

PHENOTYPIC YIELD STABILITY DEPENDENT ON PLANT DENSITY AND MEAN YIELD PER PLANT

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Introduction and problem

In many experimental investigations with Brassica-species highly significant genotype x environment interactions have been found for very different traits (Witcombe and Whittington 1971, Joarder and Eunus 1977, Posselt 1978, Joarder et al. 1978, Hühn and Léon 1985). But, nevertheless, only a few studies have been published on the estimation of parameters of phenotypic stability (Witcombe and Whittington 1971, Joarder and Eunus 1977, Posselt 1978, Schuster and Zschoche 1981, Hühn and Léon 1985, Léon 1985). Summarizing these published results no clear tendencies and no unique and generally valid conclusions can be deduced from these investigations.

Among the common agricultural crops winter-rape (Brassica napus L.) must be characterized to be especially susceptible to varying environmental conditions. The yields may show large fluctuations dependent on the effects of different years, different locations and different agronomical practices. Therefore, the still increasing interest in crop production to get reliable procedures and estimates for a quantitative characterization of phenotypic yield stability needs no further justification.

All the commonly used stability parameters (environmental variance, ecovalence, regression approach, rank parameters etc.) are based upon the actual yields of the genotypes/varieties in the different environments. No decomposition of these absolute yield values with regard to a stability analysis has been carried out. But, many investigations on yield analysis including yield components have been published, which are usually intended to an improved understanding of the yield level.

In spite of 1) the numerous existing stability parameters and 2) these extensive studies on yield analysis including yield components no sufficient explanation of yield stability and no reliable prediction of stability can be given.

In this contribution we propose a new approach of quantitative stability analysis, where the phenotypic stability of 'yield per area' can be expressed and investigated by using some properties (means, variances, correlation) of the yield determining yield components.

This inclusion of relationships between yield and yield components and, additionally, among the yield components themselves will enable an improved quantitative stability analysis.

Furthermore, the different conditions leading to the same phenotypic yield stability can be studied explicitly.

Theory

We start from the multiplicative decomposition of the yield F per area

$$F = X_1 \cdot X_2 \quad (1)$$

with

X_1 = number of plants per area (= plant density) and

X_2 = mean yield per plant.

Variability in F must be caused by fluctuations in X_1 and X_2 .

The phenotypic stability of F (measured by the variance $V(F)$ of F ; no other stability concepts than this 'environmental variance' shall be discussed in this paper) can be expressed by using some properties of the two components X_1 and X_2 .

For normal variables X_1 and X_2 the variance $V(F)$ of F can be explicitly expressed dependent on

1. the component means \bar{X}_1 and \bar{X}_2 ,
2. the component variances $V(X_1)$ and $V(X_2)$ and
3. the correlation coefficient r between X_1 and X_2 :

$$V(F) = \bar{X}_2^2 V(X_1) + \bar{X}_1^2 V(X_2) + 2r\bar{X}_1\bar{X}_2 \sqrt{V(X_1)V(X_2)} + (1+r^2)V(X_1)V(X_2) \quad (2)$$

(see, for example: Lu 1961).

$V(F)$ as a measure of phenotypic yield stability depends on 5 parameters: \bar{X}_1 , \bar{X}_2 , $V(X_1)$, $V(X_2)$ and r .

The different conditions leading to the same yield stability (measured and expressed by the same numerical value of $V(F)$) can be investigated by (2).

For many applications a standardization with regard to the yield level may be advantageous. This standardization can be realized by using the coefficient of variation v (= standard deviation divided by the mean) of the yield F instead of the standard deviation or variance itself. One obtains:

$$v = \frac{\sqrt{v_1^2 + v_2^2 + 2rv_1v_2 + (1+r^2)v_1^2v_2^2}}{1 + rv_1v_2} \quad (3)$$

with v_i = coefficient of variation of X_i ($i=1, 2$).

v as a measure of phenotypic yield stability depends on 3 parameters: v_1 , v_2 and r .

The different conditions leading to the same yield stability (measured and expressed by the same numerical value of v) can be investigated by (3).

Because we want to characterize yield stability independent from the yield level the main approach in this contribution will be the investigation of v .

