

## Multiplicative Main Cultivar Effects in Czech Official Winter Wheat Trials 1976–2005

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**Abstract:** 98 winter wheat cultivars, tested by the Czech Plant Variety Office in 554 trials between 1976 and 2005, were analysed for breeding progress, yielding capacity and behaviour in particular environments. The trials were grouped by yield level, years, altitude, precipitation, temperature and ecological regions. Within each group, least squares (LS) adjusted cultivar means and variance components were estimated. The cultivar means within groups were used as primary data for the subsequent analysis across groups. Genetic variance ( $V_g$ ) increased with increasing yield level while residual variance ( $V_r$ ) slightly decreased. Although  $V_g$  within groups was very different, phenotypic correlations between the cultivar means of the groups were very high. The cultivar yields, plotted against environment yield, followed a funnel-like distribution, expanding from the origin. The data fitted better to the assumption of multiplicative main cultivar effects than to the assumption of additive main cultivar effects, implied by standard models. Standardised relative yields (SRY), assuming multiplicative main cultivar effects on the original scale, were therefore used to analyse the data. The SRY were obtained by standardisation of cultivar means within trial groups to the variance expected from the cultivar means across the trial groups, subtraction of additive environment effects and division by the general mean. The SRY had a smaller relative error, as measured by the  $V_g/V_r$  relation, than cultivar means calculated under the assumption of additive main cultivar effects. The SRY were surprisingly consistent over environments.  $G \times E$  interactions, usually found under the assumption of additive main cultivar effects, may partly be artefacts of the assumption.

**Keywords:** trial series; cultivars; variance components; adaptation; multiplicative model

In a previous analysis, SCHWARZBACH & ATSMON (2004) studied empirically cultivars in diverse environments, using data from 353 official spring wheat trials from 1970 to 2002 in Israel. The trials were sorted by yield into several groups within which least squares (LS) adjusted cultivar means were calculated and variance components were estimated. Genetic variance was closely related to the yield level of the groups (Figure 1).

Although genetic variance in the highest yielding group was about ten times larger than in the lowest yielding group, the phenotypic correlations of cultivar means between the groups were very high, indicating multiplicative main effects of cultivars.

The genetic performance of cultivars was therefore described as relative cultivar yields (implying multiplicative cultivar effects), standardised to equal variance of cultivar means within the trial groups (SRY). The SRY had a considerably higher  $V_g/V_r$  ratio, compared with cultivar means obtained by standard techniques assuming additive cultivar effects. In Central Europe the trial yields differ less than in Israel and different environmental factors affect the yield. Therefore the question is, if in Central Europe the assumption of multiplicative main cultivar effects is also more realistic than that of additive main cultivar effects. If it is so, the use of SRY would be a useful, easy to calculate

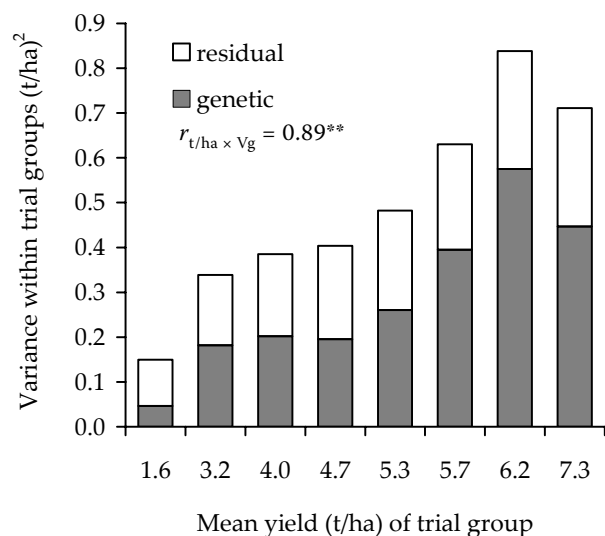


Figure 1. Genetic and residual variance of 353 wheat trials in Israel grouped by yield – after SCHWARZBACH and ATSMON (2004)

alternative for the evaluation of trial series, without the need of expensive software and experts to handle it. We therefore tried to evaluate winter wheat yield data from the Czech official trials, accumulated over 35 years, by means of SRY and the underlying multiplicative yield model.

