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The Evaluation of Horizontal Resistance of Winter Wheats by the 'Center Pivot' Method

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Summary. Twenty bread wheat varieties were sown in forty meter long plots and infected with a mixture of three races of stem rust (14, 34, 311) in the Center-pivot design. The epidemic's development and its effect on yield (factors) were studied in an experiment.

With the Center-pivot method we modelled the natural processes without chemicals. The epidemic's development and the processes connected with it can be studied quantitatively as well as by subjective evaluation.

Some of the studied genotypes were quickly infected and others slowly. The date of infection proved to be especially important to the amount of yield decrease. However, a quick spread of the epidemic does not inevitably lead to a decrease of yield and 1000-grain-weight for every genotype.

Vertical resistance has qualitative features. On the other hand, there is only a quantitative difference between field resistant and tolerant genotypes, and between horizontally resistant and susceptible ones. The tolerant genotypes cannot limit the spread of the epidemic, but they can limit the degree of damage, and so their yields and 1000-grain-weights are essentially uninfluenced. The field resistant genotypes slow down the epidemic's development, and therefore their yields and 1000-grain-weights decrease less. This fact makes possible their separation in two steps, first on the basis of epidemic development, and then by measuring the decrease of yield and 1000-grain-weight.

Tolerance and field resistance are supposed to be inherited polygenically. Consequently, breeding for horizontal resistance should work with basically different methods than those previously used for race-specific resistance.

Key words: Horizontal resistance – Vertical resistance – Field resistance – Tolerance – Center pivot method

Introduction

A. The Problems of Race-Specific (Vertical) Resistance

In wheat breeding problems have arisen in connection with the utilization of race-specific resistance during the past 15 years. Stakman not only established the race-system, but was the first to see the problem, 'Will the fight against wheat rust ever end?' (Stakman 1964).

Watson and Luig (1963) demonstrated that with the appearance of new races infection on one variety occurred within seven years and in only two years more, in three other cases. This happened even though the recombination and migration of rust races could be almost totally excluded. The incredible mutative ability of the fungus alone is enough to overcome monogenic, bigenic resistance and even resistance caused by a translocated chromosome segment of related species.

Van der Plank (1968) demonstrated that the resistant plant variety creates the selection pressure resulting in the development of more virulent and aggressive races. Consequently, breeding for resistance often results in an effect opposite to the set aim.

Klassen et al. (1975) expressed the need for continual resistance breeding (moreover, the need for total plant protection) '... crop losses caused by insects and diseases in the USA have increased both absolutely and as a percentage of crop value since the 1940's'.

B. Horizontal Resistance and its Problems

Van der Plank (1968) suggested introducing the term of 'horizontal' resistance to describe a relatively high level of resistance against all races, instead of the so called 'vertical' or race-specific resistance.

This idea flourished, especially after the American *Hel-*

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minthosporium maydis race T epidemic and the ensuring Horsfall report (1972). Most of the papers read at the IAEA/FAO resistance meetings organized in Switzerland (Brönnimann 1976) and in Vienna (Micke 1977) dealt with the problems and possibilities of horizontal resistance. At the same time many well-known researchers in this field, such as Duvick (1975) and Crill (1977), even deny its existence. Characteristic is the opinion of Ellingboe (1975) that the whole hypothesis of horizontal resistance is a spiritual 'artefact'.

This uncertainty is created by two problems which mutually fortify each other.

1) The description of different resistance types are unclear.

2) The methods applied for studying horizontal resistance are not clear enough.

The glasshouse seedlings used for studying race-specific resistance and the pathologic nursery methods (Hayes et al. 1955) have only limited use in the study of horizontal resistance, mainly because they are based on single plant testing, or at the best, a few plants.

For testing tolerance Barabás and Belea (1974) adopted the divided plot method of Simons (1966), Frey et al. (1973), and Brönnimann-Fossati (1974) for studying winter wheat stem-rust. Conclusions were drawn about the degree of tolerance from the differences in the 1000-grain-weight of protected and infected series. Several years of data, both published (Barabás et al. 1974) and unpublished, show that there are problems with these conclusions for the following reasons:

– The degree of yield loss greatly depends on the plant maturity at the date of infection, climatic conditions and other diseases of the plants, in addition to their resistance.
– The necessary use of fungicides makes real comparison difficult because of its side-effects on other diseases.
– Various types (tolerance, field resistance) of horizontal resistance cannot be differentiated by this and similar methods.

This paper reports on further studies of this type.

Material and Methods

The Center-pivot trial was planted at the 'Öthalom' station of the institute, as previously described (Barabás et al. 1974), in the years 1975/1976. By increasing the inner spreader's diameter twenty genotypes were tested in four replications on the same area, instead of the ten genotypes formerly tested.

