Aspects of durable resistance in wheat to yellow rust

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Statements (stellingen)

1 Multi-location testing is a good test for yield stability but not for durability of disease resistance.

2. Quantitative resistance is not stable but can be durable.

3. The breakdown of resistance to yellow rust in Kenya and Ethiopia of CIMMYT wheat lines is the result of a too narrow virulence spectrum in Mexico and of the breeding procedures used there.

4. If breeders want to use durable resistance, they should be prepared to put considerable and well coordinated efforts for a long period into it.

5. The international nurseries, which are distributed by the international centres to assist the national programs in their breeding program have a decreasing impact due to the strong reduction of their funds.

6. The social behaviour of an expert in the developing countries is often more important than his expertise.

7. Sustainable agriculture in the developing countries will not be able to meet the needs of the rapidly increasing populations.

8. Despite genetic engineering, traditional plant breeding in developing countries will remain essential for a long time to come.

9. The establishment of a phytopathological centre in East Africa is essential for a successful breeding program in that region.

10. The fact that in Kenya the number of missionaries and churches and the number of street children both increased strongly may not be a coincidence.

Stellingen behorende bij het proefschrift van Daniel L. Danial, getiteld "Aspects of durable resistance in wheat to yellow rust", te verdedigen op 6 april 1994 in de Aula van de landbouwuniversiteit te Wageningen.

Author's abstract

In Kenya, the number of virulence factors of the yellow rust populations showed a considerable increase and a wide variability. Selecting for complete to near complete resistance to yellow rust and other cereal rust diseases, was followed by a rapid erosion of resistance.

Partial resistance in wheat to yellow rust appeared to be difficult to select for. However, quantitatively resistant (QR) genotypes with a reduced disease severity (DS) and intermediate infection types (IT) were frequently observed. In addition, a fair number of wheat cultivars seemed to be durably resistant (DR) as their resistance was effective even after more than 25 years.

DS and area under disease progress curve proved to be suitable parameters to measure QR while IT was too unstable a trait to rely on. QR can assessed reliably in small plots since there was no interplot interference observed. During screening and selection for QR, the level of nitrogen (N), heading date, observation date and leaf position are factors that should be considered by the breeder. DS and IT increased moderately with increased Nitrogen level. The magnitude of such increase was not the same for all genotypes.

Selection for QR can be best carried out by discarding the most susceptible and most resistant plants or lines. In the field QR genotypes different significantly in DS and IT while race specificity to some yellow rust races and ineffective seedling resistance genes to race 134E150 were observed. By assessing the stability over environments of a range of genotypes, genotype x location interaction occurred fairly often for QR while the durably resistant cultivars showed by far the least interactions with location indicating high environmental stability for DR.

The resistance in five genotypes with different levels of QR seems to be based on rather few factors, one for Pr-2 to some three for Pr-7. The five genotypes seem to have factors in common or different factors that are strongly linked. The resistance in five durably resistant cultivars seemed to be based predominantly on a complex of strongly linked factors that inherited almost as a single factor in crosses with the highly susceptible Morocco.

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CONTENTS

General introduction

Yellow (stripe) rust (*Puccinia striiformis* Westend) is a major pathogen of bread wheat, (*Triticum aestivum*). The disease is confined to the cooler climates and occurs especially in N.W. Europe, Mediterranean region, Middle East, N.W of the USA, Australia, East African highlands, China, Indian sub-continent, New Zealand and the Andean region of South America.

In the last decades, yellow rust has become a major threat to wheat production in Kenya and other wheat growing areas in East Africa. This was caused by the fact that: i) the breeders concentrated mainly on developing cultivars resistant to stem rust without realizing the importance of yellow rust. ii) that national programs in East Africa were mainly dependent on advanced CIMMYT wheat lines, which could be released after a short period of testing. Soon after the release of such introduced lines the cultivars often became susceptible due to the appearance of new races of the pathogen. For instance, the cultivar Paa released in 1982 became very susceptible in 1984. This is the so called boom and bust cycle.

Effective chemical control is available but expensive especially in developing countries. The continued use of fungicides, however, may become an environmental hazard, while the pathogen is often able to become tolerant or resistant to the fungicide. Cultivars, durably resistant to yellow rust, form a good alternative in order to reduce the environmental pollution, to avoid tolerance or resistance of the pathogen to the fungicides and to avoid the boom and bust cycle introduced with non-durable resistance.

The pathogen

Name. Yellow rust was first described by Gadd in 1777 (Eriksson and Henning, 1896). It was described as a casual pathogen of rye in Sweden in 1874 by Bjerkander (Eriksson and Henning, 1896). Afterwards different names were given to the pathogen. Schmidt (1827) described yellow rust as the third cereal rust under the name *Uredo glumarum*. Westendorp (1854) described yellow rust, collected from rye (Hassebrauk, 1965), under the name *Puccinia straminis*. Erikson and Henning (1894) showed that this rust was a species on its own and called it *Puccinia glumarum*. This name remained valid until Hylander et al. (1953), followed by Cummins and Stevenson (1956), introduced the name

Puccinia striiformis Westend (Manners, 1960). The common names of yellow rust and stripe rust were given by Humphrey et al. (1924) and by Eriksson and Henning (1894), respectively.

Symptoms. Infection with yellow rust may occur at any stage of plant development. Germination of urediospores on the leaf occurs by contact with water. Yellow rust is characterized by its systemic growth in the leaf. Uredia develop in narrow, yellow, linear stripes mainly on leaves and spikelets. When the heads are infected, the pustules appear on the inner surfaces of glumes and lemmas, occasionally invading the developing kernels. The minimum, optimum and maximum temperatures for spore germination are 0°C, 9°C and 20°C respectively.

Life cycle of the pathogen. Yellow rust has a hemiform life cycle comprising of only the uredial and telial stages (Stubbs, 1985). The sexual stage of the fungus has not been encountered and so far no alternate host has been found. Mutation and possibly somatic recombination seem to be the mechanisms by which new races are formed.

Breeding for resistance

In cereals to cereal rusts, several types of resistance are described. The most important classifications are:

1. Overall resistance. High level of resistance, expressed in all development stages of the plant (Zadoks, 1961), sometimes referred to as seedling resistance.

2. Adult plant resistance. High level of resistance, expressed in the adult plant stages only and not in the seedling stage (Zadoks, 1961)

3. Partial resistance. A form of incomplete or quantitative resistance whereby a low disease severity is associated with a high infection type (Parlevliet, 1979).

4. Temperature sensitive resistance. Depending on the temperature the resistance is expressed to a lower or higher degree. It is often better expressed at higher temperatures (Lewellen et al., 1967). If expressed the reduced disease severity is associated with a lower infection type.

5. Residual resistance. When an introduced resistance breaks down due to a new race of the pathogen, the susceptibility of the cultivar hardly ever reaches the level of the most susceptible cultivar. Some resistance remains effective; residual resistance (Zadoks, 1961). This type of resistance is of a quantitative nature and can be of the above mentioned classifications 3 or 4.

6. Hypersensitive resistance. Resistance characterized by cell collapse around the point of entry of the pathogen, and resulting in a low infection type.
7. Slow rusting. A form of incomplete or quantitative resistance which describes a reduced rate of epidemic development.
8. Quantitative resistance. Resistance that shows a continuous range of variation in resistance from extremely susceptible to fairly resistant (Parlevliet, 1989).

Resistance to yellow rust is often of the race-specific, major gene type. A series of such resistance genes are identifiied and designated (*Yr1* to *Yr10* and *Yr15* express overall resistance, *Yr11* to *Yr14* are adult plant resistance genes) (Lupton and Macer, 1962; McIntosh 1983; McIntosh, 1986). Other such major genes have been detected but have to be designated still. Of the *Yr* genes so far identified, all have proved to be race-specific. Most if not all of the known *Yr* genes became ineffective in certain areas (Stubbs, 1985). This type of major gene, race specific resistance is characterized by a low infection type and proved to be not durable when exposed on large areas for longer periods. However, there are many cultivars which remained resistant and lasted for a long time after prolonged and widespread testing. Such cultivars are considered to be durably resistant and have been reported from many parts of the world (Johnson, 1988; Van Dijk *et al.*; 1988; Line, 1978). These durably resistant cultivars did not result from breeding programs directed at durable resistance, they were incidental occurrences.

The objectives of the research presented here were to characterize the durable resistance in wheat to yellow rust and to develop guidelines for its assessment and its use in the breeding programs.

The research was largely carried out in Kenya.

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I. Consequences of selection for complete resistance

Introduction

High levels of resistance, based on major genes can be easily recognized in the field and such resistance is therefore widely used in many breeding programmes. Most of this resistance is directed against specialized pathogens and is of a race-specific nature (Parlevliet and Zadoks, 1977; Parlevliet, 1981). The situation in the wheat yellow rust pathosystem is not different. The resistance used in most breeding programs appears to be based on resistance genes with a large effect (*Yr*-genes) and effective against specific races of the pathogen only.

At present a whole series of resistance genes has been identified such as *Yr1* to *Yr10* and *Yr15*, which are effective at all growth stages of the plant including the seedling stage (overall resistance), and *Yr11* to *Yr14* which are expressed in the adult plant stage only. These *Yr*-genes originate from various wheat cultivars or from related species (Lupton and Macer, 1962; McIntosh, 1986). Other resistance genes are known to be present but have not yet been designated to a *Yr* number. The resistance factors A, CV, SD, SU and SP, from the cultivars Anza, Carstens V, Strubes Dickopf, Suwon 92/Omar and Spaldings Prolific are examples of this category. There are however more resistance genes, which are as yet not identified; 2+ from 'Heines VII', 6+ from 'Peko' and 9+ from 'Clement' indicates by the + sign that besides the identified *Yr2*, *Yr6* or *Yr9* gene another unidentified resistance gene or genes is present in the cultivar mentioned.

All the resistance genes mentioned above have been shown to be race-specific (Johnson, 1988). The effectiveness of major gene resistance to yellow rust is generally of a short duration (Johnson et al., 1969; Stubbs, 1972; Johnson 1981; Johnson 1984), and all described major resistance genes became ineffective to one or more of the yellow rust races (Stubbs, 1985). This was due to the ability of the pathogen to produce races carrying new virulence factors (Johnson, 1981; Stubbs, 1985). The number of virulence factors in the yellow rust populations appear to increase rapidly in relatively short periods of time. Over the years it became very clear that high levels of resistance governed by major resistance genes were very vulnerable to the occurrence and spread of new races of the pathogen.

The fact that yellow rust populations consist of a number of races, differing in the virulence factors they carry, asked for the possibility to describe the virulence composition of the yellow rust populations. For this reason a differential set of cultivars with known resistance genes was developed (Johnson

et al., 1972). The reaction pattern of an isolate of yellow rust to this set of cultivars shows which virulence factors are present in that isolate. The present set of cultivars used here can identify some 20 virulence factors. These virulence factors are those that can neutralize the resistance genes or factors *Yr1, 2, 2+, 3N, 3V, 4+, 5, 6, 6+, 7, 7+, 8, 9, 9+, 10, A, CV, SD, SU* and *SP* (in x+, the sign + means additional virulence besides virulence against x).

When the high level of resistance of a cultivar breaks down due to the spread of a new race the disease severity on this cultivar increases significantly, but hardly ever to the levels equal to those of extremely susceptible cultivars like Morocco. This "residual resistance" is of a quantitative nature and seems much more durable (Parlevliet, 1993).

In this chapter the virulence pattern of the yellow rust populations in Kenya during the last decades and its implication for the breeding of resistant cultivars are discussed. In addition, the consequences of implementing a standard breeding programme by selecting for complete to near complete resistance are demonstrated.

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Chapter 1

Evolution of virulence patterns in yellow rust races and its implications for breeding for resistance in wheat in Kenya *

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Summary

Virulence patterns of yellow rust isolates collected in Kenya between 1986-1989 were compared with earlier results. The number of virulence factors per race and the range in virulence factors both increased considerably. Before 1976 races carried on average 4.5 to 5.0 virulence factors, whereas the races after 1986 had a mean of 6.5 virulence factors. The range in the number of virulence factors increased from some seven in the first period to 12 in the second out of the 17 evaluated. In the period 1986-1989 another three virulence factors (2,9 and A) were assessed. All three occurred at a high frequency.

Virulence neutralizing the resistance genes *Yr2, Yr2+, Yr6, Yr6+, Yr7, Yr7+, Yr8, Yr9, Yr9+* and those in the cultivars Anza (A), Strubes Dickkopf (SD) and Suwon92/Omar (SU) occurred at a high frequency, while virulence for *Yr3V, Yr4+, Yr5, CV* and *SP* (resistance in Carstens V and Spaldings Prolific resp.) were not found. The remaining three virulence factors, *Yr1*,10 and 3N were rare.

In the past ten years the resistance of most released cultivars became ineffective in less than six years. They were shown to carry race-specific major resistance genes such as *Yr7+, Yr9+, SD and A.* However, in the field, the resistance of the cultivars was not completely neutralized. A residual resistance, ranging from moderate to fairly high, was observed in all cultivars with broken resistance.

Other wheat cultivars such as Africa Mayo, Kenya Kudu, Enkoy, Kenya Leopard, Bounty, Frontatch, Bonny and Kenya Plume appeared to keep their resistance over a considerable period of time. They are considered to be durably

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*Submitted

resistant to the Kenyan yellow rust populations. This form of resistance, together with the residual resistance, can be recommended for use in breeding programmes.

Introduction

Yellow rust caused by *Puccinia striiformis* Westend is at present one of the major threats to wheat production in Kenya. Serious attacks of the pathogen occur annually and its severity increases with the altitude. Physiologic specialization of this pathogen was first demonstrated by Allison *et al.* (1930), and several genes controlling resistance to yellow rust in wheat were identified (Macer, 1972). Unfortunately, most of these genes have been overcome by one or more of the yellow rust races (Stubbs, 1985). However, some cultivars have remained resistant over a long period of time. These cultivars can be considered as durably resistant.

The main objectives of this study were:

1. To make an inventory of the virulence factors in Kenya.
2. To make an inventory of the resistance factors in the recently released cultivars.
3. To evaluate the resistance level of Kenyan cultivars before and after release.
4. To identify sources of durable resistance.