## MATERIAL AND METHODS

We analysed data from Czech official winter wheat trials from 1976 to 2005. The series comprised 599 trials. Within years the cultivars were mostly tested orthogonally, on average at 17 locations. To assess the quality of trials, correlations of cultivar means within single trials and LS-adjusted

cultivar means (LS-means) across environments within each year were calculated. Most trials were well correlated with the yearly means, with  $r > 0.65$ . To reduce noise, trials with  $r < 0.26$  were disregarded and the remaining 554 trials were analysed. The distribution of correlation coefficients is given in Figure 2.

Since the tested cultivars changed during the years, the data over years were non-orthogonal. LS-adjusted cultivar means were calculated from non-orthogonal data, as suggested by PATTERSON (1997), using the linear model  $y_{ij} = a_i + b_j + r_{ij}$ . In this paper we assume that yields are arranged in a two-way table with columns = environments and rows = cultivars. To eliminate environment effects, the actual data were first standardised to the variance expected from the cultivar means across environments. In orthogonal situations, this was done by division of the column data by their standard deviation and multiplication by the standard deviation of the overall cultivar means. In non-orthogonal situations, the column data were divided by their standard deviation and multiplied by the standard deviation that would be expected if the actually present column data were replaced by the corresponding LS-adjusted row means. With the standardised data an LS analysis was performed and the column effects were subtracted from the data. The data, now largely free of multiplicative and additive environment effects, were then expressed relative to the general mean, to be presented in a format practical breeders are used to. The effects of converting raw yields into SRY are demonstrated on data from SCHWARZBACH and ATSMON (2004) in Figure 3.

To compare the accuracy of SRY, we used the ratio of genetic to residual variance ( $V_g/V_r$ ) as a measure, regarding the SRY as primary data for the estimation of variances. This does not contradict the assumption of multiplicative cultivar effects since RY behave additively, as seen in Figure 3b. Since the data were often non-orthogonal, we defined  $V_g$  as the variance of all genetic effects actually present in the data. To estimate  $V_g$  we calculated the variance of a data matrix in which all actually present primary data were replaced by the corresponding LS-adjusted cultivar means, and subtracted from it the properly weighted error of the LS-adjusted cultivar means. This procedure yielded in Monte Carlo simulations estimates very close to expectations. The  $V_g$  estimates deviate in unbalanced situations slightly from those obtained

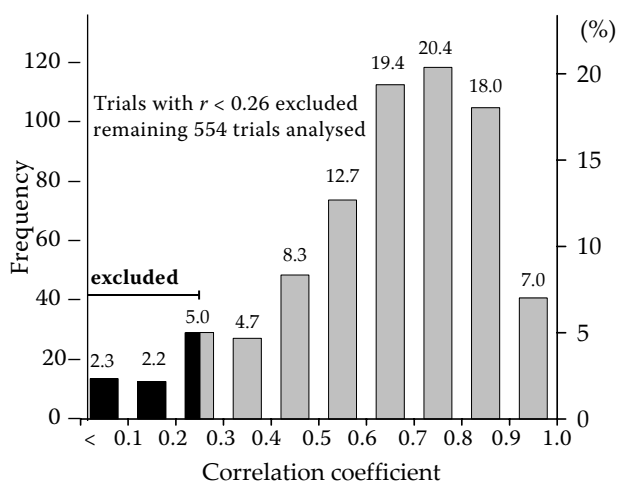


Figure 2. Correlation between cultivar yields in single trials and yearly averages in Czech official trials