The 20 entries of winter wheat (*Triticum aestivum L.*) cultivars are demonstrated in Table 1. Among the tested material are eleven cultivars as well as nine F_3, F_4, F_5 and F_6 hybrid populations.

The experimental area was a circle 50 m in radius (Fig. 1). In the center there was a circle ten meters in radius, where the spreader, a mixture of varieties susceptible to stem-rust, was sown. The 40 meter long main plots (80 strips, 75 cm wide each) were sown adjoining the central spreader circle radially in all directions at a plant density of 500 plants/m^2. The 20 entries were sown randomized in each of the four series, corresponding to the four cardinal directions to minimise atmospheric effects. At harvest each of the 40 meter long main plots was divided into 5 subplots (A-E) starting from the center. The A, B, C,D, E sectors formed by all the subplots were respectively the same distance from the center. The inner critical A and B subplots were 5 meters long each

Table 1. Entries in the Center-pivot trial

No.	Name	Abbreviation	Genotype	Origin
1.	Sava	Sv	variety	Yugoslavia
2.	GK-Szegedi 1	Sz-1	variety	Hungary
3.	Bánkuti 1201 X Sava	B 1201-Sv	F_5 bulk[a]	Hungary
4.	Martonvásári 4	Mv-4	variety	Hungary
5.	GT 76-150 X Sava	GT-Sv	F_6 bulk[a]	Hungary
6.	Bezosztaja 1	Bzt 1	variety	USSR
7.	GK-Szegedi 5	Sz-5	variety	Hungary
8.	Sava X Aurora	Sv-Au	F_4 bulk[a]	Hungary
9.	GK 8001	8001	variety	Hungary
10.	Kiszombori 2	K-2	variety	Hungary
11.	Sava X Sturdy	Sv-Sdy	F_3 bulk[a]	Hungary
12.	Zlatna Dolina X Au	ZlD-Au	F_4 bulk[a]	Hungary
13.	GK-3	GK-3	variety	Hungary
14.	Rusalka X Rannaja 12	Rsk-Rn 12	F_4 bulk[a]	Hungary
15.	GK 8001 X Sava	8001-Sv	F_5 bulk[a]	Hungary
16.	Zlatna Dolina X Sava	Zld-Sv	F_3 bulk[a]	Hungary
17.	Aurora	Au	variety	USSR
18.	Aurora X Bzt 1 X B 1201	Au-Bzt 1-B 1201	F_3 bulk[a]	Hungary
19.	Purdue	Prd	variety	USA
20.	Arthur	Art	variety	USA

[a] Degree of inbreeding

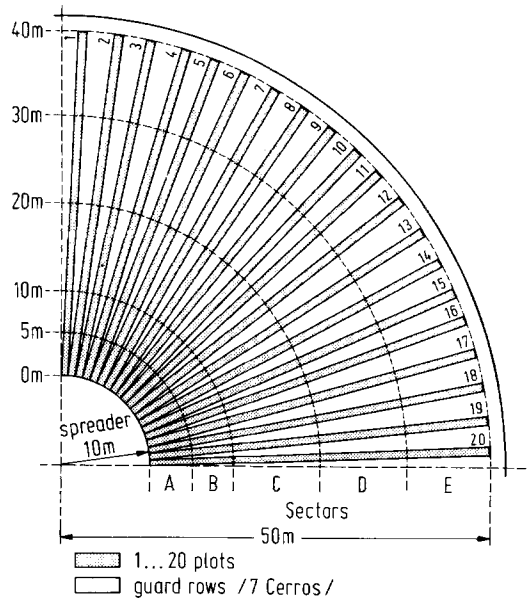

Fig. 1. The design of the 1st replication of the Center Pivot experiment

while the middle and outer C, D and E subplots were each 10 meters long. In order to diminish the inter-variety infection of the plots from the side, 'guard rows' were sown on both sides of the plots. For this purpose 'Siete Cerros', a Mexican variety, was used because it proved to be resistant to all the stem-rust races used for infection in the trial.

This arrangement makes possible the study of epidemic development under natural conditions. By the time the inner (A and B) plots had become recognisably infected the process had just started in the outer ones (C, D, E). So the effect of epidemic development at different plant maturation periods can be studied on the separate subplots. Consequently, the genotype X maturity interaction of the host plants can be examined in connection with the pathogen's infection date by its effect on yield.

For infection a mixture of the stem-rust's (*Puccinia graminis f. sp. tritici*) races 14, 34 and 311 were used.

