer use efficiency of grain yield; n Number of observations; n_G Number of genotypes G Genotype; G Genotype; G Genotype G Genotype G Genotype G Residual; G G Genotype G Geno

Genotypic, environmental, and G 2 E correlation (4)

Proof that $r_G abla 1$ and $r_{GDE} abla 1$ (Laidig et. al. 2024)

Consider two random variables Wij and Uij = Wij/Nj, where Wij = grain yield of ith genotype in jth environment and Nj = nitrogen input in jth environment. For Wij, we assume the random-effects model $W_{ij} = \mu + G_i + L_j + GL_{ij}$ (1)

with independent random effects having zero mean and variances $var(G_i) = \sigma_G^2$, $var(L_j) = \sigma_L^2$ and $var(GL_{ij}) = \sigma_{GL}^2$. Here, we will investigate what can be said about the covariance of effects for Wij and Uij assuming model (1) for Wij. For simplicity, we will assume that Nj is independent of all effects in the model for Wij. This could be relaxed by assuming a covariance with Lj, but this is not expected to have any substantive bearing on the subsequent derivation, as will be explained briefly at the end. The model for Uij can be written as

$$U_{ij} = \frac{\mu + G_i + L_j + GL_{ij}}{N_j} = \mu'_j + G'_{ij} + L'_j + GL'_{ij} \quad (2)$$
where $\mu'_j = \frac{\mu}{N_j}$, $G'_{ij} = \frac{G_i}{N_j}$, $L'_j = \frac{L_j}{N_j}$ and $GL'_{ij} = \frac{GL_{ij}}{N_j}$.

A challenge in the subsequent derivation is that all effects in (2) involve the random variable *Nj*, hence we need to check if there are correlations among the effects. It will be useful to make use of the laws of total variance and total covariance (Rudary 2009). Let *X*, *Y* and *Z* be three random variables. Then the law of total variance states that

$$var(Y) = E[var(Y|X)] + var[E(Y|X)].$$

The law of total covariance states that

$$cov(X,Y) = E[cov(X,Y|Z)] + cov[E(X|Z), E(Y|Z)].$$

Proof that r_G 2 1 and r_{GME} 2 1 (Laidig et. al. 2023)

continued

If we identify Z with Nj, and X and Y with any of the two effects in (2), then it emerges from the law of total covariance that the effects in (2) must all be uncorrelated from one another. For example, we find that

$$cov(G'_{ij}, L'_{j}) = E[cov(G'_{ij}, L'_{j}|N_{j})] + cov[E(G'_{ij}|N_{j}), E(L'_{j}|N_{j})] = E\left[\frac{1}{N_{j}^{2}}cov(G_{i}, L_{j})\right] + cov[0,0] = 0$$

Before we consider covariances among effects for W_{ij} and U_{ij} , we need to transition (2) into a model of the same form as (1). To do so, we may define

$$\mu_j' = \mu'' + F_j'',$$

where $\mu'' = E(\mu'_i)$ and $F''_i = \mu'_i - \mu''$. Similarly, we define

$$G'_{ij} = G''_i + H''_{ij},$$

where $G_i'' = E(G_{ij}'|G_i)$ and $H_{ij}'' = G_{ij}' - E(G_{ij}'|G_i)$. With these definitions, we can rewrite (2) as

$$W_{ij} = \mu'' + G_i'' + L_j'' + GL_{ij}'', \tag{3}$$

where $L''_{ij} = L'_{ij} + F''_{ij}$ and $GL''_{ij} = GL'_{ij} + H''_{ij}$.

Proof that $r_G \ 2 \ 1 \ \text{and} \ r_{G/\!\!\!/BE} \ 2 \ 1 \ \text{(Laidig et. al. 2023)}$

continued

With this reparameterization, we can now study covariances among effects between models (1) and (3), using the law of total covariance and the delta method (Johnson et al. 2003).

(i)
$$cov(G_i, G_i'') = E[cov(G_i, G_i'')|N_j] + cov[E(G_i|N_j), E(G_i''|N_j)] \approx \frac{\sigma_G^2}{\varphi_N}$$

(ii)
$$cov(L_j, L_j'') = E[cov(L_j, L_j'')|N_j] + cov[E(L_j|N_j), E(L_j''|N_j)] \approx \frac{\sigma_L^2}{\varphi_N}$$

(iii)
$$cov(GL_{ij}, GL_{ij}'') = E[cov(GL_{ij}, GL_{ij}'')|N_j] + cov[E(GL_{ij}|N_j), E(GL_{ij}''|N_j)] \approx \frac{\sigma_{GL}^2}{\varphi_N}$$

where $\varphi_N = E(N_i)$. Similarly, the variances of the random effects in (3) can be approximated as follows:

(i)
$$var(G_i'') \approx \frac{[E(G_i)]^2}{\varphi_N^4} \sigma_N^2 + \frac{\sigma_G^2}{\varphi_N^2} = \frac{\sigma_G^2}{\varphi_N^2}$$

(ii)
$$var(L''_j) = var(L'_j + F''_j) \approx \frac{\sigma_L^2}{\varphi_N^2} + \frac{\mu^2 \sigma_N^2}{\varphi_N^4}$$