Materials and methods

Virulence analysis, 1986 - 1989

Leaves carrying yellow rust were collected from various trials at the experimental farm of the National Plant Breeding Research Center (NPBRC), Njoro, Kenya. The samples were analyzed at the Research Institute of Plant Protection (IPO), Wageningen, The Netherlands. Race determination was performed as described by Stubbs (1988) on the World and European sets of differentials (Johnson *et al.*, 1972). In addition, the differential cvs Anza, Federation 4x/Kvakaz and Kalyansona, carrying the resistance factor or gene, A, Yr9 and Yr2 respectively, were added to the differentials in the second testing period. Infection types were recorded on the 0 to 9 scale (McNeal *et al.*, 1971) and classified as: resistant (0-3), intermediate (4-6) and susceptible (7-9). An isolate was usually considered to be virulent on a differential when the infection type was equal to 7, 8 or 9.

Postulation of resistance genes in Kenyan cultivars
Nine cultivars (Table 2), released in Kenya between 1982 and 1989 and widely cultivated, were used in this study. Seedlings were tested against six races of *Puccinia striiformis*, each with a different pattern of virulence factors (Table 2) in two replicates. Experiments were carried out under fully controlled conditions as described by Stubbs (1988) at IPO, Wageningen, The Netherlands.

Field evaluation of Kenyan cultivars for resistance to yellow rust
Nineteen cultivars, released between 1960-1989, were evaluated for their level of resistance. The cultivars were planted every year during the main wheat growing season from 1986 to 1991. Planting took place at NPBRC, Njoro. Each cultivar was planted in plots of 2 rows of 2m length in two replicates. The very susceptible cv Morocco was planted perpendicular to the cultivars to act as a spreader row. Disease severity (DS) was assessed after heading (stage DC 59 on the scale of Zadoks *et al.* (1974) on the 0-100 % scale of Peterson *et al.* (1948).

Results and discussion.

Virulence pattern of yellow rust isolates
Virulence factors of yellow rust races found between 1969 - 1989 are given in Table 1. The number of virulence factors in races detected between 1969-1975 varied from 0 to 7 (Stubbs *et al.*, 1974; Stubbs and Van Silfhout, unpublished data) with an average number of 4.1, while those observed between 1986-1989 ranged from 3 to 9, with a mean of 6.5. The estimate in the first period, however is an underestimation as in this period the differentials could not test the virulences for *Yr2* and *Yr9* independently from their additional factor(s), indicated by a +. *Yr2* without its additonal factor quite possible occurred in this first period. In the second period four out of the six races without the additional factor 2+ carried virulence against *Yr2*. For virulence against *Yr9* this is probably quite different. This resistance gene was not used in the first period, and even in the second period only one of the six races without the additonal factor 9+ carried the virulence against *Yr9* (race 19). This means that the corrected average number of virulence factors was probably between 4.5 and 5.0, still considerably below the average of the second period. The total number of virulence factors detected in the 8 races in the first period was probably eight if virulence against *Yr2* is included. In the second period this number had increased to 12 (in 11 races) if the virulence factors shown by the additional

differentials are excluded. This indicates a marked and rapid increase in the number of virulence factors. As there is no perfect stage known in this fungus changes in virulence must be due to mutation although parasexual recombination cannot be excluded. Unusual combinations of virulence factors can be introduced from elsewhere. Harder (1971) mentioned that there is some evidence of inoculum exchange between Tanzania, Kenya and Ethiopia. Race 19 might be such a race introduced from abroad. It deviates from the other races more than usual. As the total number of isolates evaluated in the two periods was rather restricted it is likely that not all races were detected. Table 1 therefore must be seen as representing the types of races dominating the yellow rust population in the periods concerned. Due to the scarcity of the data it is also not possible to construct the evolution tree of the races in Kenya. Races, that differ for one virulence factor only, occur quite frequently though (3 and 4, 6 and 8, 7 and 8, 4 and 12, 9 and 10, 14 and 15, 14 and 16, 15 and 17, 15 and 18, 16 and 17, 17 and 18). Most other races with similar numbers of virulence factors had very similar virulence patterns, the difference being rarely more than two factors. This indicates that single step mutations played an important role in the evolution of the yellow rust races in Kenya towards wider virulence spectra. The races 14, 15, 16, 17 and 18 provide a good example of this single step evolution pattern.

Virulence corresponding with the resistance *Yr2, 2+, 6, 6+, 7, 7+, 8, 9, 9+, A, SD and SU* is very frequent in Kenya (Table 1). Virulence against *Yr1, 3N,* and *10* appeared rather infrequent and virulence against *Yr3V, 4+, 5, CV* and *SP* was not detected.

The genes still fully effective in Kenya, *Yr3V, Yr4+, Yr5, CV and SP,* and the recently introduced *Yr15* (Gerechter-Amitai *et al.*,1989) may not be so for long. It is worth noting that *Yr3V, Yr4+, and CV* are no longer effective in Europe and virulence to *Yr5* was reported in India (Nagarajan, 1983) and Australia (Wellings, 1986). Gene *Yr15* is not yet fully exposed to the yellow rust populations in the world. Nevertheless, virulence to this gene has been observed.

Postulation of resistance genes to yellow rust

Postulated resistance genes in nine cultivars are shown in Table 2. Kenya Popo seems to carry the resistance factors A and SD as races carrying only one of the corresponding virulence factors gave a resistance reaction on this cultivar. The high frequency of virulence to *A* and *SD* (Table 1) is in agreement with the rapid break down of K.Popo's resistance. The cvs K.Kulungu, K.Kima, K.Tumbili and Mbuni showed a similar reaction to the six test races. 'K.Kulungu', though, showed a variable reaction with race 14 in the two

replicates (IT= 4-7) and is therefore considered to be susceptible to this race. These cultivars are assumed to carry *Yr7+*. The appearance of virulence to *Yr7+* in the eighties (Table 1) supports this conclusion as these cultivars too lost their resistance rapidly. The sister cvs K.Chiriku and K.Mlembe showed an R/S pattern to the test races indicating a resistance not belonging to any of the 16 resistance genes/factors tested with these races. The cvs Kwale and Pasa were only susceptible to race 14 indicating the presence of *Yr9+* and *A*. Here too the high frequency of the virulence factors corresponding to these genes could explain the break down of the resistance of these cultivars.

Of the cultivars released in the eighties only a few are still resistant and they were released very recently (K.Chiriku and K.Mlembe in 1989). It shows the rapid adaptation of the yellow rust population to the introduced resistances.

Resistance levels of Kenyan cultivars before and after release

The DS for six cultivars is shown in Table 3. All cultivars were completely resistant during the process of selection and at release. Soon after their release, all six cultivars showed a noticeably increased susceptibility. After this loss of complete resistance the level of susceptibility among the cultivars varied from low to moderately high. Cv Paa, for instance, became very susceptible at the end of 1982 (Bonthuis,1986) and was withdrawn from the list of recommended cultivars. It is assumed to possesses *Yr9*, a gene derived from rye and introduced through the IB/IR translocation (Zeller, 1973). The cvs K.Popo and K.Kulungu showed a high level of resistance during the first five years of cultivation, but since 1987 they showed a moderate level of resistance (residual resistance). The cvs K.Kima and K.Tumbili were released in 1984. Their resistance did not last for more than three years. The cv Pasa, released in 1989, was already showing a DS of 30% in its first year of cultivation in 1991. These examples demonstrate the consequences and the danger of breeding for race-specific resistance and how fast a resistance gene can be overcome.

After the breakdown of the resistance in these cultivars, their average DS varied from 17 % to 53 %. Even 'Paa' is considerably less susceptible than the extremely susceptible cv Morocco. Apparantly all cultivars carry moderate (Paa) to good levels (K.Popo, K.Kima and K.Kulungu) of residual resistance which may be conditioned by minor genes and could be of great importance in any breeding programme (Van Dijk *et al.*, 1988).

Sources of durable resistance

DS on cultivars, highly resistant at their release in the sixties, are given in Table 4. The cvs Africa Mayo, K.Kudu, Enkoy, K.Leopard, Bounty, Frontatch,

Bonny, and K.Plume, have shown a high level of resistance since 1976. Only Trophy lost some, but not much of its resistance, a high residual resistance similar to that of K.Popo and K.Kima (Table 3) remained. The resistance of these cultivars has therefore lasted for more than 20 to 30 years, and suggest that these cultivars are durably resistant. Such a form of resistance has been reported in various parts of the world. 'Cappelle Desprez' never lost its resistance in Great Britain although it occupied more than 80 % of the total wheat area, for more than 10 years (Johnson, 1978). The cvs Wilhelmina and its daughter Juliana were grown for 50 years in The Netherlands without loss of their resistance (Van Dijk *et al.*, 1988). 'Enkoy,' released in 1974 in Ethiopia, 'Gaines', 'Nugaines' and 'Luke' in the Pacific North West of USA (Line, 1978), 'Fan Lui' from China, 'Bonza 63', 'Crespo 63', 'Napo 63' and 'Amazonas' 69 from Ecuador (Broers, pers.comm.) seem to be durably resistant. Such durably resistant cultivars can be utilized in a breeding program with great effect particularly in areas were race-specific resistance is usually overcome rapidly by the pathogen.

To increase the possibility of achieving such resistance, the breeders should select parents with satisfying agronomic traits and having either a fair amount of residual resistance after the complete resistance broke down or carrying proven durable resistance. By crossing parents with residual resistance to parents with durable resistance the chance of obtaining a high level of durable resistance in the progenies is greatly increased.

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Table 1. Yellow rust races and their virulence factors detected in Kenya from 1969 to 1989. The virulence factors are indicated by the *Yr* resistance genes they neutralize.

Race	Year[1]	Virulence factors[2]		No. of vir. factors	
1	1975	-		0	
2	1969	6,7,SU		3	
3	1973	6,7,8		3	
4	1974	6,7,8,SD		4	
5	1970	3N,8,SD,SU		4	
6	1972	6,6+,7,8,SD,SU		6	
7	1971	3N,6,6+,8,SD,SU		6	
8	1972	3N,6,6+,7,8,SD,SU		7	
9	1986	6,7,8	(2,A)[3]	3	(5)[4]
10	1988	6,7,8,SD	(2,A)	4	(6)
11	1987	6,7,7+,8,SD	(A)	5	(6)
12	1989	6,7,8,SD,SU	(A)	5	(6)
13	1989	6,7,7+,8,10,SU	(2,A)	6	(8)
14	1986	2+,6,6+,7,7+,8,9+	(2,9,A)	7	(10)
15	1986	2+,6,6+,7,7+,8,9+,SD	(2,9,A)	8	(11)
16	1989	2+,6,6+,7,7+,8,9+,SU	(2,9,A)	8	(11)
17	1989	2+,6,6+,7,7+,8,9+,SD,SU	(2,9,A)	9	(12)
18	1986	2+,3N,6,6+,7,7+,8,9+,SD	(2,9,A)	9	(12)
19	1987	1,6,6+,7,7+,8,SD,SU	(2,9,A)	8	(11)

1) Data from 1969-1971 from Stubbs et al, 1974; data from 1972-1975 from Stubbs and van Silfhout, personal comm.

2) In total at least 17 virulence factors were studied over the whole period, which were those neutralizing the resistance genes in the 17 differentials used; *Yr*1 in Chinese, 2+ in Heines VII, 3V in Vilmorin 23, 3N in Nord Desprez, 4+ in Hybrid 46, 5 in *Triticum speltum album*, 6 in Heines Kolben, 6+ in Heines Peko, 7 in Lee, 7+ in Reichersberg 42, 8 in Compair, 9+ in Clement, 10 in Moro, SD in Strubes Dickkopf, SU in Suwon92/Omar, CV in Carstens V, and SP in Spalding Prolific. In the period 1986-1989 three additional virulence factors were studied (2 in Kalyansona ,9 in Federation 4/kavkaz and A in Anza). The factors SD, SU, CV, SP and A refer to resistance factors not yet designated and found in the cultivars mentioned; x+ refers to a virulence factor additional to x.

3) The additional factors not assessed in the period 1969-1975.

4) Including the additional factors.

Table 2. Infection types (R=0-3, I=4-6, S=7-9) of nine Kenyan wheat cultivars for six yellow rust races with known virulence factors and the postulated resistance genes.

No. and origin of race	Virulence factors of race[1]	Cultivar[2]								
		1	2	3	4	5	6	7	8	9
22 Rwanda	2,2+,6,6+,7,7+,8,9,A,SD	S	S	S	S	S	R	R	R	R
21 Zambia	2,3N,6,9,A	R	R	R	R	R	S	S	R	R
9 Kenya	2,6,7,8,A	R	R	R	R	R	R	R	R	R
14 Kenya	2,2+,6,6+,7,7+,8,9,9+,A,	R	I	S	S	S	S	S	S	S
23 The Netherlands	2,2+,3V,3N,4+,7,7+,9,9+, CV,SD,SU	I	S	S	S	S	R	R	R	R
24 Chile	2,2+,3V,3N,4+,6,6+,9,9+, SD,SU	R	R	R	R	R	S	S	R	R
Postulated resistance genes/factors		A,SD			7+			?	9+,A	

[1] See for explanation Table 1, note 2)

[2] 1=Kenya Popo, 2=Kenya Kulungu, 3=Kenya Kima, 4=Kenya Tumbili, 5=Mbuni, 6=Kenya Chiriku, 7=Kenya Mlembe, 8=Kwale, 9=Pasa

Table 3. Yellow rust disease severity (DS) on the 0-100 % scale of six Kenyan wheat cultivars before and after their release.

Year of release	Cultivar	Before release	After release			
			1987	1989	1991	mean
1981	Paa	0	70	60	30	53
1982	K.Popo	0	10	30	15	18
1982	K.kulungu	0	5	30	30	22
1984	K.Kima	0	10	30	10	17
1984	K.Tumbili	0	40	60	20	40
1989	Pasa	0	–	–	30	30

Table 4. Yellow rust disease severity (DS) on the 0-100 % scale of 9 Kenyan wheat cultivars over a period of 16 years.

Year of release	Cultivar	Mean DS in two periods		Overall mean[2]
		1976-1979[1]	1986-1991	
1960	Africa Mayo	0	1	0.8
1966	Kenya Kudu	1	2	1.4
-	Enkoy[3]	–	2	2.6[4]
1966	Kenya Leopard	3	7	5.4
1967	Bounty	9	5	6.8
1963	Frontatch	12	4	7.4
1968	Trophy	0	15	–[5]
1967	Bonny	10	10	9.8
1965	Kenya Plume	20	10	14.0

1) Data derived from the national variety trials of Kenya, NPBRC, Njoro.
2) Mean DS over the four years in the seventies and the six years in the later period.
3) Not released in Kenya, but widely grown in Ethiopia from 1974 onward.
4) Means calculated by correcting for the missing values.
5) For Trophy no mean is given as the DS in the second period was significantly higher than the DS in the first period.