The spreader plants were artificially infected at an early stage (Feekes scale: 7) of their development by injection. The infection was repeated. In 1976 the dates of infection were May 12 and May 21.

The level of infection was scored according to the following scale of 9 degrees: 0 = no infection; 1 = mild infection, sporated layers on 1-10% of plants; 2 = 11-40%; 3 = 41-70%; 4 = 71-100%; 5 = strong infection with coatedness on 1-10% of plants; 6 = 11-40%; 7 = 41-70%; 8 = 71-100%.

The date of evaluation was July 7 because the epidemic spread late. The degree of infection was determined at least two points of each subplot.

The weather was favourable for epidemic development in the year of the trial. So the factors (host plant, stem-rust, yield, etc.) and their relations could be well studied. Spring was colder than usual. It was followed by a warm May and a cooler, wet beginning of June. Flowering of the wheat was delayed a week.

The experiment was sown with a Wintersteiger small plot driller and harvested with a Hege 125 plot combine by subplots. The yield, test weight, and 1000-grain-weight were measured after cleaning.

Variance, correlation and regression analyses were used to aid the evaluation of the data (Sváb 1973).

The data of the trial were evaluated by two way variance analysis for a split plot arrangement (Sváb 1973). One of the factors was genotype (G), and the other, the sector. In order to make counting and comparison easier the yield results of the outer 10 m long subplots (C, D and E) were divided by 2 to be numerically related to the same area of the inner sectors. In all countings this reduced average yield was used.

Regression and correlation analyses were made to study the relation between the infection level and the decrease of the 1000-grain-weight, and between the infection level and the decrease of yield for each variety. For this purpose 20 pairs of data were available for each variety (4 replications X 5 sectors = 20 plots). The infection level used in these countings for the appropriate sector in each plot was chosen from the appropriate infection (estimation) scoring values made in two meters.

Results

A. General Relations Between Stem-Rust Infection and the Grain-Yield of Wheat

Variance analysis (Table 2) shows significant differences between genotypes in relation to all four parameters

Table 2. The variance table of yield, 1000-grain-weight, test-weight, and infection severity data per plot

Source of variance	FG	Grain-yield MQ	1000-grain-weight MQ	Test-weight MQ	Infection severity MQ
Total	399				
Replications	3				
Genotype (G)	19	2.40***	425.33***	112.42***	36.99***
Error (G)	57	0.11	2.60	2.19	3.22
Sector (A, B, C, D, E) (I)	4	1.84***	154.41***	37.25***	221.21***
G X I Interaction	76	0.05*	4.40**	1.37***	1.38*
Error (I)	240	0.03	2.75	0.56	0.90

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

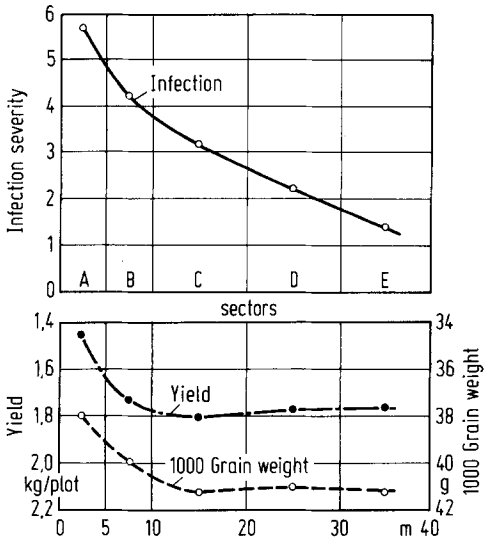

Fig. 2. Average performance of winter wheat genotypes to *P. graminis* tritici according to the distance from the spreader (A, B, C, D and E sectors)

(yield, 1000-grain-weight, test-weight, infection severity). The same can be established for the differences between sectors as well (I). The genotype × sector interaction is also significant in the case of all four parameters. That is, different genotypes react differently with different infection times.

The value of the level of infection is the highest and yield the lowest in the inner A and B sectors near the spreader (Fig. 2). The infection level decreases steadily with the distance from spreader. The yield is relatively greater in the B and C sectors as compared with A because the level of infection decreases. However, the yield does not increase further in the outer D and E sectors in spite of the further decreasing infection.

For judging the yield decrease it is very important to mention that the yield of both uninfected varieties ('Purdue' and 'Arthur') decreased in the innermost sector as compared with sector B. The same phenomenon is described in the report of Barabás et al. (1974) for non-infected varieties.