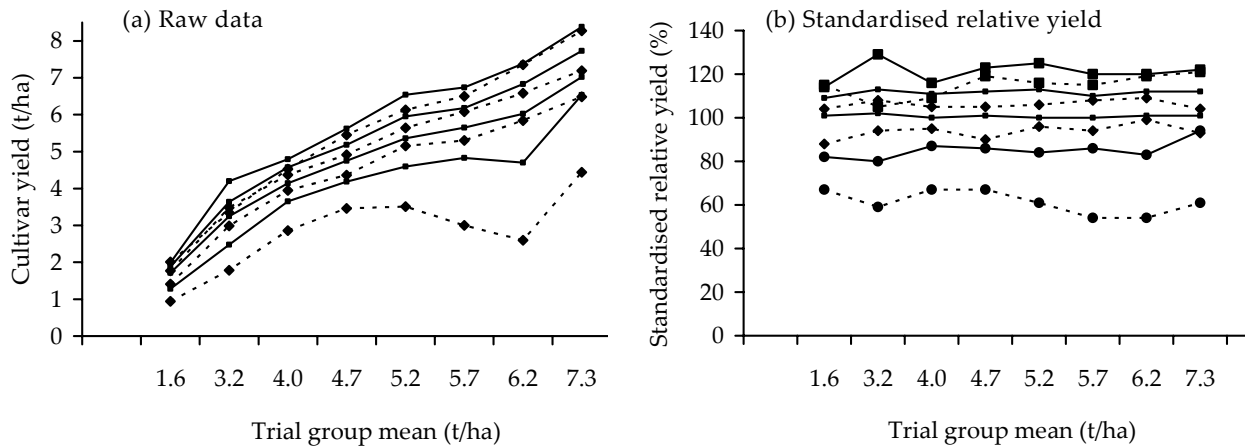


Figure 3. Yield of 8 cultivars at different yield level in Israel (after SCHWARZBACH & ATSMON 2004)

with standard statistical packages due to a different  $V_g$  definition. The SAS statistical package was used for the analysis of variance (ANOVA) and to fit the multiplicative model.

## RESULTS AND DISCUSSION

When yield data from the regional trials in Israel and from the Czech official trials were plotted against environment means, in both series the distribution was hardly a two-dimensional normal one, but looked rather funnel-like, expanding from the origin of the diagram (Figures 4 and 5).

A similar distribution can be observed in the data of FINLAY and WILKINSON (1963). The funnel-shaped distribution, seen also in Figure 3a,

should be expected with multiplicative cultivar effects and if  $V_g$  is correlated with the trial yield. The regression lines in both series went through the origin, as it should be, since negative yield is biologically impossible and at zero trial yield all cultivars must also have zero yield. The trials were sorted by yield into 6 groups of approximately 92 trials. Within groups LS-adjusted cultivar means were calculated and genetic and residual variances were estimated.

The estimated variance components are summarised in Figure 6.

$V_g$  was significantly correlated with yield, while  $V_r$  slightly decreased. The relation  $V_g/V_r$  increased approx. fourfold from the lowest to the highest yield group. The differentiation of cultivars was

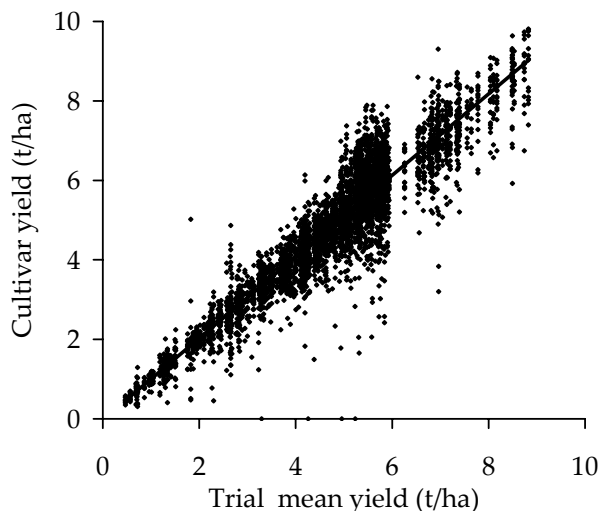


Figure 4. Cultivar yield and mean trial yield in 353 wheat trials in Israel

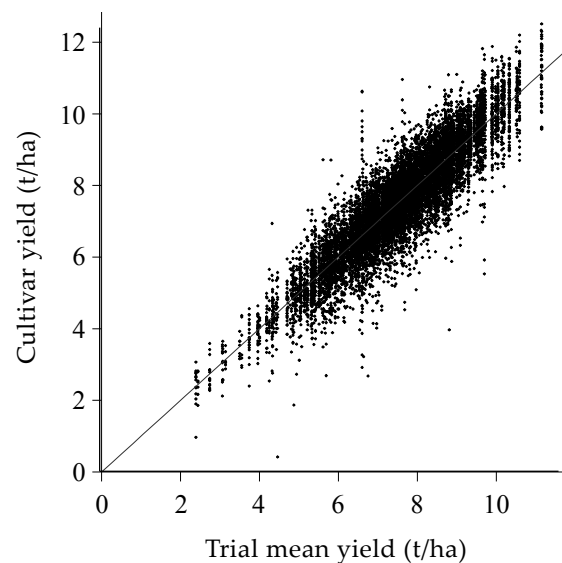


Figure 5. Cultivar yield and mean trial yield in 554 Czech official winter wheat trials