Chapter 2

Lack of durability of resistance to cereal rusts in wheat when selection is for complete resistance.*

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Summary

Twenty one bread wheat entries were selected after careful screening for complete or near complete resistance to yellow rust (*Puccinia striiformis*), stem rust (*P. graminis*), and leaf rust (*P. recondita*). In only a few cases such as 'Kenya Tembo' for yellow rust and Kenya Kongoni for stem rust the resistance was not complete but moderate. In 1987, the 21 entries were intercrossed in a near half diallel scheme. The resulting 190 F2 populations were advanced to the F7 under selection for complete resistance for all three rusts and for good agronomic types. In 1992 the selected lines (140) and all parents were assessed for their resistance to the three rusts. Of the 21 parents twelve showed a break down of yellow rust resistance, five a break down of stem rust resistance and two a breakdown of leaf rust resistance. In addition several of the 140 selected F7 lines, all still resistant in the F6, had become susceptible to one or more of the rusts. Apparently, a build up towards more complex races, especially of yellow rust, is inevitable for the wheat-cereal rust pathosystems when the selection is for complete or near complete resistance.

Introduction

The major diseases of bread wheat in East Africa are (*Puccinia striiformis*), stem rust (*P. graminis*), and leaf rust (*P. recondita*). Due the world wide resistance breeding, stem rust seems by and large controlled and leaf rust too does not form a great threat at present. Yellow rust, however, is far from controlled. Newly introduced resistant cultivars loose their resistance within a few years

*Submitted

due to the appearance of new, often more complex races (Danial and Stubbs, 1992).

The development of new races as a response to the introduction of resistant cultivars is especially associated with breeding for major gene resistance and these major genes are typically selected for when the breeding is for high levels of resistance (Parlevliet, 1993).

This research aimed at initiating a standard breeding program where the selection is for complete or near complete resistance and to follow the effectiveness of the resistances used.

Materials and methods

Screening

The research was carried out predominantly at Njoro, Kenya by using both the main season, April to September, and the off season (by the use of irrigation when needed), November to March.

Screening of entries for complete or near-complete resistance to the three rusts and for a good agronomic performance started in 1984, main season, with over 5000 entries at Njoro (Table 1). The selected entries were re-assessed in the subsequent off-season. Those selected after two cycles at Njoro were tested in the main season of the second year at seven locations, Njoro, Molo, Eldoret, Endebess, Narok, Timau and Ol Joro Orok to expose the selected lines to possibly different pathogen populations of each rust. In the second main season, 1985, another large number of entries, over 3000, were screened following exactly the same procedure. In 1986 another set of entries was screened (Table 1). This resulted in the end in 35 selected entries, whereby the number of selection cycles varied from five to one. All tested entries originated from CIMMYT germplasm.

Table 1. Number of wheat entries in the various screening stages.

Year of planting	Season of screening 1984		1985		1986	
	main	off	main	off	main	off
1984	5491	458	262[1]	173	112[1]	16
1985	–	–	3334	492	127[1]	10
1986	–	–	–	–	2363	9

[1] tested at seven locations

Planting was carried out in blocks containing 50 to 100 plots. Each plot consisted of two rows of 2m length and 20 cm apart. Between the blocks a spreader row was planted of the cv. Morocco highly susceptible to all three rusts. At Njoro, plots were usually inoculated by spores of yellow rust which were collected during the previous season while at all other sites and to the other rusts in Njoro, the epidemics started from natural infection.

Disease severity (DS) of the three rust species was assessed according to the Peterson scale (0-100%) (Peterson *et al.*, 1948). The infection type (IT) was evaluated within the range R (resistant), MR (moderate resistant), MS (moderate susceptible) and S (susceptible).

The 35 entries selected for a good agronomic performance and high level of resistance to the three rust species were exposed to six yellow rust races of known virulence spectrum (Table 2) at the seedling stage at the Research Institute for Plant Protection (IPO), Wageningen, The Netherlands. Per entry 10-15 seedlings were grown under controlled conditions in a growth chamber at 15 °C with 16 hrs of light (about 22.000 lux) and were inoculated in the first leaf stage with urediospores suspended in mineral oil (soltrol 170). The plants were then incubated at 10 °C for 24 hrs in a dew chamber and placed in a growth chamber with a day/night profile of 16/8 hrs, at about 28.000 lux and a temperature profile of 18/15 °C respectively. Infection types (IT) were recorded 16 days after inoculation by using the 0-9 scale of McNeal *et al.* (1971). The races used represented together 16 virulence factors. The races were avirulent to *Yr1, Yr4 and Yr5*. The *Yr4* and *Yr5* resistance genes are not used in East Africa and virulence to *Yr1* was not yet detected at the time of testing in Kenya.

Of the 35 entries 15 were resistant (R) to all six races (Table 3) and they were selected as parents for the breeding program. To add locally adapted materials to the breeding program six widely tested Kenyan cultivars for resistance to the three rusts were selected as well (Table 5, entries nr. 16-21).

Table 2. Virulence factors of six yellow rust races compatible with specified resistance genes in wheat.

Race	Origin	Virulence factors*	nr. of virulence factors
1	Kenya	2,6,7,8,A	5
2	Zambia	2,3N,6,9,A	5
3	Rwanda	2,2+,6,6+,7,7+,8,9,A,SD	10
4	Kenya	2,2+,6,6+,7,7+,8,9,9+,A	10
5	Chile	2,2+,3V,3N,4+,6,6+,9,9+,SD,SU	11
6	Netherlands	2,2+,3V,3N,4+,7,7+,9,9+,CV,SD,SU	12

*) Virulence factors are designated by the number of the *Yr* resistance gene it is compatible with.
a + means an additional resistance gene(s) present together with the known one. A, SD, SU and CV refer to resistance factors not yet designated in the cultivars Anza, Strubes Dickkopf, Suwon 92/Omar and Carstens V respectively.

Breeding program

Crosses were made between the 21 selected entries and cultivars in a half diallel scheme. Of a number of crosses no or insufficient F2 seeds were obtained, leaving 190 crosses to proceed with. About 20.000 F2 seeds, representing these 190 crosses were planted early May, 1989. Each cross was planted in two rows of 10 m long. Seeds were space planted (15-20 cm) and the cv. Morocco was planted between each plot to act as a spreader row for the three rusts. The infection was started by inoculating the spreader row with race 134E150. After single plant selection in the F2, line selection was carried out in the subsequent generations (Table 4). In each generation lines were selected for complete to near complete resistance to the three rusts and for a good agronomic performance as before. In each selected line, five plants were advanced to the next generation to give five sister lines. In the F6, the seed of each selected line was bulk harvested for a more extensive test in the F7. The F7 and the parents were planted on the 28th of May, 1992 in a non-replicated trial with plots measuring 1.44 m x 6 m. The level of resistance to yellow rust, stem rust and leaf rust was assessed as described above. Yield of each plot was determined and the best F7 lines were harvested for a further yield test. Thirteen F8 lines and their twelve parents were planted in four replicates in a randomized complete block design on 13th of November 1992 at Njoro. Each plot measured 1.44 m x 6 m and the seed rate was 120 kg/ha.

Results

Screening

The 35 selected lines were not tested equally thorough, 16 were tested in six seasons of which twice at seven locations, 10 in four seasons and once at seven locations and 9 in two seasons only. The three rusts were nearly always present, stem rust only at the end of the season. 1984 was a very dry year and the selection for yellow rust was poor but the selection for stem rust and leaf rust resistance was successful. The years 1985 and 1986 were characterized by severe epidemics of yellow rust and selection for high levels of resistance was easily done. A race survey of yellow rust, carried out in 1986, revealed that race 4 (Table 2) with 10 virulence factors was the most prevalent one. These 35 entries with a good agronomic performance, assessed by eye, had a high level of resistance to the three rust species. Mean DS for yellow rust, stem rust and leaf rust was 0.0, 2.2 and 1.7%, respectively.

The 35 entries, exposed to six yellow rust races, could be classified into five groups (Table 3). Group A with 15 entries was resistant to all six races. The other groups (B-E) showed a differential pattern, with susceptibility to 2, 3 or 5 of the races. The differential patterns suggest the presence of *Yr7* and an unidentified gene in B, *Yr6* and *Yr7* in C, *Yr6* and an unidentified gene in D, and *Yr2* and an unidentified gene in E.

Table 3. Wheat entries classified into five resistance groups according to the reaction pattern with six yellow rust races. An entry was classified as resistant (R) if its infection type (IT) was on average 3 or less and as susceptible (S) if its average IT was more than 7. There were no entries with an intermediate IT (4 to 6).

Resistance group	n	Races					
		1	2	3	4	5	6
A	15	R	R	R	R	R	R
B	7	S	R	S	R	R	S
C	2	S	R	S	S	R	R
D	3	S	S	R	R	S	R
E	8	S	S	S	R	S	S

Breeding program

In 1988, the F2 population was exposed to a severe yellow rust epidemic in which races with 10 and 11 virulence factors predominated. From 20.000 F2 plants of the 190 crosses, 487 plants were selected originating from 62 crosses. The F3 lines were planted during the off season of 1988/89 and were again exposed to a severe epidemic of yellow rust where highly complex races dominated. During this season, 209 lines belonging to 22 crosses were selected. At all generations, only lines were selected with no or very little yellow, stem and leaf rust. Ultimately, 140 lines were selected in the F6 coming from 14 crosses only (Table 4). The 140 F7 lines were planted in 1992 and yellow rust started at the seedling stage and continued to increase in time while stem and leaf rust appeared at the end of the season. The F7 lines showed a large variation in disease severity to all three rusts. For yellow and stem rust, about 24% of the lines could be classified as moderately to fairly susceptible. Of the 140 lines, 107 showed a complete to near complete resistance to yellow rust in the field in the adult plant stage and 33 were moderately susceptible to susceptible.

Table 4. Number of wheat lines selected and number of crosses involved in the selected lines in the generations F2 to F6.

Generation and season	Year planted	No. of lines selected	No. of crosses involved
F2-main	1988	–	190
F3-off	1988/89	487	62
F4-off	1990/91	209	22
F5-main	1991	282	15
F6-off	1991/92	205	14
F7-main	1992	140	14

The IT had been recorded in the seedling stage (in the field) as well. Of the 107 lines with complete or near complete resistance in the adult plant stage, 24 had a low IT (0-3), 12 an intermediate IT (4-6) and 71 a susceptible IT (7-9) in the seedling stage. Apparently seedling resistance (=overall resistance) and adult plant resistance to yellow rust both occurred in these lines.

Of the 14 crosses, from which the 140 selected F7 lines originated, six were between entries that had lost their high level of resistance in 1992 (Table 5). Of the F7 lines derived from these six crosses 57 were still highly resistant

with a DS of 5% or less. For instance, of the cross between entries 19 (DS=30%) and 13 (DS=50%) six highly resistant F7 lines were obtained, and from the cross 17 (DS=60%) x 21 (DS=20%) three. This much higher level of resistance in the F7 lines strongly indicates that accumulation of resistance genes occurred. It can be accumulation of residual resistance, which occurs with a high frequency (Danial *et al.*, 1994), but accumulation of "broken resistance genes" is another possibility, if the parents lost their resistance to different races.

Table 5. Disease severity (DS) of yellow rust (*YR*), stem rust (*SR*) and leaf rust (*LR*) of 21 spring wheat entries measured in 1984, 1985 and 1986 for YR at Njoro and Molo, for Stem rust at Njoro and Narok and for leaf rust at Njoro and Endebess. DS for *YR*, *SR* and *LR* was recorded in 1992 at Njoro.

Entry	Mean DS in 1984-1986			DS in 1992[2]		
	YR	*SR*	*LR*	*YR*	*SR*	*LR*
1[1]	0	2	0	**40**[2]	0	0
2[1]	0	2	0	0	0	0
3	0	5	0	5	**20**	0
4[1]	0	5	0	**40**	5	0
5[1]	0	5	0	5	**20**	0
6	0	5	0	0	5	0
7	0	5	5	**40**	5	**30**
8[1]	0	0	0	0	2	0
9	0	2	5	tr	**40**	**20**
10	0	0	5	tr	**90**	tr
11[1]	0	0	0	**20**	0	5
12[1]	0	0	0	**20**	**20**	0
13[1]	0	1	0	**50**	0	0
14	0	0	0	**20**	0	0
15	0	0	8	**25**	0	2
16 K.Kongoni	10	20	0	10	0	tr
17 K.Tausi[1]	0	0	0	**60**	tr	0
18 K.Tembo	30[3]	2	0	30	2	tr
19 K.Fahari	10	5	0	**30**	0	0
20 Kwale[1]	0[4]	0	0	**25**	2	0
21 Mbuni[1]	0	1	0	**20**	2	tr

1) parents of the selected F7 lines, 2) bold figures indicate a break down of resistance compared to 1984-86, and tr = trace; 3) resistance already broken, 4) observation from 1987

Level of resistance of the parents

A general shift towards susceptibility was observed for the three rust species (Table 5). Twelve parents out of the 21 lost their resistance to yellow rust within this short time span. For stem rust, this was five out of 21 parents and for leaf rust, two out of 21 parents. The DS of K.Tembo apparently represents residual resistance (Danial and Stubbs, 1992) as this moderate level of susceptibility has not changed after the complete resistance of this cultivar broke down in 1978. This cultivar still occupies a large part of the wheat acreage in Kenya.

Despite the break down of resistance to the three rusts in some of the lines and the parents selected (Table 5), the mean yield in kg/ha of the thirteen lines selected in the F7 was higher than the mean yield of the twelve parents (Table 6). For instance, the mean yield of the cvs. Kenya Tausi and Mbuni in 1992 and 1993 was 2805 and 3326 kg/ha, respectively, while the mean yield of the lines derived from these parents was 4043 and 4319 Kg/ha, respectively.

Table 6. Mean yield and range in kg/ha of 12 parental and 13 selected wheat lines planted at Njoro in 1992 and 1993, respectively.