Table 3. The average infection level values per sector and genotype

No.	Variety	Sectors					Mean of genotypes
		A	B	C	D	E	
1.	Sv	7.5	6.8	5.5	4.5	3.8	5.59
2.	Sz-1	6.5	5.8	4.9	4.1	2.8	4.79
3.	B 1201-Sv	7.1	6.1	4.3	3.1	1.4	4.50
4.	Mv-4	7.3	5.8	4.3	2.7	2.0	4.41
5.	GT-Sv	6.8	5.4	4.2	3.6	1.8	4.33
6.	Bzt 1	7.2	5.4	3.9	2.9	1.9	4.26
7.	Sz-5	6.3	4.6	3.7	3.2	2.3	4.00
8.	Sv-Au	6.3	4.8	3.7	2.3	1.5	3.72
9.	8001	6.0	4.5	3.5	2.3	1.6	3.56
10.	K-2	6.0	4.3	3.5	2.2	1.6	3.52
11.	Sv-Sdy	6.1	4.4	2.7	1.9	0.9	3.21
12.	ZlD-Au	5.6	4.2	3.3	1.7	1.3	3.21
13.	GK-3	6.0	4.1	3.2	1.7	1.1	3.19
14.	Rsk-Rn 12	5.7	4.1	2.9	1.9	1.2	3.12
15.	8001-Sv	5.5	3.6	2.3	1.7	1.1	2.84
16.	ZlD-Sv	5.8	4.2	2.0	1.0	0.9	2.74
17.	Au	5.3	3.2	1.7	1.1	0.6	2.35
18.	Au-Bzt 1-B 1201	4.3	2.4	2.0	1.4	0.9	2.16
19.	Prd	1.1	0.0	0.1	0.0	0.0	0.30
20.	Atr	0.4	0.0	0.0	0.0	0.0	0.08
Mean of sectors		5.64	4.20	3.08	2.16	1.43	3.30

LSD 5%		
	between the mean of varieties	1.13
	between the mean of sectors	0.30
	between 2 genotypes on the same or different sectors	1.64
	between sectors of the same genotype	1.32

Table 4. Means of the 1000-grain-weights (g) per sector and genotype

No.	Variety	Sectors					Mean of genotypes
		A	B	C	D	E	
1.	Sv	32.2	34.6	34.5	34.8	35.0	34.2
2.	Sz-1	36.8	40.5	42.4	42.1	41.2	40.6
3.	B 1201-Sv	34.1	38.0	39.6	39.7	40.6	38.4
4.	Mv-4	41.1	44.5	44.0	44.9	45.4	44.0
5.	GT-Sv	31.9	34.8	36.4	35.4	34.8	34.6
6.	Bzt 1	39.9	39.2	46.8	45.9	45.4	43.4
7.	Sz-5	46.4	47.1	47.5	46.7	46.6	46.9
8.	Sv-Au	38.7	40.5	42.3	42.2	42.3	41.2
9.	8001	34.9	38.3	36.6	38.5	39.4	37.5
10.	K-2	43.1	46.3	46.6	45.8	46.1	45.6
11.	Sv-Sdy	32.1	34.8	35.6	35.4	34.5	34.5
12.	ZlD-Au	40.2	41.5	44.3	43.2	44.7	42.8
13.	GK-3	35.9	36.7	38.6	40.1	39.9	38.8
14.	Rsk-Rn	40.6	42.8	42.8	42.7	42.8	42.3
15.	8001-Sv	29.1	29.8	31.5	31.0	30.0	30.3
16.	ZlD-Sv	35.3	35.3	37.2	37.6	37.7	36.6
17.	Au	44.4	45.4	47.2	46.7	47.9	46.3
18.	Au-Bzt 1-B 1201	34.9	37.2	38.9	38.1	40.9	38.0
19.	Prd	44.8	44.0	45.4	43.5	45.6	44.6
20.	Atr	41.8	42.9	43.8	43.4	43.4	43.1
Mean of sectors		37.9	39.9	41.1	40.9	41.2	40.2

LSD 5%		
	between the means of genotypes	1.0
	between the means of sectors	0.5
	between 2 genotypes of similar or different sectors	2.3
	between sectors of the same genotype	2.1

B. Relationships Between the Level of Infection and the 1000-Grain-Weight

In addition to acquiring knowledge of general reactions, breeders are interested in the individual reactions of genotypes. The entries can be ordered on the basis of the values of their infection levels. They fall between the extreme values in the A sector of 0,4 and they approach the maximum of 7,5 in the A sector (Table 3). The level of infection difference between the A and E sectors is 4.21 units in the mean of 20 genotypes. However, there are genotypes for which this value is nearly 6 units. That is, a strong initial infection is followed by a very quick decrease (Entries 3 and 11). At the same time, for entries 1 and 2 the initial high level of infection is followed by a low decrease. If we compare the data of the 1000-grain-weight (Table 4) and the level of infection values we find that infection severity further decreases in B, C and E sectors, but 1000-grain-weight does not increase further. This means that infection values below these 4-5 severity values did not result in any more change. This is proved unambigously by the equalized 1000-grain-weights of genotypes 14 to 18.