Table 1. Phenotypic correlations between LS-adjusted cultivar means within the six yield groups

| Yield<br>(t/ha) | G 1 | G 2  | G 3  | G 4  | G 5  | G 6  |
|-----------------|-----|------|------|------|------|------|
|                 | 5.2 | 6.4  | 7.1  | 7.7  | 8.3  | 9.3  |
| G 1             |     | 0.84 | 0.87 | 0.88 | 0.86 | 0.87 |
| G 2             |     |      | 0.90 | 0.89 | 0.87 | 0.87 |
| G 3             |     |      |      | 0.93 | 0.96 | 0.96 |
| G 4             |     |      |      |      | 0.93 | 0.96 |
| G 5             |     |      |      |      |      | 0.98 |

All correlation coefficients are significant at  $P = 0.01$

No significant differences between correlation coefficients

therefore much better at a high yield level than at a low yield level. Since phenotypic correlations of the LS-adjusted cultivar means between the groups were very high (average  $r = 0.904$ ) and the correlation coefficients did not differ significantly (see Table 1), the relationship between the cultivars remained basically the same, regardless of the yield level and the actual genetic variance.

The selection of superior cultivars therefore appears most efficient at a high yield level. The phenotypic correlations were also similarly high if the trials were grouped by other criteria, i.e. years, regions, altitude or temperature, as described in more detail elsewhere (SCHWARZBACH & HARTMANN 2007). The above findings indicate multiplicative main cultivar effects and justify the expression of cultivar performance in relative terms. The main effects of cultivars, disregarding non-linear interactions, can thus be symbolised visually by the heuristic model given in Figure 7.

The empirical findings suggest that the main effects of cultivars in this data set are multiplicative and that environment effects are both additive and multiplicative. This corresponds to the joint regression model  $y_{ij} = a_i b_j + e_j + r_{ij}$ , where  $y_{ij}$  denotes the yield of cultivar  $i$  in environment  $j$ ,  $a_i$  the multiplicative effect of cultivar  $i$ ,  $b_j$  the multiplicative effect of environment  $j$ ,  $e_j$  the additive effect of environment  $j$  and  $r_{ij}$  the residual effect.

Table 2. Summary of fitting the SRY model  $y_{ij} = a_i b_j + e_j + r_{ij}$  (excerpt from SAS output)

| Source          | Sum of squares | DF  | Mean square | $F$ value | approx pr > $F$ |
|-----------------|----------------|-----|-------------|-----------|-----------------|
| Model           | 518.24         | 62  | 8.36        | 318.27    | < 0.0001        |
| Error           | 6.6969         | 255 | 0.0263      |           |                 |
| Corrected total | 524.92         | 317 | 1.66        |           |                 |

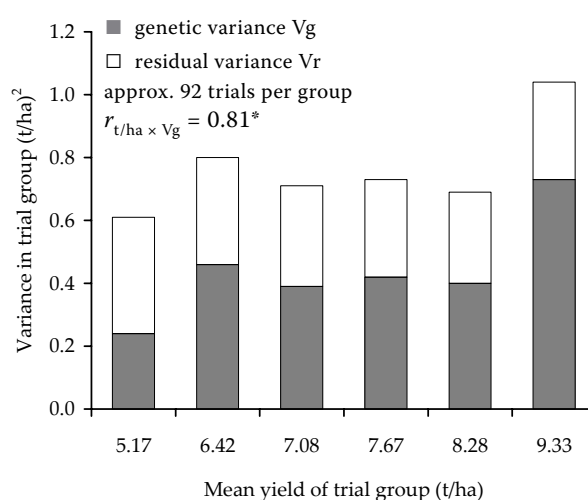


Figure 6. Genetic and residual variance in 554 Czech wheat trials grouped by yield

To test the model with minimum noise, we reduced the original data set to cultivars present at least ten times in each of the six trial groups. We fitted the joint regression model  $y_{ij} = a_i b_j + e_j + r_{ij}$  to the reduced data set as explained in the appendix. The results are summarised in Table 2.

To compare the above model with the standard additive model  $y_{ij} = a_i + b_j + r_{ij}$ , we performed a usual ANOVA on the reduced data set. The results are summarised in Table 3. Although the requirements for the analysis are not met (inhomogeneous variances and non-additivity according to the Tukey test with  $F = 82.2$ ), the error mean square of 0.042, almost twice that for the multiplicative model, confirms the better fit of the multiplicative model. For practical purposes the SRY, which are based on the above multiplicative model, offer a simple tool to evaluate trial series, without the need of expensive software and skilled experts, able to use it properly. The SRY can be calculated easily even with a pocket calculator and provide a straightforward, easily understandable information to the breeder. To give an impression how consistent and reproducible the standardised relative cultivar yields are, these are presented for the reduced data set in Table 4.