Year	Parents		Selected lines	
	Mean	Range	Mean	Range
1992(F7)	2686	1360-3578	4070	2000-5550
1993(F8)	3218	2728-3871	3372	2706-4319

Discussion

Because of the pressure of yellow rust inoculum in Kenya throughout the year, seedling resistance to this rust is also required, especially for late plantings at high altitudes. Of about 11.000 entries ultimately 15 entries were selected that had yellow rust resistance at all plant stages combined with stem rust and leaf rust resistance and a good agronomic performance. Despite the fact that nearly all the parental materials were highly resistant to the three rusts (Table 5), and despite a continued selection from the F2 to the F7 for complete to near complete resistance, still some 25% of the selected F7 lines were not resistant any more for yellow rust and or stem rust. Of the 21 parents selected for high resistance to all three rusts, twelve became susceptible to yellow rust, five to

stem rust and two to leaf rust in a period of about five years. This selection program shows clearly that vigorous selection for complete resistance to any of the three rusts, and especially to yellow rust, is of no avail. The best that can be achieved is just to keep out of reach of the new more complex races. For yellow rust, Danial and Stubbs (1992) showed the rapid increase of complexity of yellow rust races in Kenya, but with stem rust and leaf rust, the situation is the same although the erosion of resistance seems less rapid than with yellow rust resistance.

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II. Quantitative resistance: aspects of assessments

Introduction

In a breeder's selection field, evaluation for quantitative resistance of the host genotypes usually takes place by assessing the amount of tissue affected by the pathogen at a given moment. The amount of tissue affected reflects the amount of pathogen present and so the level of resistance. However, there are other factors besides resistance that may influence the amount of tissue affected and so interfere with a proper assessment of the resistance. Interfering factors could be interplot interference, earliness, soil fertility, assessment dates, leaf layer and plant height, all factors which may affect plant habit and inoculum distribution and density.

The importance of interplot interference in the evaluation of the host-parasite interactions has been reported for different hosts and parasites (Van der Plank, 1968; Paysour and Fry, 1983; Parlevliet and Danial, 1992). Screening of a large number of wheat entries in a breeders field is generally carried out in small plots, adjacent to each other. In this situation, the level of resistance of an entry can be underestimated (positive interference) if substantial amounts of inoculum from a highly susceptible neighbour is imported, which can easily happen with wind borne pathogens.

Earliness is another factor that may affect the assessment of the resistance of entries to different pathogens. In the screening trials, assessment for resistance is usually done for all entries at one moment. If the entries show large differences in earliness, the period of exposure to the pathogen will differ considerably for late and early entries. Late entries tend to be less affected and therefore considered more resistant because they are exposed for a shorter period to the pathogen and not because they are more resistant. For instance, the resistance of wheat cultivars to Septoria leaf and glume blotch were found to be associated with lateness, the later the entries, the lower the glume blotch score (Tavella, 1978; Rosielle and Brown, 1980; Shaner et al. 1975).

Soil fertility too may influence the level of the disease and so the assessment of the level of resistance and/or the ranking order for resistance of the entries. Higher fertilizer rates may encourage greater vegetative growth and better environmental conditions for certain pathogens. The incidence of the cereal rusts, and especially that of yellow rust were often observed to increase with an increased level of nitrogen (Darwinkel 1980; Daamen et al. 1989 and Ash et al., 1991) but rarely reported, whereas fertilization with phosphorous decreased the incidence of both leaf rust and powdery mildew (Bouquet and Johnson, 1987).

Observation date too is a factor that can affect the assessment of resistance. As the epidemic development is not expected to follow exactly the same pattern in all wheat genotypes, the ranking order of wheat entries may vary with different observation dates. Especially when entries with small differences in quantitative resistance are concerned, this aspect may play a significant role.

Different methods have been reported on how to assess the level of resistance in the field for the cereal rusts. Disease severity (DS) on a scale of 0-100% (Peterson et al, 1948), is often used to estimate the percentage of tissue affected by the rust at a certain moment during the epidemic development. From DS's, measured at several dates, the apparent infection rate (r) can be calculated (Van der Plank , 1963) and or the area under disease progress curve (AUDPC), (Wilcoxson et al, 1975) can be computed. Shaner and Finny (1980) found that AUDPC was a better criterion for measuring the partial resistance than the apparent infection rate *r*. Broers (1989) compared various methods and concluded that the DS and AUDPC were the most suitable parameters to measure the partial resistance in the field to leaf rust in wheat, whereas the r value seemed an unsuitable estimator of partial resistance.

The assessment of infection types (IT) on a scale of 0-9, according to McNeal et al, 1971., is a parameter for resistance often used and quite different from DS. It can be assessed at any plant stage.

The average coefficient of infection (ACI) is another method used by several scientists and by CIMMYT for rating or ranking entries for their resistance to the rust diseases (Stubbs et al, 1986). This method has clearly some disadvantages. Roelfs (1988), for instance questioned how a reaction of 60MR could be considered equal to 20S, just because their ACI's where so similar, especially if interplot interference plays a significant role.

In this chapter the main objectives are:

1. To investigate the type and magnitude of interplot interference for yellow rust in wheat.
2. To study the association between DS and IT
3. To examine the effect of nitrogen rates on the level and assessment of resistance to yellow rust.
4. To study the effect of earliness on the assessment for resistance.
5. To find out whether the assessment on one observation date and on one leaf layer is sufficiently representative for the disease severity as measured by the AUDPC.
6. To find out whether observation date affects the ranking order of the wheat genotypes for their resistance to yellow rust.

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Chapter 3

Does interplot interference affect the screening of wheat for yellow rust resistance?*

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Summary

In small plots, adjacent to one another, a representational error can be expected when screening for quantitative forms of resistance to airborne pathogens. The representational error or interplot interference may occur as an underestimation of the level of resistance and/or as an error in the ranking of the entries tested.

Four experiments were carried out with wheat (*Triticum aestivum*) exposed to yellow rust (*Puccinia striiformis*), three in Kenya, one in Mexico (exp. III).

In experiment I 57 entries were compared in an unreplicated trial with three adjacent and one isolated plot situation. The range in, the standard deviation of and the ranking order for disease severity (DS) between the 57 entries were the same for all plot situations at all observation dates.

In experiment II nine entries from experiment I, representing a wide range of quantitative resistance and having a similar heading date, were compared in adjacent plots consisting of two rows of 10 m in eight replicates and isolated plots of one, six and ten rows of 4 m in three replicates. The range in, the standard deviation of and the ranking order for DS between the entries were very similar for the four plot situations.

The 10 entries in experiment III differed from those in experiment II, but represented a similar wide range of resistance. Three adjacent plot situations of 0.9 x 0.5 m, 0.9 x 2.0 m and 2.7 x 2.0 m respectively were compared with one isolated one with plots of 2.7 x 2.0 m. The ranking order was not affected, the range in and the standard deviation of the DS in the isolated plots were slightly larger than in the adjacent plots.

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In experiment IV two mixtures of two entries each were made. Per mixture one entry was fairly resistant (R) the other rather susceptible (S). Within each mixture the entries had a similar heading date. The ratios of the R:S mixtures were 0:100, 50:50, 67:33, 75:25, 82:18 and 100:0. The DS of each entry was the same as its DS in monoculture irrespective of the mixture ratio. There was no mixture effect on DS.

The three experiments in Kenya gave no indication of any interplot interference occurring. In Mexico there was a very slight underestimation of the resistance in adjacent plots. The ranking order was always the same irrespective of the test plot situation. The screening of wheat for yellow rust resistance in small adjacent plots is representative for the farmers fields. This is contrary to what has been found in other windborne pathosystems such as barley-barley leaf rust (strong under estimation of resistance), barley-powdery mildew (some under estimation of resistance and different ranking order) and durum wheat-stem rust (fair under estimation of resistance).

Introduction

Screening for resistance is normally carried out in small plots neighbouring each other. The assessment does not take into account whether the lesions developed from inoculum produced by the plot itself or by a neighbouring plot. The more resistant entries may receive substantial amounts of inoculum from more susceptible neighbours while the latter ones may receive much smaller amounts from the more resistant neighbours. The amount of disease on the more resistant entries may therefore be overestimated, that on the highly susceptible ones underestimated. This interplot interference, operating especially with wind borne pathogens, may seriously underestimate the level of partial or quantitative resistance (Van der Plank, 1963). Van der Plank called it representational error. This error may vary greatly. From very large in barley to barley leaf rust, *Puccinia hordei*, (Parlevliet and Van Ommeren, 1975, 1984) to moderate in barley to powdery mildew, *Erysiphe graminis* f.sp. *hordei* (Nørgaard Knudsen et al., 1986) and maize - *Puccinia sorghi* (Randle et al., 1986).

The representational error may take two forms (Parlevliet and Danial, 1992):

i) The level of quantitative resistance is underestimated, which is expressed by a reduced range and standard deviation of the entries tested.

ii) The ranking order for resistance of the entries is affected. The ranking in adjacent plots is different from those in isolated plots, which represent the farmers' situation.

The amount of disease present is assessed either at one representative observation date, disease severity (DS), or as the area under the disease progress curve (AUDPC). Both parameters can be used in studying the interplot interference. The AUDPC uses more information; with DS one can study the effect of observation date on both the interplot interference and the ranking order of the tested entries.

As yellow rust is a wind borne pathogen the research reported here aimed at investigating the magnitude of the representational error if present with regard to both the level and ranking of the resistance. Both the AUDPC and the DS were used to study the effects mentioned in the former paragraph.

Materials and methods

Experiment I, 1988

Hundred and fifty spring wheat entries, originating from the International Maize and Wheat Improvement Center, CIMMYT, were used. The entries were evaluated for their level of resistance under field conditions in four plot situations:

A1: adjacent plots of one row of 2.0 m length;
A2: adjacent plots of five rows of 2.0 m length;
A3: adjacent plots of ten rows of 2.0 m length;
I: isolated plots of ten rows of 2.0 m length. Each plot was isolated from all others by 2 m of oats in all directions.

Sowing took place at Njoro, Kenya, altitude 2160 m on the 15th of March at a seed rate of 120 Kg/ha and a row distance of 20 cm in an unreplicated trial. On 28 April, one pot containing 3 to 4 spreader plants of the susceptible cv Morocco was placed in each plot for a period of one week. The spreader plants were grown, inoculated under shed conditions and were transferred to the field just before the sporulation started. Race 134E150 (race designation according to Johnson et al., 1972), the predominant race in Kenya, was used for inoculation. Disease severity (DS) was assessed on the upper three leaves at four dates (D1 to D4) on 21 July, 27 July, 3 August and 11 August. DS was recorded according to the 0-100 scale (Peterson et al., 1948) and subjected to logistic transformations and 10 was added to obtain positive values. Entries with a DS below 5% were excluded from data analysis as they were considered not to represent quantitative resistance. This resulted in 57 genotypes suitable for analysis. Area under the disease progress curve (AUDPC), derived from the four observation dates was calculated as 3.5 x D1 + 7 x D2 + 7 x D3 + 3.5 x D4. This formula disregards the disease prior to July 21st and measures the

AUDPC in days x DS for the period from D1 to D4 assuming a linear course of the transformed DS's.

Experiment II, 1989

From experiment I, nine wheat entries representing different levels of quantitative resistance and with a similar maturity were selected. The entries were evaluated at Njoro in five plot situations:

A1: adjacent plots of two rows of 10 m length in four replicates in a randomized complete block design;

A2: adjacent plots of two rows of 10 m length in four replicates in a non randomized design. With A1 and A2 two spreader rows of the highly susceptible cv Morocco were planted perpendicular to the rows to be assessed. Each replicate of 9 double row plots started and ended with a two-row plot of cv Hindi-62, a moderately susceptible cultivar and a two-row spreader plot of cv Morocco. Between entry 4 and 5 again a two-row spreader plot of Morocco bordered on both sides by a two-row plot with "Hindi-62" was inserted. "Hindi" was inserted between Morocco and the entries to be tested to prevent a differential exposure of the entries to be tested to the enormous spore production of the spreader cv Morocco;

I1: isolated plots of one row of 4 m length ;

I2: isolated plots of six rows of 4 m length;

I3: isolated plots of ten rows of 4 m length.

The isolated plots were isolated from one another by 4 m of oats in all directions. Planting took place on 25 April, at a seed rate of 120 kg/ha and a spacing of 20 cm. A1 and A2 were planted in four, I1, I2 and I3 in three replicates. Inoculation of I1, I2 and I3 took place on 5 June with the same race and in the same way as described in experiment I. For A1 and A2, one pot containing 3 to 4 almost sporulating plants of Morocco was placed every 4m inside the double spreader rows. After one week the pots were removed from the field.

DS was recorded on each of the upper three leaves individually on each of 15 tillers taken at random from each plot on 7 July, 14 July and 21 July.

Experiment III, 1992

This experiment was carried out at El-Batan (CIMMYT), Mexico, altitude 2250 m, to study the interplot interference in an environment different from that in Kenya. Ten spring wheat entries representing a wide range in quantitative resistance were studied in four plot situations.

A1: adjacent plots of 0.9 x 0.5 m (2 rows of 50 cm on a bed, beds 90 cm apart)

A2: adjacent plots of 0.9 x 2.0 m (2 rows of 2 m on a bed, beds 90 cm apart)
A3: adjacent plots of 2.7 x 2.0 m (6 rows on 3 beds) and
I: isolated plots of 2.7 x 2.0 m (6 rows on 3 beds).

The experimental design was a randomized complete block design with three replicates. The isolated plots were separated from one another by 10 m of oats in all directions.

Planting took place on 15 January 1992 at a seed rate of 120 kg/ha. On 20 February sporulating (race 14E14) spreader plants of the cv Morocco were placed in each plot at the rate of one pot containing 1 to 3 plants per one bed per m row length. After one week the pots were removed from all plots. Between tillering and heading, the plots were supplemented with an additional irrigation twice a week for 30 minutes in the afternoon.

After heading the DS was measured on the upper two leaves at two observation dates with seven days interval. Subsequently, DS was transformed as described before.

Experiment IV, 1992

This experiment, carried out at Njoro, studied the development of yellow rust in two cultivar mixtures each consisting of a resistant and susceptible cultivar at different ratios. Two fairly resistant (R), awnless cultivars (Bounty and Frontatch) and two rather susceptible (S), awned genotypes (PR-2 and PR-46) were used to produce the two mixtures. Bounty and PR-2 formed mixture A and Frontatch and PR-46 mixture B. In this way, each entry could be recognized in each mixture. Days to heading (DH) of the two entries in each mixture were similar. Mixture A was considered as late maturing (DH = 75) and mixture B as early maturing (DH = 65).