Theoretical results

For a given correlation coefficient r between 'plant density' and 'mean yield per plant' the coefficient of variation v of the 'yield per area' only depends on v_1 and v_2 . Therefore, in a two-dimensional space with axes v_1 and v_2 "isolines" (= lines consisting of points with equal v -values) can be constructed and discussed. For $r = -0.80$ and the intervals $0 < v_1 \leq 1$ and $0 < v_2 \leq 1$ such "isolines" are presented in Figure 1. (The numerical v 's belonging to the different "isolines" have been assigned to the graphs at the two axes).

Some results of the theoretical investigations are:

1. For $r \geq 0$ we have $v_1 < v$ and $v_2 < v$, that means: The phenotypic stability of 'yield per area' cannot be higher than the phenotypic stability of each of the components X_1 and X_2 .
2. For $r < 0$ there exist situations, where the phenotypic stability

$$R = -0.8$$

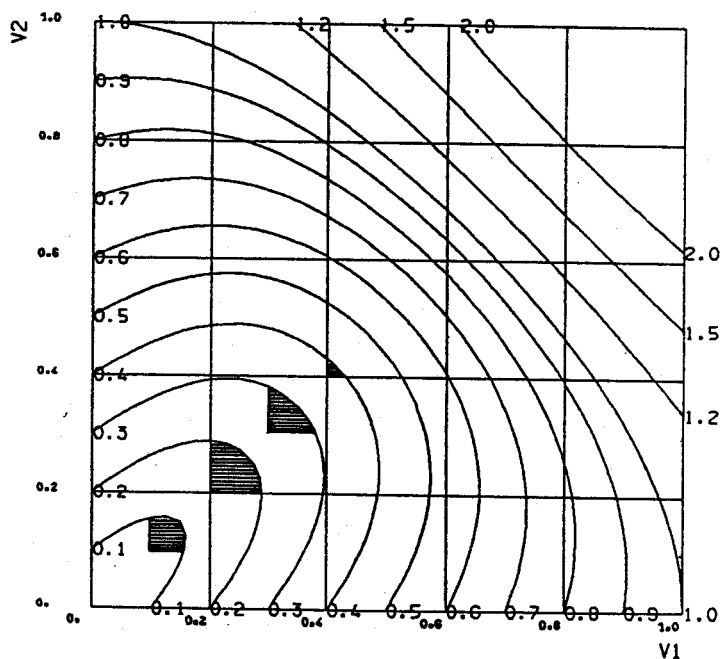


Figure 1: Graphical representation of "isolines" (= lines consisting of points with equal v -values) for $r = -0.80$.

of 'yield per area' is higher than the phenotypic stability of a component.

For low or medium v and simultaneously a high negative correlation r this result can be strengthened:

3. Here we have situations, where the phenotypic stability of F is higher than the phenotypic stability of both components X_1 and X_2 .

Such situations have been indicated in Figure 1 by the hatched areas.

These situations can be described numerically and many other interesting results and conclusions have been derived from the theoretical studies. But, these results will be published elsewhere in a more theoretical orientated paper.

In the present contribution we want to apply the previous theoretical models and approaches to an extensive winter-rape field trial.

Material and methods

This trial with rape-seed (*Brassica napus* L.) has been conducted for the 6 years from 1978/79 to 1983/84 with one cultivar ('Garant') at one location (Hohenschulen near Kiel, FRG) and designed with 3 different distances between rows (14, 31, 41 cm) and 4 different plant densities (40, 80, 120, 180 plants/m²) as a completely randomized block design with 6 replications. For the resulting 12 different treatments the traits 'plant density', 'mean yield per plant' and 'yield per area' have been measured for each plot separately.

This trial has been originally initiated for other purposes (yield analysis under different plant-distribution patterns). But, these data can be used for demonstration purposes of the application of the previous theoretical approaches on quantitative stability analysis.

Details on the design and analysis of this field trial are given by Sierts et al. (1987) and Hühn (1987).

Finally, we want to compare the theoretically expected values of the phenotypic stability (computed by (3)) with the experimental estimates of v for the trait 'yield per area'.