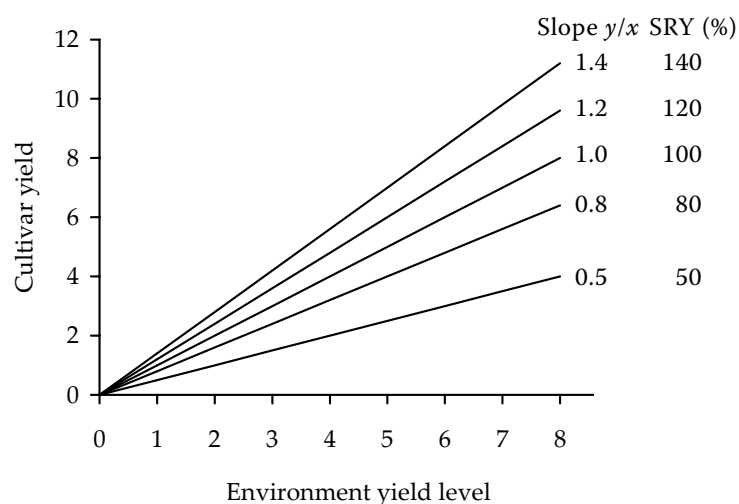


Figure 7. Graphical heuristic model of main cultivar effects

SRY = standardised relative yields

It is tempting to interpret fluctuations of SRY of individual cultivars in the table in terms of yield stability, using for example the ratio of variance within a cultivar to the residual variance of the remaining cultivars ( $F$ -test). This would identify cultivars with below or above average fluctuations. However, the error of variance estimates from a small number of data is enormous (PIEPHO 1998b). Considerably more data per cultivar would be necessary to obtain meaningful estimates. The fluctuations within the rows in Table 4 depend also on the number of trials per group of a given cultivar, which is not constant. We therefore give just the standard deviation within cultivars. This might indicate suspect cultivars which could then be compared in a balanced comparison in a maximum number of environments, which is not, however, within the intention of this paper.

Standardisation to equal variance of cultivar means substantially reduced the residual variance relative to  $V_g$  and thus improved the statistical separation of cultivars. The improvement is mainly due to the minimisation of interactions created in additive models as artefacts by the multiplicative behaviour of cultivars. The improvements, in terms of the  $V_g/V_r$  ratio, are summarised in Table 5.

SRY are very suitable to visualise breeding progress, especially periods of stagnation or sud-

den shifts to another level of performance. In Figure 8 the breeding progress, observed in the Czech official trials, is visualised. In the graph the performance of the top three cultivars in each year is represented by their SRY, calculated from all available data.

YAU and HAMBLIN (1994) used yields relative to the environment mean to measure cultivar performance and adaptation in an orthogonal trial series with very large differences in the mean trial yield. It could be shown (SCHWARZBACH *et al.* 2007) that the obvious advantages of relative yields in these series were partly offset by the errors of the trial means and additive effects of environments. In unbalanced trial series the error is still higher since the trial means depend also on the tested entries. Standardisation, as described above, removed these problems. The question remains if the SRY are superior also over measuring cultivar performance according to more advanced statistical models, such as the regression model of FINLAY and WILKINSON (1963), the AMMI (additive main and multiplicative interactions) model (GOLLOB 1968; GAUCH 1988; VAN EEUWIJK *et al.* 2004) and its further extensions, for example by PIEPHO (1997, 1998a). These models have in common additive main effects of cultivars and split the residual term of the linear model into one or more

Table 3. ANOVA for the additive model  $y_{ij} = a_i + b_j + r_{ij}$  (excerpt from SAS output rounded to 2 digits)

| Source          | Sum of squares | DF  | Mean square | $F$ value |
|-----------------|----------------|-----|-------------|-----------|
| Cultivar        | 114.29         | 52  | 2.20        | 52.34     |
| Environment     | 399.71         | 5   | 79.94       | 1903.77   |
| Error           | 10.92          | 260 | 0.0419      |           |
| Corrected total | 524.92         | 317 | 1.66        |           |