Mixture A and mixture B were represented by four ratios of R:S. These were 50:50, 67:33, 75:25 and 82:18. In addition, the individual entries were planted in monoculture (ratio 0:100 and 100:0). The sowing took place on 4 April in plots of eight rows of 4.0 m and with a row spacing of 20 cm in four replicates as a randomized complete block design at a seedrate of 120 kg/ha. DS was recorded when heading had been completed at three consecutive dates a week apart on the upper three leaves on each component of the mixtures separately and the AUDPC was calculated as 3.5 x D1 + 7 x D2 + 3.5 x D3 disregarding the disease prior to D1 as in experiment I.

Results

Experiment I

Treatments A1, A2 and A3 did not differ from each other. The mean DS was about the same at each observation date and both the range between the 57 entries and the standard deviation varied little. The isolated plots (I) showed a slightly reduced DS, but range and standard deviation were very similar to those of the other plot situations. If AUDPC is considered alone the mean decreased, the range increased and the standard deviation decreased from A1 to I (Table 1). The tendency of the DS and AUDPC to decrease from A1 to I could be due to a gradient across the field as there were no replications.

Plot situations did not affect the ranking order of genotypes. This is shown by the Pearson linear correlation coefficients of the AUDPC between isolated plots (I) and adjacent plot situation A1, A2 and A3 respectively. Correlation coefficients between all treatments were extremely high and varied from 0.97 to 0.99. Between A1 and I, the most extreme plot situations, r was 0.97.

Table 1. Mean, range and standard deviation of the yellow rust disease severity (transformed) and area under the disease progress curve (AUDPC) of 57 wheat entries in four plot situations.

	Plot situation[1]	Observation date				AUDPC
		21 July	27 July	3 Aug	11 Aug	
Mean	A1	8.7	9.3	9.8	10.4	201
	A2	8.2	9.0	9.5	10.2	194
	A3	8.0	10.0	9.4	10.2	192
	I	7.5	8.6	9.0	9.6	184
Range[2]	A1	6.0	5.9	5.4	6.8	117
	A2	5.7	6.3	5.9	7.2	123
	A3	5.5	6.8	7.5	6.6	134
	I	5.0	7.5	9.2	9.2	138
St.dev.[2]	A1	1.40	1.46	1.34	1.35	96.0
	A2	1.27	1.37	1.33	1.33	92.9
	A3	1.38	1.40	1.35	1.27	92.1
	I	1.31	1.49	1.53	1.41	88.2

[1] A1, A2, A3 = adjacent plots of one, five and ten rows wide resp. and I = isolated plots.
[2] Range and standard deviation between the entries measuring difference between extremes and spread resp.

Experiment II

Treatments A1 and A2 were very similar. The Spearman rank correlation coefficient for DS between A1 and A2 for the three observation dates were 0.89, 0.96 and 0.99 respectively. Therefore A1 and A2 were taken together as one plot situation with eight replicates (A).

Table 2 shows the mean DS for the nine entries. The range and the standard deviation for the adjacent plots (A) was at all three observation dates not smaller than those for the isolated plots (I1, I2, I3). On the contrary, at the observation dates 14 and 21 July the adjacent plots tended to have a somewhat larger range and standard deviation than the isolated plots. In the Anova this tendency appeared significant as the entry x plot situations interaction had a significant F-value (at $P = 0.01$).

The ranking of the entries was not affected by the plot situation within observation dates. The Spearman rank correlation coefficients between the DS's of the adjacent plots (A) and those of the isolated plots (I1, I2 or I3) within observation dates ranged from 0.88 to 0.99 with a mean of 0.94.

The observation dates did affect the ranking order of the entries (Table 2). Pr-63 for instance had a DS not different from that of PR-2 and significantly higher than that of PR-6 on 7 July. On 21 July PR-63 did not differ significantly from PR-6 and was significantly lower than PR-2. This is also shown by the Spearman rank correlation coefficients for the four plot treatments between 7 and 21 July which were 0.88, 0.92, 0.87 and 0.82 for A, I1, I2 and I3 respectively. These values are considerably lower than those between A and the isolated plot situations within observation dates (see above).

Table 2. Mean yellow rust disease severity (transformed) at three observation dates of four plot treatments for nine wheat entries.

	7 July					14 July					21 July				
Entry	A	I1	I2	I3	Mean[1]	A	I1	I2	I3	Mean[1]	A	I1	I2	I3	Mean[1]
Morocco	9.9	9.7	9.0	8.1	9.2 a	11.6	11.9	11.5	11.6	11.7 a	15.2	15.3	15.3	15.3	15.3 a
PR-2	8.1	7.0	6.2	5.2	6.6 b	10.4	10.6	10.1	9.5	10.2 b	12.1	11.5	11.2	11.2	11.5 b
PR-63	6.6	6.4	7.0	6.2	6.5 b	8.3	8.7	8.8	8.6	8.6 c	9.1	9.9	9.6	9.8	9.6 cd
PR-45	6.9	7.5	5.4	4.4	6.1 b	8.2	9.0	8.5	7.4	8.3 cd	9.8	10.5	10.2	10.1	10.2 c
PR-105	5.8	5.3	3.9	3.0	4.5 c	7.6	8.2	7.7	7.0	7.6 def	8.5	9.7	9.1	8.3	8.9 de
PR-41	5.6	4.5	4.3	4.0	4.6 c	7.7	7.5	7.0	7.0	7.3 efg	8.4	8.4	8.4	9.1	8.6 e
PR-6	4.6	4.6	4.1	3.8	4.3 c	7.8	7.8	7.7	7.9	7.8 de	9.6	10.1	9.6	10.1	9.9 c
PR-103	4.4	3.1	3.2	3.0	3.4 d	5.7	7.0	6.7	7.0	6.6 g	6.9	8.0	8.3	7.7	7.7 f
PR-134	3.9	3.2	3.8	2.2	3.3 d	6.8	7.0	7.2	6.9	7.0 fg	8.2	9.3	8.3	8.5	8.6 e
Range	6.0	6.6	5.8	5.9	5.9	5.9	4.9	4.8	4.7	5.1	8.3	7.3	7.0	7.6	7.6
St.dev.[2]	1.92	2.16	1.88	1.83	1.89	1.78	1.67	1.58	1.58	1.64	2.49	2.15	2.21	2.26	2.26
Mean	6.2	3.7	5.2	4.4	5.4	8.2	8.6	8.4	8.1	8.3	9.8	10.3	10.0	10.0	10.0

[1] Means with different letters are significantly different at P = 0.01 according to the LSD test
[2] Standard deviation of the nine entries measuring their spread

Table 3. Mean yellow rust disease severity (transformed) at two observation dates of four plot treatments (S) for ten wheat entries.

Entry	22 May					8 June				
	A1	A2	A3	I	Mean[1]	A1	A2	A3	I	Mean[1]
Taichung	11.5	11.0	10.1	10.8	10.8 a	12.3	12.5	11.7	12.5	12.3 a
E-3	10.0	9.8	9.8	10.1	9.9 b	11.3	10.8	10.5	11.1	10.9 b
E-35	10.6	9.5	8.9	9.8	9.7 b	11.4	10.7	10.2	10.8	10.8 b
E-2	10.1	9.7	8.6	9.2	9.4 bc	10.5	10.2	8.3	10.5	10.4 b
E-12	9.6	8.7	8.5	8.8	8.9 c	10.2	9.7	9.3	9.3	9.6 c
E-5	8.7	8.1	7.4	7.4	7.9 d	9.4	8.8	8.3	8.3	8.8 d
E-1	7.9	6.7	6.1	6.5	6.8 e	10.1	9.9	8.9	9.4	9.6 c
E-90	6.9	6.2	6.4	6.7	6.5 ef	9.4	10.0	9.2	9.4	9.5 c
Jupatec-73 R	6.5	6.7	6.0	5.4	6.1 f	7.9	7.7	6.4	5.7	6.9 f
E-78	5.6	5.1	4.6	4.6	5.0 g	8.1	8.1	7.8	7.5	7.9 e
Range	5.9	5.9	5.5	6.2	5.8	4.4	4.8	5.3	6.8	5.4
St. dev.[2]	1.94	1.89	1.83	2.08	1.92	1.41	1.39	1.51	1.97	1.55
Mean	8.7	8.2	7.6	7.9	8.1	10.1	9.8	9.0	9.4	9.7

[1] Means with different letters are significant different at P = 0.01 according to the LSD test
[2] Standard deviation of the ten entries measuring their spread

Experiment III

The plot situations A1, A2 and A3 represented differently sized adjacent plots, while I represented the isolated plot situation with the same plot size as in A3. Table 3 gives the DS for the 10 wheat entries. At the first observation date the range and standard deviation did not differ significantly between the four treatments, although the range and standard deviation for the isolated plots tended to be slightly larger than those of the adjacent plots. At the second observation date this tendency had become clearer and significant ($P = 0.05$). The range and standard deviation between the three adjacent plot treatments were very similar at both observation dates.

The ranking order was not affected by the plot situations within observation dates. The Spearman rank correlation coefficients (r_s) between the DS's of the three types of adjacent plots and the isolated plots ranged from 0.94 to 0.95 at both observation dates. Between observation dates the ranking order of the entries changed somewhat as in experiment II. E1, E90 and E78 changed rank between the observation dates.

Experiment IV

Table 4 shows the AUDPC of each entry in the various mixtures and in monoculture. Within each mixture each entry could be recognized not only by its morphological features, but also by its DS. The DS of each entry in all the mixtures was practically the same as the DS in monoculture. The disease development in an entry apparently was independent of the presence of another entry with a clearly different disease development. In short there was no mixture effect on disease development observed.

Table 4. Area under the disease progress curve (after transformation of the yellow rust disease severities) of four wheat entries in six different mixture ratios.

Ratio in mixture			Mixture A[1)]		Mixture B[1)]	
R	:	S	Bounty	PR-2	Frontatch	PR-46
0	:	100	–	159 b	–	138 b
50	:	50	109 a	159 b	96 a	134 b
67	:	33	108 a	161 b	97 a	133 b
75	:	25	107 a	160 b	99 a	132 b
82	:	18	107 a	161 b	99 a	134 b
100	:	0	105 a	–	94 a	–

[1)] Different letters (within mixture A or B) mean significant differences at $P = 0.05$ according to the LSD test.

Discussion

Test plots are meant to represent farmers' fields (Van der Plank, 1963). But this is only so if the plots do not interfere with one another. When testing for resistance interference may easily occur in the case of airborne pathogens such as rusts. Spores produced within a given plot may remain within the confines of the plot or leave it. Van der Plank (1963) calculated that with normal air turbulence some 31% of the spores leave a plot of 1.0 m square. Even in such small plots the majority of the spores remain inside the plot area. But this small proportion leaving the area can have large effects on neighbouring plots. Parlevliet and Van Ommeren (1984) estimated that in the case of barley-barley leaf rust the contribution of the spores produced by a plot of 1 m^2 of the fairly resistant cv Vada to the spores produced and remained within the confines of a similar plot next to it with the highly susceptible cv Akka would be less than 1%, while the reverse contribution would be over 90%. In this pathosystem the interplot interference is very large, the resistance of Vada being over a hundred fold under estimated in adjacent plots compared to the isolated plot testing. But the ranking order was not affected (Parlevliet et al., 1980). With barley and barley powdery mildew Nørgaard Knudsen et al. (1986) observed a much smaller underestimation but also a change in ranking in very small plots compared to isolated plots.

In contrast to these results the experiments in Kenya showed no sign of interplot interference whatsoever. The entries kept the same ranking order irrespective of the test plot situation including the situation where the plot size consisted of a single plant, the cultivar mixture experiment. This was unexpected and one of the possible causes were sought in the very high natural yellow rust inoculum pressure in the Njoro area of Kenya where the experiments were performed. This could explain the results in experiment I, but not in those of experiments II and IV. In II, of the area with the adjacent plots, about 20% of the area was taken up by the extremely susceptible cultivar Morocco creating a much higher inoculum level in this area than in the adjacent area with the isolated plots and without doubt also much higher than the inoculum level floating in from outside the experimental area. The results of experiment IV too cannot be explained with a high natural inoculum level as the susceptible plants were directly bordering the resistant ones.

The experiment in Mexico (III) was done to see what the results would be when the natural inoculum level is much lower. The experiment was done in El Batan where normally no wheat is grown in that season. The results were quite similar although a small interplot interference effect emerged, too small to be of any significance.

The explanation of the large differences in interplot interference might be sought in a quite different direction. Within the cereals the leaf pathogens differ in the degree of systemic growth, expressed by the size of the area occupied by the mycelium derived from a single infection. The average colony size in case of unhampered growth is very small for leaf rust in barley, clearly larger for stem rust in durum wheat, again larger for powdery mildew in barley and much larger (reaching over the whole leaf) for yellow rust in wheat. The interplot interference expressed as underestimation of quantitative resistance seems associated with it, being very large for barley to *P. hordei* (Parlevliet and Van Ommeren, 1975, 1984), much smaller for durum wheat to *P. graminis* (Broers, unpublished data), again smaller for barley to *E. graminis* powdery mildew (Nørgaard Knudsen et al., 1986) and hardly if at all existing for wheat to *P. striiformis*.

As for wheat to yellow rust testing for resistance in small adjacent plots gives results that are very representative for the farmers fields both in level and ranking order. Only the moment of scoring can have some effect on the selection, although only a slight one, as the ranking of the entries can change somewhat during the development of the epidemic. Calculation of the AUDPC would of course take care of this problem, but would be too cumbersome for initial screening.

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Chapter 4

Effect of nitrogen fertilization on disease severity and infection type of yellow rust in wheat*

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Summary

Two experiments were carried out to study the effect of nitrogen (N) level on disease severity of wheat genotypes (*Triticum aestivum*) varying in quantitative resistance to yellow rust, caused by *Puccinia striiformis*.

In 1990, nine wheat genotypes were exposed to 0, 20, 40 and 80 kg N per ha. In 1991, six genotypes selected from experiment 1, were examined at 0, 30 and 90 kg N per ha. The N was applied in the form of calcium ammonium nitrate [$Ca(NH_4NO_3)_2$].

In both years the disease severity increased two fold from 0 to the highest N-level. The infection types too increased with the N-level. Genotypes responded differentially to the increase in N-level. Moderately resistant genotypes responded more to nitrogen than the most resistant and the most susceptible genotypes. The ranking order for quantitative resistance of the genotypes was significantly affected by the N-treatments.