Experimental results

If we summarize the complete data of this field trial (all row distances and all plant densities) for each year or all possible year combinations separately a normal distribution for such a heterogeneous material (inclusion of extremely different plant densities) cannot be assumed (see: Hühn 1987). More homogeneous data subsets are the single plant density/row distance-combinations. These 12 combinations can be investigated for each year and all possible year combinations separately. For only one year combination (79/80/81/83/84) the experimental estimates of r (= correlation coefficient between 'plant density' and 'mean yield per plant'), v_1 (= coefficient of variation for 'plant density'), v_2 (= coefficient of variation for 'mean yield per plant') and v_{exp} (= coefficient of variation for 'yield per area') are presented in Table 1. The theoretically expected measures of phenotypic stability of 'yield per area' (computed by (3)) are denoted by v_{theor} and they are included in Table 1.

material 79/80/81/83/84 plant row density distance		yield per area v_{exp} v_{theor}		yield components v_1 v_2 r		
40	14	0.46	0.45	0.20	0.40	-0.07
40	31	0.39	0.39	0.17	0.32	+0.20
40	41	0.40	0.46	0.18	0.41	+0.08
80	14	0.44	0.57	0.16	0.52	+0.20
80	31	0.36	0.63	0.22	0.59	-0.06
80	41	0.32	0.89	0.17	0.87	-0.37
120	14	0.39	0.54	0.22	0.55	-0.44
120	31	0.35	0.87	0.25	0.81	-0.15
120	41	0.40	0.66	0.27	0.66	-0.55
180	14	0.32	0.78	0.26	0.72	-0.07
180	31	0.39	0.64	0.19	0.65	-0.47
180	41	0.38	0.74	0.30	0.66	-0.09
plant density (plants/m ²)						
"	40	0.41	0.45	0.23	0.38	-0.03
"	80	0.38	0.71	0.20	0.68	-0.13
"	120	0.38	0.73	0.29	0.68	-0.31
"	180	0.36	0.74	0.28	0.68	-0.18

Table 1: Results for v_{exp} , v_{theor} , v_1 , v_2 and r for the 12 plant density/row distance-combinations and, additionally, for the 4 plant densities (over all row distances) for the summarized data of the years 1979, 1980, 1981, 1983 and 1984.

The agreement between v_{exp} and v_{theor} is extremely good for the lowest plant density (40 plants/m²). This is true for the separate combinations with each row distance as well as for the total material of the lowest plant density (over all row distances). This agreement between v_{exp} and v_{theor} don't hold true for the higher plant densities 80, 120 and 180 plants/m².

For further results and conclusions see: Hühn 1987.

Discussion

A critical discussion of the proposed theoretical approaches and their conclusions and numerical results has been given by Hühn (1987) with special reference to the simplifying assumptions and their possible resulting restrictions. Therefore, here only a few comments shall be mentioned: For plant populations it is a well-known fact, that with increasing plant density (= increasing intensity of competitive effects) the distribution-characterizing parameters skewness and kurtosis change substantially. Therefore, increasing deviations from the normal distribution must be

expected. The good agreement between v_{exp} and v_{theor} for the lowest plant density and their bad agreement for the higher plant densities (Table 1) seems to find a clear explanation. But this conclusion is not true: If we reject the assumption of a bivariate normal distribution for X_1 and X_2 by allowing an arbitrary distribution the previous disagreement between v_{exp} and v_{theor} (Table 1) will be only slightly reduced. The disagreement remains substantial (see: Hühn 1987).

Therefore, other causes must be predominantly responsible: A main source of error may be the mode of trait-measurement in this field trial. The 'plant density' has been counted at the beginning of spring vegetation. Plant losses up to maturity have not been measured. This procedure, therefore, implies, that damages within the stands could be neglected. But, many experimental investigations have been published demonstrating an increasing loss of plants from the beginning of spring vegetation to maturity with an increasing plant density. With regard to this aspect, therefore, the optimal situation (= minimal plant losses) must be the lowest plant density. We think, just this statement is the main cause for the good agreement between v_{exp} and v_{theor} for the lowest plant density (40 plants/m²) and the extremely bad agreement for all higher plant densities.

Literature

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