Table 4. Standardised relative cultivar yields in groups of trials sorted by yield

| Group mean (t/ha) | 5.17  | 6.42  | 7.08  | 7.67  | 8.28  | 9.33  | s    | Mean   |
|-------------------|-------|-------|-------|-------|-------|-------|------|--------|
| Apache            | 108.1 | 116.1 | 115.2 | 112.5 | 114.9 | 111.3 | 2.02 | 114.36 |
| Corsaire          | 108.1 | 117.6 | 113.7 | 110.5 | 112.9 | 111.6 | 2.59 | 113.62 |
| Vlasta            | 106.9 | 111.1 | 112.9 | 115.3 | 112.6 | 111.8 | 1.43 | 112.83 |
| Complet           | 105.8 | 112.0 | 111.0 | 114.1 | 114.9 | 112.1 | 1.56 | 112.58 |
| Rialto            | 106.4 | 111.8 | 115.8 | 113.0 | 113.2 | 111.6 | 2.41 | 112.29 |
| Semper            | 98.5  | 113.4 | 110.5 | 112.8 | 110.0 | 112.6 | 1.45 | 111.62 |
| Ludwig            | 101.7 | 112.4 | 113.1 | 112.2 | 108.4 | 108.0 | 2.28 | 111.09 |
| Drifter           | 102.1 | 108.2 | 108.5 | 114.2 | 112.4 | 113.4 | 3.37 | 110.42 |
| Estica            | 101.9 | 109.2 | 109.8 | 106.5 | 110.0 | 109.5 | 1.86 | 109.55 |
| Sarka             | 96.5  | 110.1 | 107.9 | 108.6 | 107.0 | 105.4 | 2.28 | 108.47 |
| Alana             | 102.5 | 108.8 | 102.5 | 106.7 | 103.6 | 106.2 | 3.05 | 106.41 |
| Versailles        | 102.5 | 105.4 | 104.8 | 103.9 | 109.8 | 106.0 | 2.08 | 106.11 |
| Siria             | 104.9 | 105.7 | 104.3 | 104.0 | 106.2 | 105.7 | 1.45 | 105.67 |
| Nela              | 99.8  | 107.8 | 104.6 | 105.3 | 104.2 | 104.9 | 1.41 | 105.64 |
| Trane             | 101.0 | 106.7 | 106.4 | 104.8 | 101.6 | 103.8 | 1.92 | 104.86 |
| Samara            | 93.9  | 104.6 | 98.0  | 105.3 | 103.5 | 103.8 | 2.92 | 103.60 |
| Astella           | 97.2  | 100.4 | 109.3 | 102.2 | 102.9 | 105.8 | 3.87 | 103.18 |
| Ina               | 97.0  | 103.8 | 102.1 | 105.3 | 100.3 | 104.8 | 1.96 | 103.02 |
| Torysa            | 98.9  | 104.3 | 103.6 | 104.0 | 103.3 | 100.3 | 1.52 | 102.94 |
| Ebi               | 98.5  | 106.3 | 99.5  | 104.8 | 100.9 | 103.0 | 2.51 | 102.73 |
| Sida              | 97.0  | 101.4 | 105.4 | 103.9 | 104.2 | 103.6 | 3.22 | 102.49 |
| Alka              | 98.4  | 101.2 | 103.0 | 101.9 | 100.9 | 101.0 | 0.85 | 101.74 |
| Samanta           | 92.6  | 100.4 | 101.6 | 101.8 | 101.2 | 101.5 | 0.69 | 101.49 |
| Rexia             | 106.0 | 96.8  | 103.1 | 96.2  | 101.9 | 101.4 | 3.50 | 100.72 |
| Asta              | 96.9  | 104.6 | 97.0  | 95.1  | 101.2 | 103.4 | 3.65 | 100.18 |