Introduction

Soil fertility as an environmental factor may differ from soil to soil and year to year and might affect the assessment of resistance in breeding programs. Especially nitrogen (N) levels may vary greatly. Darwinkel (1980) and Ash *et al.* (1991) reported increased yellow rust severity with increased N-rates. In addition, the incidence of many wheat diseases depends on the form of N (Huber *et al.*, 1974). In most cases rust severity increased by the nitrate-N form rather than by the ammonium N-form (Huber *et al.*, 1974; Huber (1980).

*Submitted

The objectives of this research were to 1) determine the effect of N on yellow rust severity in wheat, 2) study whether wheat genotypes respond differentially to increases in N-levels.

Materials and methods

Experiment 1

Of each of nine wheat entries originating from CIMMYT and selected in Kenya a single plant was taken and multiplied to give the nine genotypes used in this study. The nine genotypes represent a wide range of quantitative resistance and have a similar earliness. Planting took place at Njoro on 10 May 1990 at a seed rate of 120 kg/ha. It was a randomized complete block design including four N-treatments in three replicates. Each plot consisted of 10 rows of 2.0 m at a spacing of 20 cm. The plots were separated from each other by one meter in all directions. Four nitrogen rates (0, 20, 40 and 80 kg N per ha) were applied in the form of calcium ammonium nitrate [$CaNH_4(NO_3)_2$]. The N was divided into two parts, with half the rate applied at tillering and the remainder at booting. P_2O_5 was applied at the rate of 150 kg/ha at planting to all plots. On 14 June, one pot containing 3 to 4 spreader plants of the susceptible cv. Morocco was placed in each plot for a period of one week. The spreader plants were previously grown and inoculated under shed conditions and were transferred to the plots just before sporulation started. Race 134E150, the predominant race in Kenya, was used for the inoculation.

From each plot, 15 tillers were taken at random at 20 and 27 july and 3 August. Disease severity (DS) and infection type (IT) were recorded on each of the upper three leaves individually (F, F-1 and F-2). DS was recorded according to the 0-100% scale of Peterson *et al.* (1948) and IT according to McNeal *et al.* (1971).

Experiment 2

From experiment 1, six genotypes were selected. Planting took place on 5 April 1991. The experimental design was a randomized complete block one in three replicates with three N rates (0, 30 and 90 kg N per ha). Plot size and seed rate were as in experiment 1. N was applied in the same form and at the same two growth stages as described above. P_2O_5 at a rate of 150 kg/ha was given to all plots at the time of planting.

Inoculation took place on 18 May with the same race and in the same way as described in experiment 1. DS and IT were recorded on the upper three leaves individually as described in exp. 1 on 6 June, 13 June and 20 June.

Results

For the analyses of variance the DS data were logit transformed while the IT's were not transformed. The analyses of variance for DS of both experiments showed highly significant main effects, which were expected. The genotype x N-level interaction and the genotype x observation date interaction too were significant ($P=0.01$). The leaf position x N-level interaction and the observation date x N-level interaction were not significant. Because of that the data of the three leaf layers and of the three observation dates were taken together for each genotype x N-level treatment.

In both years the DS, averaged over the genotypes, increased with increased N-rates. The DS was about twice as high at the highest dose as at the lowest one (Tables 1 and 2). This increase in DS coincided with an increase in IT (Tables 1 and 2). The magnitude of increase in DS and in IT was not the same for all genotypes. The genotype x N-level interaction was for a fair part due to the tendency that the moderately resistant genotypes responded stronger to the increase in N than the most susceptible and most resistant genotypes. This resulted in a different ranking order with the different N-rates, both for DS and IT for several genotypes. For instance, PR-105 and PR-118 were equally resistant at N1 with DS's of 1.3 and 1.2%, while the corresponding DS's at N4 were 11.9 and 2.6 %, respectively. For IT's, PR-6 increased from 4.8 at N1 to 5.2 at N4 only, while PR-103 increased at the same time from 2.4 to 6.0.

Both DS and IT responded similarly to N-rate increases, which is expected as there is an association between both as shown in Table 1 and 2. The spearman rank correlation, r_s between DS and IT in 1990 and 1991 was 0.82 and 0.63, respectively and the weighted mean was 0.75.

Discussion

In agreement with the general knowledge, but supported by few scientific results, the DS of yellow rust increased moderately with increased N rates. Genotypes, however, did not respond in the same way. There were clear genotype x N-level interactions causing some changes in ranking order with changing N-levels. This is of some concern to the breeder, especially when screening for quantitative resistance is carried out. This is even more pronounced when DS and the IT are combined into one disease score, used for selection as is done in several breeding programs. If that was done with the present data the disease scores (DS x IT), as shown in Table 3, would have

been obtained. The ranking order correlation, r_s for DS between N1 and N4 in 1990 was 0.73. The corresponding r_s for the disease scores appeared to be 0.62, considerably lower. With such a scoring, because DS and IT are only partially associated, with an r_s in the order of 0.6 to 0.8, it is even more important to screen at the right N-level.

It should be realized that the r_s values would have been considerably lower when the two most susceptible genotypes had not been present. Such a situation is actually the reality as breeders want to distinguish between the various moderately resistant genotypes and these smaller differences are much more likely to be strongly affected by N-level effects, changing the ranking order markedly.

The breeder must therefore screen for quantitative resistance at N-levels similar to those used in the area for which the breeding is meant for.

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Table 1. Mean yellow rust disease severity (DS) and infection type (IT) of nine wheat genotypes at four nitrogen (N) treatments (1=0, 2=20, 3=40 and 4=80 Kg N per ha) in 1990.

Genotype	DS					IT				
	N1[1]	N2[1]	N3[1]	N4[1]	Relative increase, %	N1	N2	N3	N4	N4-N1
PR-2	33.4a	44.6a	47.6a	44.9a	34	5.5	5.9	6.1	6.3	0.8
PR-124	24.0a	27.6ab	37.9ab	35.6ab	48	5.2	5.4	5.0	5.6	0.4
PR-6	5.3b	7.0c	10.2bc	13.5bc	155	4.8	4.7	5.2	5.2	0.4
PR-109	3.0bc	2.5cd	7.1cd	9.1c	203	1.7	2.7	3.3	3.7	2.0
PR-46	2.7bc	5.6cd	2.4de	11.8c	337	3.1	3.9	4.7	5.8	2.7
PR-103	2.1c	9.1bc	5.6cde	12.4c	490	2.4	5.9	5.5	6.0	3.6
PR-41	1.8c	2.6cd	3.8cde	6.9c	283	2.6	4.2	4.9	5.0	2.4
PR-105	1.3c	5.0cd	11.1bc	11.9c	815	3.5	5.1	7.0	7.2	3.7
PR-118	1.2c	1.4d	2.1e	2.6d	117	1.7	1.8	2.2	2.4	0.7
Mean[1]	8.3d	11.7c	14.2b	16.5a		3.4d	4.4c	4.9b	5.2a	

[1] Means with different letters within a column are significantly different at (P=0.05) according to the LSD test carried out on tranformed data.

Table 2. Mean yellow rust disease severity (DS) and infection type (IT) of six wheat genotypes at three nitrogen (N) treatments (1=0, 2=30 and 3=90 kg N per ha) in 1991

Genotype	DS				IT			
	N1[1]	N2[1]	N3[1]	Relative increase, %	N1	N2	N3	N3-N1
PR-2	41.2a	49.9a	56.7a	38	6.8	7.6	7.5	0.7
PR-124	21.4b	29.2b	43.9b	105	5.7	5.2	6.3	0.6
PR-46	9.7c	15.6c	22.4c	131	5.7	6.4	6.3	0.6
PR-109	7.0d	17.4c	28.8c	311	6.2	6.9	7.3	1.1
PR-103	3.8e	6.6d	10.4d	174	6.6	6.7	7.1	0.5
PR-118	0.8f	1.4e	4.6e	475	2.9	2.9	2.9	0.0
Mean[1]	14.0c	20.0b	27.8a		5.7c	6.0b	6.2a	

[1] See Table 1.

Table 3. Disease scores (disease severity x infection type) for yellow rust of nine wheat genotypes at four nirtrogen (N) treatments (see Table 1) in 1990.

Genotype	N1	N2	N3	N4
PR-2	183.7	263.0	290.4	282.9
PR-124	124.8	149.0	189.5	199.4
PR-6	25.4	32.9	53.0	70.2
PR-109	5.1	6.8	23.4	33.7
PR-46	8.4	21.8	11.3	68.4
PR-103	5.0	53.7	30.8	77.4
PR-41	4.7	10.9	18.6	34.5
PR-105	4.6	25.5	77.7	85.7
PR-118	2.0	2.5	4.6	6.2

Chapter 5

The effect of earliness, observation date and leaf layer on the assessment of resistance to yellow rust in wheat

D.L. Danial

Summary

When selecting for quantitative resistance in wheat (*Triticum aestivum*) to yellow rust (*Puccinia striiformis*) the assessment is based on differences in disease severity (DS) and/or infection type (IT). However, differences in DS can be caused by other variables such as earliness, observation date and leaf layer as well.

Twenty spring wheat genotypes were assessed for DS and IT at three observation dates on each of the upper three leaf layers. The rank correlation coefficient, r_s, between IT and area under the disease progress curve (AUDPC) was 0.35 (not significant) if two highly susceptible and one very resistant genotypes were excluded, indicating that IT is not a suitable parameter to assess quantitative resistance. Earliness tended to increase the DS slightly, irrespective of the resistance level, but the confounding effect was small. There were small but significant genotype x observation date interactions and genotype x leaf layer interactions.

The r_s between AUDPC and DS at each of the three observation dates was very high, 0.93, 0.99 and 0.95 respectively. Therefore DS of one observation date, preferably not too early, could be used instead of the more laborious AUDPC to assess quantitative resistance. The r_s-values at the 2nd and 3rd observation date of the DS of the flag leaf and of the second leaf individually with the AUDPC ranged from 0.95 to 0.99. This means that DS assessed on either one of these leaf layers at a not too early observation date gives accurate and quite representative assessments of the quantitative resistance of a genotype.

Introduction

An accurate assessment of resistance is essential in breeding for disease resistance, especially if quantitative resistance is concerned. There are several

factors that may interfere with an accurate assessment in the bread wheat/yellow rust pathosystem such as interplot interference, nitrogen level, earliness, date of observation and leaf layer. Danial *et al.* (1993) showed that there was no interplot interference. Danial and Parlevliet (1994) reported that the ranking order of entries could be affected by the N-level.

Earliness, observation date and leaf position are the factors discussed in this study. Resistance can be deduced from the disease severity (DS) measured at a given date, from the area under the disease progress curve (AUDPC) and from the infection type (IT). The relevance of these parameters for an accurate assessment of resistance is a second aim of this study.

Materials and methods

Of each of 20 spring wheat entries, originating from CIMMYT, a single plant was taken and multiplied at Njoro, Kenya to give the 20 genotypes in this study Sowing was done on 8 March 1989, in four replicates in two row plots of 10 m length in a randomized complete block design. Two spreader rows of the highly susceptible cv Morocco were planted perpendicular to each block. On 18 April, one pot containing 3-4 almost sporulating plants of "Morocco" was placed every 4 m inside the double spreader rows for a period of one week. The spreader plants were previously grown and inoculated with race 134E150 in a shed.

DS and IT were recorded on each of the upper three leaves individually of each of 15 tillers taken at random from each plot on 28 June (D1), 5 July (D2) and 12 July (D3). DS was recorded using the 0-100% scale, (Peterson et al. 1948) and IT was recorded using a 0-9 scale (McNeal et al.1971). The AUDPC was calculated from the DS's of the three observation dates as 3.5 x (D1 + 7 x D2 + 3,5 x D3). Heading date (HD) was used as a measurement for earliness and recorded for all plots when the upper half of the ear had emerged in 50% of the tillers. The DS data were logit transformed for the analysis of variance

Results

Analysis of variance for DS showed that the main effects were highly significant. In addition, the genotype x observation date and the genotype x leaf position interaction were significant at (P=0.01). Table 1. shows the DS's, AUDPC's, IT's and heading date (HD) of the 20 genotypes. The DS increased clearly with later assessment, while the IT declined only slightly.

Table 1. Disease severity (DS) and infection type (IT) of three observation dates (D1 to D3) and area under disease progress curve (AUDPC) of 20 wheat genotypes exposed to yellow rust and the heading dates (HD) in days from sowing of these genotypes.

Genotype	DS			AUDPC	IT			Mean	HD
	D1[1]	D2[1]	D3[1]		D1	D2	D3 IT		
MOROCCO	80.9 a	97.1 a	100.0 a	1312.7	9.0	8.8	8.8	8.9	60
PR-2	69.7 ab	79.3 b	90.3 b	1111.2	7.7	7.7	7.3	7.6	72
PR-78	55.8 bc	65.9 c	63.8 c	880.2	3.3	3.2	3.0	3.2	60
PR-91	52.8 bc	64.9 c	64.8 c	865.9	7.2	7.5	6.9	7.2	68
PR-45	39.4 def	56.1 d	62.1 cd	747.6	4.8	5.5	5.0	5.1	75
PR-31	44.5 cde	53.5 de	54.2 de	719.8	6.4	6.6	6.3	6.4	68
PR-27	45.4 bcd	53.1 de	48.1 ef	698.8	3.8	3.6	3.1	3.5	65
PR-6	30.6 fghi	52.8 de	60.5 cd	688.6	4.9	3.9	3.9	4.2	73
PR-124	31.3 efghi	54.8 de	55.0 de	685.1	5.3	4.0	3.6	4.3	70
PR-46	35.8 defg	41.0 fg	59.8 cd	621.3	7.4	7.5	6.2	7.0	72
PR-96	31.9 defgh	46.4 ef	41.3 fg	581.1	3.1	2.9	3.0	3.0	60
PR-105	29.8 fghij	40.0 fg	47.8 ef	551.3	7.6	7.5	6.8	7.3	73
PR-134	25.8 ghijk	39.3 fg	49.4 ef	537.8	7.7	7.9	7.6	7.7	75
PR-38	23.8 ghijk	39.4 fg	34.4 g	479.4	3.2	3.4	3.0	3.2	62
PR-41	18.5 ijkl	29.0 h	35.4 g	391.7	4.7	3.7	3.4	3.9	72
PR-118	22.2 hijk	29.3 h	23.2 h	363.5	2.8	2.9	2.9	2.9	72
PR-109	15.8 jkl	21.3 i	22.0 h	281.2	2.9	2.9	2.7	2.8	74
PR-52	13.6 kl	18.4 ij	16.6 i	234.0	2.9	2.9	2.7	2.8	63
PR-103	10.7 lm	15.8 j	23.4 h	230.4	5.2	6.1	4.4	5.2	73
PR-119	6.7 m	5.7 k	10.0 j	98.3	2.7	2.7	2.5	2.6	78
Mean[1]	34.2 c	45.1 b	48.1 a		5.1	5.1	4.7		

[1] Means with different letters are significantly different at (P=0.05) according to LSD test carried out on transformed data.