(iii)
$$var(GL''_{ij}) = var(GL'_{ij} + G'_{ij} - E(G'_{ij}|G_i)) \approx \frac{\sigma_{GL}^2}{\varphi_N^2} + var[G_i(\frac{1}{N_i} - \frac{1}{\varphi_N})] \approx \frac{\sigma_{GL}^2}{\varphi_N^2}$$

where $\sigma_N^2 = var(N_i)$. From these results, the correlations can be approximated as

(i)
$$corr(G_i, G_i'') \approx 1$$

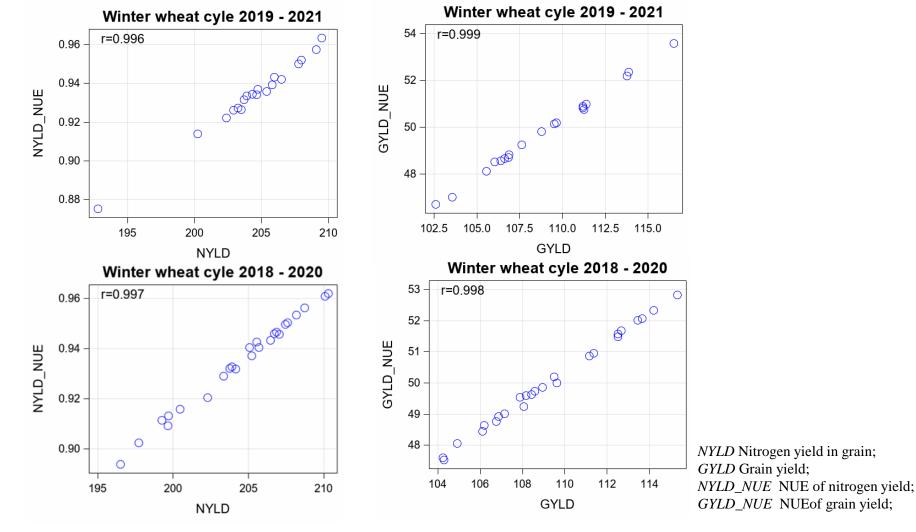
(ii)
$$corr(L_j, L_j'') \approx \frac{1}{\sqrt{\left(1 + \frac{\mu^2 \sigma_N^2}{\varphi_N^2 \sigma_L^2}\right)}} < 1$$

(iii)
$$corr(GL_{ij}, GL_{ij}'') \approx 1$$

As noted before, we have assumed here that L_j and N_j are uncorrelated. If a covariance is allowed, this will only affect the correlation $corr(L_j, L_j'')$, but it will still be the case that $corr(L_j, L_j'') < 1$.

Genotypic, environmental, and G E correlation (5)

Examples: Correlation between cycle means (LS means) of varieties





Heritability (1)

Broad sense heritability of 3-year cycle means

$$h^2 = \sigma_{G'}^2 / \left(\sigma_{G'}^2 + \frac{v_d}{2} \right), \tag{5}$$

where $\sigma_{G'}^2$ is the genotypic variance and v_d is the average variance of a difference between the BLUE-means of two varieties tested in the same 3-year cycle (Piepho & Möhring 2007).

Broader sense heritability of cycle means (3 years)

										NUE	of	
		Nι	ımbe	r of l	locatio	ons	NYLD	GPC	GYLD	NYLD (GYLD	
Crop	n	n_1	n_2	n_3	n ₁₂	n ₁₃	n ₂₃	H^2	H^2	H^2	H^2	H^2
Winter wheat	24	8	8	8	0	0	4	0.83	0.96	0.90	0.82	0.90
Winter rye Hyb	24	8	8	8	0	0	6	0.61	0.89	0.65	0.54	0.63
Spring wheat	21	7	7	7	5	6	5	0.74	0.90	0.62	0.69	0.59
Spring barley	23	8	8	7	0	0	3	0.57	0.78	0.72	0.56	0.72
Winter oil seed rape	36	9	13	14	0	1	7	0.85	0.94	0.80	0.84	0.79
Mean	25.7	7.9	8.8	8.9	1.0	1.4	5.0	0.72	0.89	0.74	0.69	0.73

N yield equally reliable as grain yield, should be given higher attention in registration trials

Since 2023, N yield of winter wheat varieties is reported as quality trait in the Descriptive Variety List

n Number of trials per cycle; n_1 , n_2 , n_3 number of locations in cycle year 1, 2 and 3; n_{12} , n_{13} , n_{23} overlapping locations NYLD Nitrogen yield in grain; GYLD Grain yield; GPC Grain protein concentration; NUE N use efficiency



Conclusions

- N fertilizer rate was considerably reduced in the last 26 years (in all crops except spring barley)
- Grain yield increased despite lower N fertilzer rates
- N accumulated in grain was not significantly reduced, despite reduced N fertilizer rates
- Considerable breeding progress achieved for NUE
- Rank order of genotypic values of varieties for grain and N yield is identical with NUE, i.e., selection for high grain and nitrogen yield is equivalent to high NUE
- Heritability of N yield is about as high as for grain yield, therefore N yield should be considered as additional criterion in registration trials

Literature

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