| Sulamit           | 93.9  | 101.8 | 97.4  | 102.5 | 98.7  | 99.5  | 1.95 | 100.18 |
| Blava             | 94.4  | 97.1  | 101.6 | 101.5 | 102.8 | 101.1 | 3.43 | 99.67  |
| Ilona             | 96.5  | 97.1  | 100.3 | 99.2  | 100.3 | 101.7 | 1.83 | 99.32  |
| Simona            | 100.6 | 98.8  | 99.2  | 99.4  | 99.5  | 99.6  | 0.96 | 98.92  |
| Saskia            | 86.6  | 99.4  | 98.0  | 100.2 | 97.9  | 98.4  | 0.88 | 98.79  |
| Bruta             | 93.9  | 98.5  | 97.7  | 99.6  | 97.9  | 98.9  | 0.70 | 98.53  |
| Sparta            | 95.7  | 96.0  | 98.9  | 98.8  | 100.0 | 100.0 | 1.61 | 98.47  |
| Boka              | 88.8  | 96.7  | 100.0 | 97.1  | 98.0  | 100.7 | 1.59 | 98.47  |
| Iris              | 92.2  | 95.8  | 98.9  | 98.0  | 101.6 | 100.2 | 3.25 | 97.85  |
| Zdar              | 92.2  | 97.9  | 98.0  | 95.3  | 94.8  | 95.1  | 4.24 | 97.85  |
| Sofia             | 90.9  | 94.2  | 100.0 | 96.3  | 99.0  | 97.1  | 2.06 | 97.23  |
| Selekta           | 89.4  | 96.4  | 97.0  | 96.1  | 98.9  | 97.2  | 1.64 | 96.56  |
| Vega              | 90.3  | 94.8  | 94.4  | 98.7  | 97.0  | 98.3  | 1.98 | 96.28  |
| Brea              | 89.6  | 94.8  | 97.0  | 96.8  | 94.4  | 98.0  | 1.38 | 96.25  |
| Regina            | 89.4  | 96.4  | 94.7  | 94.7  | 92.1  | 92.6  | 3.08 | 95.19  |
| Mona              | 82.5  | 95.8  | 97.9  | 95.9  | 96.3  | 96.6  | 4.11 | 94.85  |
| Viginta           | 82.9  | 93.4  | 93.4  | 94.2  | 95.6  | 94.2  | 0.80 | 94.11  |
| Hana              | 95.7  | 93.4  | 94.9  | 92.1  | 92.7  | 93.8  | 1.36 | 93.77  |
| Vala              | 88.8  | 92.1  | 92.5  | 91.9  | 94.3  | 92.8  | 1.79 | 92.06  |
| Slavia            | 92.2  | 91.6  | 92.3  | 92.7  | 92.0  | 91.2  | 0.54 | 92.00  |
| Vlada             | 92.2  | 89.6  | 91.3  | 90.0  | 94.7  | 94.1  | 2.12 | 91.97  |
| Odra              | 90.9  | 91.2  | 92.0  | 90.9  | 91.4  | 91.2  | 0.42 | 91.27  |
| Mara              | 89.4  | 89.5  | 88.0  | 90.0  | 90.4  | 90.9  | 1.02 | 89.68  |
| Roxana            | 90.3  | 87.2  | 87.8  | 89.2  | 90.2  | 88.5  | 1.26 | 88.88  |
| Hela              | 89.6  | 88.5  | 88.7  | 88.4  | 87.8  | 88.7  | 0.59 | 88.61  |
| Kosutka           | 89.4  | 86.7  | 89.5  | 88.2  | 87.6  | 88.6  | 1.05 | 88.35  |
| Iljicovka         | 82.5  | 84.6  | 79.4  | 81.1  | 78.3  | 77.9  | 2.62 | 80.63  |
| Mironovskaja      | 82.9  | 80.8  | 75.6  | 76.3  | 73.9  | 70.4  | 4.56 | 76.65  |