The ranking order for DS of the genotypes did change with the observation date. PR-105 and PR-6 for instance had almost the same DS at D1, while they differed considerably at D3. The spearman rank correlation, r_s, between D1, D2 and D3 and the AUDPC were 0.93, 0.99 and 0.95, respectively. The r_s between AUDPC and IT was 0.57. The r_s between HD and AUDPC and HD and IT were -0.41 and 0.02, respectively.

In Table 2, the DS's of the three leaf layers averaged over the three observation dates are shown. The IT's are not shown as there were no differences in IT of any significance between leaves. The r_s between HD and F, F-1 and F-2 were -0.46, -0.40 and -0.32, respectively.

In order to see how strong the DS at the three observation dates for the three leaf layers were associated, the r_s-values are shown in Table 3. The r_s values between the adjacent observation dates (D1, D2 and D3) were in all instances higher than the r_s between the first and last observation date. This effect was very pronounced for the flag leaf and hardly if at all visible at the third leaf (F-2) indicating that the ranking order for DS of the genotypes varied with the observation date most pronounced in the flag leaves and least so in the F-2 leaves.

In order to evaluate which observation date and which leaf layer would give the best assessment, several r_s values are shown in Table 4. If the AUDPC is assumed to represent the best estimate of the real DS of a genotype, the DS's on the individual leaves, often represented an almost equally good assessment with r_s-values above 0.95. This was especially the case for the second and third observation dates. The flag leaf always correlated considerably less well with the other parameters at the first observation date. The correlation of DS on either the flag leaf or the second leaf with the AUDPC was at least 0.95.

Discussion

The genotypes studied varied greatly in their level of resistance to yellow rust and for their earliness. In case of early genotypes one expects them to have a higher DS as the upper three leaves of these genotypes have been exposed for a longer time to the pathogen at a given observation date. This expected tendency might exist since the r_s between HD and AUDPC was 0.41 (almost significant at $P=0.05$) but is at best fairly weak. For instance, the cv. Morocco indeed was the earliest and most severely affected, but PR-78, PR-96, PR-38 and PR-52 were also among the earliest and varied in DS from a high level to a fairly low level. This is easily explained by genotypic differences in resistance independent from the earliness effect. On the other hand PR-2, is almost as late

as PR-103 but is far more affected; they represent a large part of the whole range of AUDPC (230.4 to 1111.2).

Apparently a large part of the variation in the observed DS is due to real genotype differences, but a small part, about 16 % (r_s^2) could be due to differences in heading date. As long as HD's, vary within 2 to 2.5 weeks, the disturbing effect of earliness on the assessment of resistance seems sufficiently small, if present at all, not to warrant special measures for correction. However, when the HD shows extreme differences the disturbing effect of HD can be expected to be too large. In such cases the breeder is advised to classify the genotypes into earliness groups for a representative comparison.

The high correlation coefficients between DS and AUDPC suggests that DS is a reliable epidemiological parameter and can be used as a parameter to evaluate the resistance in the field rather than using AUDPC which is too laborious.

IT, another variable sometimes used in the assessment of resistance, appeared poorly associated with DS. The r_s between IT and AUDPC was 0.57 and if Morocco, PR-2 and PR-119, not really representing quantitative resistance, are left out, the r_s-value is reduced to 0.35 (not significant). So IT appears to be an unsuitable parameter for assessing quantitative resistance. Danial (1993), already showed that IT is not a stable trait, at least not under Kenyan field conditions.

The extremely high r-values between mean DS and AUDPC for the individual upper two leaves (F and F-1), (Table 4), indicate that DS measured on the flag leaf or the second leaf can be a reliable criterion to measure resistance in the field which is practically as accurate as the AUDPC or mean DS over the three leaf layers, provided the assessment is not taken at a too early stage. In this study, ranking order of the genotypes appeared to be somewhat affected by the observation dates. A similar observation was reported by Danial and Parlevliet (1994).

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Table 2. Disease severity of yellow rust for 20 wheat genotypes on the upper three leaves (F= flag leaf; F-1=second leaf and F-2=third leaf), their mean and their heading date (HD) in days from sowing. DS's are means of three observation dates.

Genotype	DS				HD
	F[1]	F-1[1]	F-2[1]	Mean	
Morocco	89.7 a	93.8 a	94.6 a	92.7 a	60
PR-2	65.6 b	83.5 b	90.2 b	79.8 b	72
PR-78	42.3 bc	63.0 bcd	80.3 bcd	61.9 bc	60
PR-91	35.1 bcd	64.9 bc	82.5 bc	60.8 cd	68
PR-45	25.4 cdef	56.2 bcd	75.9 bcde	52.5 cde	75
PR-31	26.2 cdef	54.5 bcde	71.5 bcdef	50.7 cde	68
PR-27	25.2 bcdef	51.3 bcdef	70.1 bcdef	48.9 cde	65
PR-6	23.1 cdefg	49.2 cdef	71.7 bcdef	48.0 cde	73
PR-124	26.6 cde	46.5 cdefg	67.8 bcdef	47.0 cdef	70
PR-46	21.0 cdefg	47.8 cdefg	67.7 bcdef	45.5 cde	72
PR-96	18.9 cdefg	40.1 cdefg	60.7 cdefg	39.9 defg	60
PR-105	14.4 cdefgh	39.3 cdefg	63.9 cdefg	39.2 efg	73
PR-134	12.4 defgh	38.8 cdefg	63.2 cdefg	38.1 efg	75
PR-38	18.1 cdefg	30.8 cdefg	48.7 cdefg	32.5 efghi	62
PR-41	11.2 defgh	26.0 cdefgh	45.8 defg	27.6 fghi	72
PR-118	7.6 efgh	23.6 defgh	43.4 efgh	24.9 ghi	72
PR-109	7.8 efgh	16.3 efgh	35.1 fgh	19.7 hi	74
PR-52	4.3 gh	15.8 fgh	28.3 gh	16.2 ij	63
PR-103	6.2 fgh	14.3 gh	29.6 gh	16.7 ij	73
PR-119	2.9 h	6.7 h	12.9 h	7.5 j	78
Mean[1]	24.2 c	43.1 b	60.2 a		

[1] Means with different letters are significantly different at (P=0.05) according to LSD test carried out on transformed data.

Table 3. Spearman rank correlation coefficients of DS between three observation dates (D1 to D3) for the upper three leaves (F, F-1 and F-2) and for the mean of the three leaf layer's (mean).

	F	F-1	F-2	Mean
D1/D2	0.85***	0.98***	0.91***	0.96***
D2/D3	0.94***	0.94***	0.90***	0.98***
D1/D3	0.72**	0.91***	0.89***	0.91***

** = significant at P=0.01
*** = significant at P=0.001

Table 4. Spearman rank correlation coefficients (r_s) of DS of the upper three leaves F, F-1 and F-2, mutually and with AUDPC at three observation dates.

r_s between	D1	D2	D3
F/F-1	0.88***	0.95***	0.96***
F/F-2	0.77**	0.97***	0.94***
F-1/F-2	0.97***	0.98***	0.98***
F/AUDPC	0.83***	0.96***	0.96***
F-1/AUDPC	0.98***	0.99***	0.95***
F-2/AUDPC	0.97***	0.97***	0.92***

** = significant at P=0.01
*** = significant at P=0.001

Chapter 6

Factors affecting expression of infection type of *Puccinia striiformis* in spring wheat and the association between disease severity and infection type

D.L. Danial

Summary

Observation date, year and level of nitrogen are factors that appear to affect the expression of infection type (IT) of yellow rust in wheat. IT increased with increased nitrogen level and the response of wheat genotypes was differently. The association between IT and DS is not clear and seemed to vary depending on the genotype. It is assumed that IT is an unstable character and does not seem to be a suitable tool in order to measure quantitative resistance.

Introduction

Various methods have been suggested to assess the levels of resistance in the field for the cereal rusts. Peterson *et al.* (1948) measured disease severity (DS) by estimating the percentage of tissue affected by the rust at a certain moment during the epidemic development. Van der Plank (1963) used the apparent infection rate (r) which is calculated from the DS measured at several dates, while Wilcoxson *et al.* (1975) proposed the use of the area under disease progress curve (AUDPC) to be computed from the DS assessed at various dates as well. Broers (1989) compared different methods and concluded that DS and AUDPC were the most suitable parameters to measure the partial resistance to leaf rust in wheat, whereas the r value seemed an unsuitable estimator of partial resistance. Similarly, Danial (1994), showed a high correlation between AUDPC and DS for yellow rust in wheat.

Infection type (IT) on a scale 0-9 (McNeal *et al.*, 1971), is another parameter used to assess the resistance at any plant stage. Generally IT 0 to 3 are classified as resistant, IT 4 to 6 as intermediate and IT 7 to 9 as susceptible. Various factors may interfere with or affect the expression of IT such as the environmental conditions, observation date, leaf age, age of infection and the level of nitrogen fertilizer.

The effect of various factors on IT and the association between DS and IT are discussed here.

Effect of environmental conditions

In selection experiments carried out to select for quantitative resistance, the disease severity (DS) and infection type (IT) were used to evaluate the level of resistance (Danial, 1993). Table 1 shows the mean DS and mean IT of nine wheat genotypes selected and reassessed between 1988-1991. The genotypes varied greatly for the DS and did not change much in the ranking over the years, the average r_s between years being 0.96 (Table 2). Contrary to the DS, the genotypes initially selected on the basis of a high IT showed a decline in IT that varied with the genotype and resulting in IT's that were hardly associated with the initial ones, r_s between 1988 and 1991 being 0.15 (Table 2). The mean r_s between years was 0.46. Some genotypes showed a strong decrease, like Pr105, and others only a slight one, such as Pr134. Spearman's rank correlation coefficients (r_s) between four years for the DS and for the IT for the nine genotypes is given in Table 2. For the DS, the r_s values were very high with an average of 0.96 ranged from 0.92 to 0.99 while low r_s values for the IT were obtained with an average of 0.46 and range from 0.15 to 0.82.

Table 1. Disease severity (DS) and infection type (IT) of yellow rust for nine wheat genotypes between 1988-1991. DS measured on a 0-100 scale and IT on a 0-9 scale.

Genotype	DS				IT			
	'88	'89	'90	'91	'88	'89	'90	'91
Pr134	5	15	15	23	7.5	8.0	6.5	7.0
Pr7	10	15	18	15	7.5	8.0	6.5	7.0
Pr105	15	35	30	38	8.5	7.5	7.0	4.0
Pr6	15	25	35	30	7.0	4.5	4.0	5.0
Pr46	30	35	40	33	7.0	8.0	5.0	5.0
Pr31	40	50	60	60	8.0	6.5	6.5	4.0
Pr124	45	45	50	50	7.0	4.5	4.0	3.5
Pr91	60	60	65	60	8.0	9.0	7.5	7.0
Pr2	65	80	75	80	8.5	8.0	4.5	6.0
Mean	32	40	43	43	7.7	7.1	5.7	5.4

Table 2. Spearman's rank correlation coefficient of disease severity and infection types between four years for nine wheat genotypes.

Year	Disease severity			Infection types		
	1989	1990	1991	1989	1990	1991
1988	0.97***	0.98***	0.92***	0.25	0.60i	0.15
1989		0.97***	0.99***		0.55	0.82*
1990			0.93***			0.40

i=Significant at P= 0.10; *= Significant at P=0.05; ***= Significant at P= 0.001.

The instability of IT was also observed in an another experiment which was carried out to study the level of resistance to yellow rust in spring wheat at different nitrogen levels in two consecutive years (Table 4). The results demonstrate the fluctuation of IT between years for the same genotype. For instance, Pr46 and Pr109 have shown the same DS in both years while the IT reacted differently in the two years.

The correlations between DS and IT were low and not significantly different from zero (Table 3). A similar observation was reported by (Danial, 1994), whereby the r_s-values between IT and AUDPC for 20 genotypes appeared to be low (r_s=0.35, not significant).

Table 3. Pearson's and Spearman's correlation coefficient between mean disease severity and infection types at three years for nine genotypes.

Year	Pearson's	Spearman's
1989	0.15	-0.01
1990	-0.18	-0.12
1991	-0.20	-0.29

Table 4. Mean disease severity (DS) and mean infection type (IT) of yellow rust of six wheat genotypes in two years.

Genotype	DS		IT	
	1990	1991	1990	1991
Pr2	42.6	49.3	6.0	7.3
Pr124	31.3	31.5	5.0	5.7
Pr103	7.3	6.9	4.4	6.8
Pr46	5.6	15.9	5.3	6.1
Pr109	5.4	17.7	2.9	6.8
Pr118	1.9	2.3	2.0	2.9
Mean	15.7	20.6	4.3	5.9

Effect of observation date

Observation date is another factor that may affect the IT and so the assessment of resistance level and/ or ranking order for resistance of the genotypes. This can be shown by an experiment designed to study the interplot interference in wheat to yellow rust (Danial *et al.*, 1993) by assessing DS and IT of 57 genotypes representing a wide range of quantitative resistance at different plot situations. Table 5 shows mean DS and IT for the four plot situations. The IT decreased clearly with the later assessment. In all plot situations at the first observation date (O1), the IT showed a high value ranging from 6.1 to 6.9 while at the fourth observation date (O4) the IT showed a declined value ranging from 3.4 to 3.7. Similar results were obtained from an experiment carried out over two years to study the effect of nitrogen on IT (Danial and Parlevliet, 1994). Mean IT for six wheat genotypes at the three observation dates in 1990 and 1991 is given in Table 6. In both years, the genotypes varied greatly in their IT's and showed a decreasing value at later observation dates. In addition, some genotypes showed a noticeable change in IT from one year to another. For instance, Pr109 showed at O1 in 1990 an IT of 2.9 while in 1991 at O1 the IT was 7.6.