When evaluating the 1000-grain-weight, or yield, the fact must be considered that the sectors did not become infected at the same time. Some of them became infected earlier, and some of them later, depending on the speed of the epidemic spread. Different varieties flowered at different times. Therefore, the same infection value does not always result in the same degree of yield and 1000-grain-weight decrease. On nine occasions the correlation between the level of infection and yield was significant and on nine occasions the correlation between the level of infection and the 1000-grain-weight was significant (2 entries were resistant).

C. Trial for the Separation of Different Resistance Types on the Basis of the 1000-Grain-Weight

1) A synonym of 'race-specific' resistance is 'vertical' resistance. This form was represented here by the varieties 'Arthur' and 'Purdue'. These varieties were resistant to the races tested. However, it seems probable that other naturally occurring races could have infected them to a very low extent. Another possibility would be that the very strong infection pressure led to a low degree of infection. Although they cannot be tested for tolerance, it was necessary to include them as checks in the experiment.
2) 'Horizontal' (syn. 'lateral') resistance gives certain, but not total, protection against all races. However, they may have race specific resistance genes as well. We separated two types within horizontal resistance.

a) 'Field' resistance. The plant becomes infected but the epidemic develops slowly for certain reasons. The plant ripens quicker than the infection spreads and remains un- or very little damaged, and therefore the decrease of yield (and 1000-grain-weight) is not significant. Thus the ultimate reason for this is the low and slow development of the infection process.

b) 'Tolerance'. The plant shows susceptibility reactions, and the pathogen spreads quickly, but the yields (1000-grain-weight) do not decrease.
The infection spread is judged quick or slow if the level of infection in the E sector is higher or lower than the mean of all entries, respectively.

The classification of the eighteen considerably infected genotypes is shown in Table 5. They are arranged on the basis of the infection level (Table 3) and the 1000-grain-weight data (Table 4).

Table 5. Determination of resistance types of the entries based on the development of infection and the 1000-grain-weight interaction

Development of infection in the A – E sectors	Entries	Effect of infection on the 1000-grain-weight	Entries	Type of resistance
Quick	1, 2, 4, 5, 6, 7, 9, 10	does not increase[ns]	6, 7	tolerant
		increase[a]	1, 2, 3, 4, 5, 8, 9, 10, 11, 14, 15, 18	susceptible
Slow	3, 8, 11, 12, 13, 14, 15, 16, 17, 18	does not increase[ns]	13, 16, 17	field resistant

[ns] For these varieties there is no significant difference between the 1000-grain-weights in the A and B sectors
[a] For these genotypes there is a significant difference between the 1000-grain-weights in the A and B sectors at P = 5%

Discussion

If we accept the above premises about resistance it becomes possible to determine the kind of resistance shown by a genotype. According to this, two of the tested genotypes are tolerant, and three of them are more or less field resistant. The susceptibility of the other genotypes can be classified. Twelve of them were susceptible, in different degrees. Naturally, race-specific resistance is totally different from these. There is no infection or if there is, it is only minimal and there is no 1000-grain-weight decrease at all.

If one takes the infection circumstances into consideration, one realizes that tolerance or field resistance evaluation can be difficult. It is possible that the varieties may not behave similarly in case of an earlier and stronger epidemic. The decrease of yield and 1000-grain-weight is influenced by the complicated interrelation of the host-pathogen-environment complex.

Even we regard the yield decrease as the most ideal parameter for characterizing tolerance, in the present experiment it could not be used because of the considerations mentioned above. However, the 1000-grain-weight (oscillation of the extreme values is 8.2%) has a constant value in every subplot of the uninfected varieties so this characteristic is good for an objective analysis.

Changes in the test-weight are very small; the oscillation is only 2.2% Therefore this characteristic is not considered to be good for further examinations.

Although final conclusions cannot be drawn from the data of the experiments, they are promising. Differences between genotypes could be demonstrated by the present methods. There must also be enough data to provide a basis for selection and improvement. However, as the differences are quantitative, not only tolerance, (Van der Plank 1975; Brönnimann and Fossati 1976) but also field resistance, are polygenically determined. Consequently, breeding methods should be basically changed.

It is more difficult to determine polygenic resistance and to breed for it rather than for race-specific resistance. However, the first is more durable and effective (Van der Plank 1968; Hooker and Saxena 1971).

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