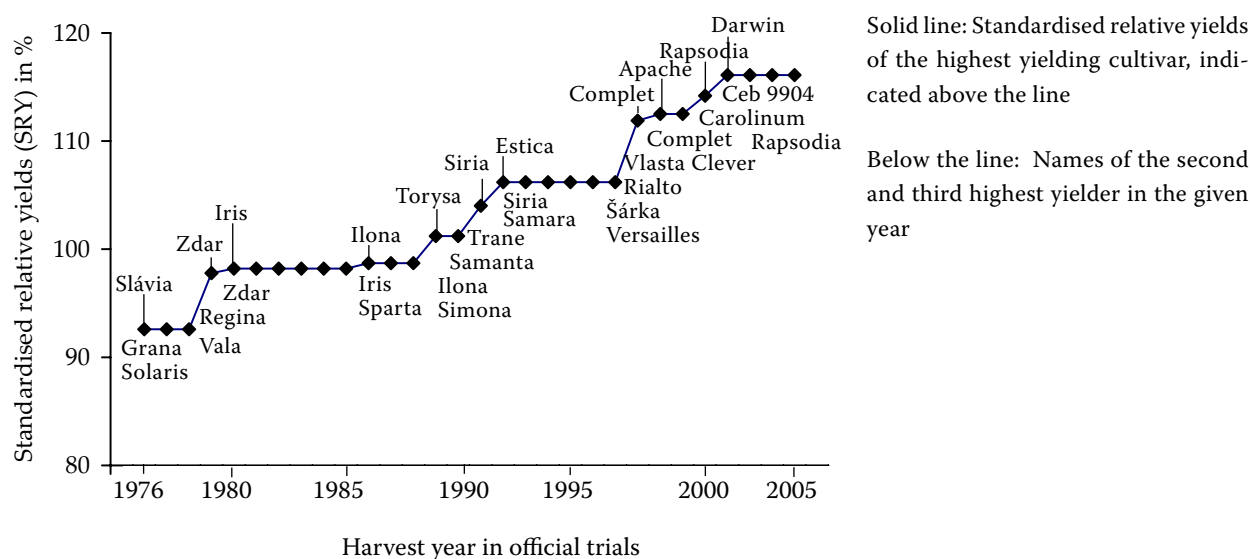


Figure 8. Winter wheat breeding progress 1976–2005 in official trials in the Czech republic

multiplicative parameters, obtained by regression or factor analysis, and an error term. The tested entries are then characterised apart from their main effect, which is supposed to be additive, also by one or more additional parameters with not well understood biological meaning. If the main effects of cultivars are really multiplicative, then SRY should be better than all the models with additive main cultivar effects. So far, however, a comparison of SRY with evaluations based on advanced statistical models like AMMI still remains to be investigated with real data.

### Appendix: mathematical considerations

We fitted the joint regression model  $y_{ij} = a_i b_j + e_j + r_{ij}$  to the original data by nonlinear least squares subject to the usual identifiability constraints  $\sum a_i = \sum (b_j - 1) = 0$  (NG & GRUNWALD

1997). The expected value under this model is given by  $\mu_{ij} = a_i b_j + e_j$ . This model is equivalent to the Finlay-Wilkinson regression (FINLAY & WILKINSON 1963) with the roles of genotypes and environments reversed (DIGBY 1979).

The standardization to SRY is consistent with the multiplicative model used in this paper as will be now shown. Observing the constraints, this is found to have environment means equal to  $\bar{\mu}_{\cdot j} = e_j$  and environment variances equal to  $b_j^2 \text{var}(a_j)$ . Also, the genotype means over environments have means  $\bar{e}_{\cdot}$  and variance  $\text{var}(a_j)$ . It emerges that, provided that errors  $r_{ij}$  are negligible, subtracting the environment mean from the raw data and standardizing to constant variance yields a model with expected value approximately equal to  $a_i$ . It remains to be investigated how this model fitting compares with the SRY when the errors are large. If the  $b_j$ , obtained from model fitting, are used

Table 5. The  $V_g/V_r$  ratio of standardised relative yields (SRY) compared with  $V_g/V_r$  ratios from the additive model

| Kind of primary data. LS-adjusted cultivar means                  | No. of trial groups | Additive model    | SRY               |
|---|---------------------|-------------------|-------------------|
| from single trials within years                                   | no                  | 0.67 <sup>1</sup> | 0.77 <sup>1</sup> |
| within years 1976–2005  | 30                  | 5.59              | 6.46              |
| within ecological regions   | 5                   | 8.29              | 9.45              |
| of trials grouped by temperature                                  | 7                   | 8.16              | 9.05              |
| of trials grouped by yield (all 98 cultivars)                     | 6                   | 5.58              | 9.16              |
| of trials grouped by yield, only cultivars with $n > 9$ per group | 6                   | 8.42              | 12.15             |

<sup>1</sup>average per year;  $V_g$  – genetic variance;  $V_r$  – residual variance

to standardise the data, a  $V_g/V_r$  ratio of 11.89 is obtained, which is slightly worse than 12.15 for the SRY. Strictly speaking, our procedure for obtaining SRY implicitly assumes that the standard deviation of  $r_{ij}$  is proportional to  $b_j$ , which corresponds to a variance-covariance structure known as heterogeneous compound symmetry (WOLFINGER 1996). By contrast, our least squares fit assumes that residuals  $r_{ij}$  have constant variance, which explains, at least in part, the slight lack of perfect correlation ( $r = 0.99918$ ) between the least squares fits for  $a_j$  and SRY.

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