Table 5. Mean disease severity (DS) and infection type (IT) of yellow rust of 57 wheat genotypes at four observation dates (O1, O2, O3 and O4) and in four plot situations (A= one row of 2m, B= five rows of 2m; C=ten rows of 2m not isolated and D=10 rows of 2m isolated. DS was recorded on the upper three leaves according to the Peterson scale (Peterson et al.,1948) and transformed to logits and 10 was added. IT was assessed by using scale 0-9 (McNeal et al., 1971).

Plot situation	DS				IT			
	O1	O2	O3	O4	O1	O2	O3	O4
A	8.7	9.3	9.8	10.4	6.1	5.4	4.0	3.5
B	8.2	9.0	9.5	10.2	6.3	5.6	4.2	3.5
C	8.0	9.0	9.4	10.2	6.6	6.2	4.3	3.7
D	7.4	8.6	9.0	9.6	6.9	6.3	4.2	3.4
Mean	8.1	9.0	9.4	10.1	6.5	5.9	4.2	3.5

Table 6. Mean yellow rust infection types of six wheat genotypes at three observation date in 1990 and 1991.

Genotype	1990			1991		
	O1	O2	O3	O1	O2	O3
Pr2	7.1	5.1	5.7	7.3	7.3	7.3
Pr124	6.4	4.6	4.9	6.9	5.1	5.2
Pr103	5.1	5.0	4.8	7.7	6.8	5.8
Pr46	4.6	4.3	4.2	7.2	6.4	4.8
Pr109	2.9	2.8	2.9	7.6	6.9	5.9
Pr118	0.4	2.6	3.0	3.2	2.9	2.6
Mean	4.4	4.1	4.3	6.7	5.9	5.3

Effect of the nitrogen level

The nitrogen level may affect the assessment of IT of yellow rust in wheat. Danial and Parlevliet (1994) reported increased yellow rust severity with increased N-rates and IT responded similarly to N-rate increases. The effect of different N-rates in two years on the IT for six wheat genotypes is shown in Table 7. In both years the IT, averaged over the genotypes, increased with increased N-rates and the magnitude of increase was not the same for all genotypes. For instance, Pr2 increased from 5.5 at N1 to 6.3 at N4 in 1990 which is not significant (P=0.05), while Pr103 increased in that year from 2.4 to 6.0, a highly significant increase (P=0.01). There was also an interaction between years and genotypes to increased N-rates. For instance, in 1990 the IT of Pr103 was 2.4 at N1 and 6.0 at N4, while in 1991, the IT of the same genotype was 6.6 at N1 and 7.1 at N6. The former increase was highly significant (P=0.01), the latter was not significant. Pr109 and Pr118 did not differ at N1 in 1990, while they were highly significantly different in 1991 (P=0.01).This resulted in a different ranking order of the genotypes with the different N-rates and years.

Table 7. Mean yellow rust infection types of six wheat genotypes at various nitrogen treatments (N1=0, N2=20, N3=40, N4=80, N5=30 and N6=90 kg N per ha.) in 1990 and 1991.

Genotype	1990				1991		
	N1	N2	N3	N4	N1	N5	N6
Pr2	5.5	5.9	6.1	6.3	6.8	7.6	7.5
Pr124	5.2	5.4	5.0	5.6	5.7	5.2	6.3
Pr103	2.4	5.9	5.5	6.0	6.6	6.7	7.1
Pr46	3.1	3.9	4.7	5.8	5.7	6.4	6.3
Pr109	1.7	2.7	3.3	3.7	6.2	6.9	7.3
Pr118	1.7	1.8	2.2	2.4	2.9	2.9	2.9
Mean	3.3	4.3	4.5	5.0	5.7	6.0	6.2

Discussion

The infection type appears to be a rather unstable characteristic, at least within quantitatively resistant genotypes. Observation date, Nitrogen level and year affect the IT, but genotypes may be affected differently. This agrees with other studies. Stubbs (1967) observed that the IT varied with the light intensity, depending on the wheat cultivars.

In the above mentioned experiments, DS and IT were assessed together. The DS appeared to be a more consistent and reproducible characteristic. The association between DS and IT appeared to be poor.

For assessing quantitative resistance IT therefore must be considered an unsuitable parameter, which agrees with the observation of Danial (1993) that it is not possible to select for true partial resistance (a low DS despite a high IT) as the IT is an unstable characteristic, too unstable to base selection on.

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III. Selection for partial or for quantitative resistance

Introduction

In the cereal rusts different forms of resistance are recognized and reported. Hypersensitive resistance can be expressed in the seedling and/or adult plant stage. The hypersensitive resistance can be classified into complete resistance (no sporulation) and incomplete resistance (some sporulation). This type of resistance is usually based on major genes. Resistance induced by these major genes is vulnerable to genetic adaptation in the pathogen population and is generally considered to be non-durable.

In the wheat-yellow rust system, 18 major resistance genes have been identified (McIntoch, 1988) and the effectiveness of such genes is generally of a short duration. There is a long history of cultivars which initially were resistant at the time of release and became susceptible as new races of the pathogen appeared (Johnson, 1981; Stubbs, 1985; Danial and Stubbs, 1992). Selection and breeding for partial resistance in wheat to this pathogen has received less attention than other rust disease.

Besides the hypersensitive resistance, other descriptions of resistance have been given such as adult plant resistance, temperature sensitive resistance, slow rusting, quantitative resistance (QR) and partial resistance (PR) (general introduction). The concept of partial resistance was introduced by Parlevliet, 1979; Parlevliet and Van Ommeren, 1975) as a form of quantitative resistance in which spore production is reduced even though the host plants have a susceptible infection type, indicating that no hypersensitivity resistance is present. Attention of breeders has been drawn to PR because it is assumed to be polygenically inherited and durable.

In this part the application of selection for partial resistance in wheat to yellow rust is examined, different selection criteria were applied and the selection results compared. In addition, the expression and stability of the resistance of cultivars which have shown durable resistance for a long period of time in their own region is studied at widely different environments.

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Chapter 7

Is partial resistance a suitable approach to obtain durable resistance in wheat to yellow rust?*

D.L. Danial

Summary

Over the period 1987 - 1989 a total of over 15,000 spring bread wheat entries were screened for partial resistance (PR) to yellow rust, i.e. exhibiting a reduced disease severity (DS) together with a high infection type (IT). Only 31 entries were identified as having PR. The selected entries were retested in replicated trials for four (9 entries), three (14 entries) and two (8 entries) consecutive years. The selected entries varied greatly in DS, all having a significantly lower DS than the highly susceptible 'Morocco'. The DS of the entries remained constant over the years, but the IT decreased. Out of the 31 selected entries only 7 retained a high IT (7.0 to 9.0). The IT of the remaining 24 entries decreased to values ranging from 6.5 to 3.5.

It is concluded that PR for yellow rust in wheat does exist, but that the combination of a sufficient high level of resistance together with a high IT is so rare that partial resistance against yellow rust does not seem to be a promising approach for breeders.

Introduction

In wheat (*Triticum aestivum*), yellow rust, (*Puccinia striiformis* Westend.) is one of the most important pathogens in the highlands of Kenya and in other regions with a temperate climate. Breeding for yellow rust resistance usually involves the use of major, race-specific resistance genes (*Yr*-genes)(Röbbelen and Sharp 1978). However, the resistance obtained is often elusive (Beaver and Powelson 1969; Johnson *et al.*, 1969; Stubbs 1972; Stubbs 1974; Danial and Stubbs 1992) as almost all described *Yr* genes have been overcome by one or more of the many yellow rust races (Stubbs 1985). The virulence factors of yellow rust

*In: Durability of disease resistance: Th.M.G.M. Jacobs and J.E. Parlevliet (Eds), 185-189 Kluwer, Dordrecht, Netherlands

races appear to increase in a step-wise manner (Stubbs 1985; Danial and Stubbs 1992) suggesting the need for a more durable form of resistance. Parlevliet and Van Ommeren (1975) studied a type of resistance, described as partial resistance (PR), characterized by a reduced level of rust on the host plant despite a susceptible infection type. This type of resistance has been assumed to be durable (Parlevliet 1985), in contrast to the race-specific *Yr* genes used by breeders.

The objective of this study was to investigate whether selection for PR can be a useful approach in breeding for durable resistance in this pathosystem, i.e can one recognize PR and does it occur with an adequate frequency and level.

Materials and methods

Three experiments were carried out from 1987 - 1989 in which a total of 15.028 spring bread wheat entries from various origins were tested. In 1987 5.046 entries were tested, in 1988 4.970 entries were tested, in 1990 5.012 entries were tested (Table 1). The experiments were carried out on the experimental fields of the National Plant Breeding Research Centre at Njoro, Kenya. Entries were planted in duplicate in two-row plots of 2 m length. Strips, containing from 50 to 100 plots, were separated by a spreader row of the highly susceptible cultivar Morocco planted perpendicular to the plots. The spreader rows were inoculated by dusting with a mixture of spores of race 134E150 and talc powder. Inoculation of spreader rows and plots was carried out just after tillering, when stem elongation had started. Race 134E150 possesses virulence to the resistance factors *Yr2, Yr2+, Yr6, Yr6+, Yr7, Yr7+, Yr8, Yr9, Yr9+* and *Anza* and was the predominant race in Kenya in this period. Disease severity (DS) and infection type (IT) were assessed on the upper three leaves on three successive dates at one week intervals. DS was recorded using the 0-100 Peterson scale, (Peterson *et al.*, 1948) and IT using a 0-9 scale (McNeal *et al.*, 1971). Selection for PR was carried out when the DS of the susceptible cultivar Morocco reached or exceeded 70%. Entries characterized by a low DS and a high IT were selected. One single head was harvested per selected entry for multiplication under irrigation during the off-season. The selected entries were reassessed in 4, 3 or 2 consecutive years. Only data from the third reading were used for the analysis presented here.

Table 1. Disease severity (DS) on a 0-100% scale and infection type (IT) on a 0-9 scale for 15 wheat entries selected for partial resistance to yellow rust in experiments I, II and III in four, three and two years of assessment, respectively.

Entry		DS					IT*				
		'88	'89	'90	'91	Mean	'88	'89	'90	'91	Mean
I	PR-134	5	15	15	23	15	7.5	8.0	6.5	7.0	7.3
	PR-7	10	15	18	15	15	7.5	5.0	5.0	4.5	5.5
	PR-105	15	35	30	38	29	8.5	7.5	7.0	4.0	6.8
	PR-46	30	35	40	33	34	7.0	8.0	5.0	5.0	6.3
	PR-91	60	60	65	60	61	8.0	9.0	7.5	7.0	7.9
	PR-2	65	80	75	80	75	8.5	8.0	4.5	6.0	6.8
II	PR-3	–	40	40	40	40	–	7.0	8.0	4.0	6.3
	PR-114	–	60	52	60	58	–	9.0	7.0	7.0	7.7
	PR-123	–	70	60	55	62	–	9.0	7.0	4.0	6.8
	PR-116	–	70	65	60	65	–	8.5	7.5	8.0	8.0
	PR-115	–	75	65	75	72	–	8.5	7.5	7.5	7.8
	PR-127	–	75	70	75	73	–	9.0	8.5	5.0	7.5
III	PR-19	–	–	18	28	23	–	–	8.0	3.5	5.8
	PR-93	–	–	25	35	30	–	–	7.0	5.0	6.0
	PR-112	–	–	75	40	58	–	–	7.5	3.0	5.3
	Morocco	90	90	90	90	90	9.0	9.0	8.8	8.3	8.8

* a difference of 1.5 within each year represents a significant difference at P = 0.01.

Results

Of the 15.028 entries only 31 were classified as possessing PR, having an IT being of at least 7.5, and a DS lower than that of the highly susceptible Morocco. All other entries exhibited a low or intermediate IT. Without exception, the IT of the 31 selected entries decreased over the subsequent years. Table 1 lists the DS and IT of 15 representative entries. The decrease in IT ranged from 0.5 (PR-116) to 5.0 (PR-123). Table 2 summarizes the decrease of IT of all selected entries. Even considering the slight decrease in DS for the extremely susceptible cultivar Morocco, the downward trend is clear. The degree by which the IT decreased differed greatly amongst entries. At the first reassessment the IT of most entries did not differ much from the time of selection. At the last assessment, in 1991, the differences were large and highly significant (Table 1). In 1991, only seven of the 31 selected entries could still be classified as being partially resistant (Table 3). Of these, six had a level of partial resistance too low to be of practical interest. Only the level of PR-134

was satisfactory.

Contrary to the IT, the DS of the entries did not change much over the years (Tables 1 and 2). Also the differences between entries were consistent over the years. Entries, PR-134, PR-105, PR-124, PR-91 and PR-2 had mean DS values of 15, 29, 41, 61 and 75%, respectively, all differing significantly from each other at the 1% level of significance.

Table 2. Mean disease severity (DS) on a scale 0 - 100 % and infection type (IT) on a 0 - 9 scale of wheat entries selected from experiments I, II and III over successive years of reassessment.

Number of entries	DS				IT			
	1988	1989	1990	1991	1988	1989	1990	1991
9 (I)	29	41	41	41	7.8	7.2	6.1	5.4
14 (II)	–	65	60	60	–	8.5	7.5	6.0
8 (III)	–	–	46	42	–	–	7.5	3.8
Morocco	90	90	90	90	9.0	9.0	8.8	8.3

Discussion

Most of the entries screened were modern types of spring bread wheat. Among these, PR appeared to be very rare. Resistance genes resulting in an intermediate or low IT seemed to occur at a very high frequency in the entries tested. Most entries selected for having PR did not represent true PR after reassessment as the IT invariably decreased over the years. It seems unlikely that erratic environmental factors such as light intensity or temperature could be responsible for this consistent tendency. A change in racial composition in the direction of a decrease in virulence factors is unlikely as such a postulated annual loss of virulence factors is contradicted by the observed general tendency for an increase in the number of virulence factors (Danial and Stubbs 1992). A decrease in IT due to a decrease in virulence of the pathogen populations should have been accompanied by an increase in resistance and a decrease of DS. This tendency was totally absent (Tables 1 and 2). Apparently, IT is an inherently unstable characteristic, not stable enough to rely on.

Truly high IT and adequate levels of resistance did not seem to occur together, the only entry that came fairly close to these criteria was PR-134, combining a fair level of resistance with a fairly high IT.

In order to be of agronomic interest, the level of resistance expressed as DS, should be at least below 20 % compared to Morocco. The results presented here tend to disqualify PR as a promising selection criterion. PR does not seem to be a suitable approach to select for a durable type of resistance in this pathosystem. This is supported by the accumulated experience in various areas, such as Western Europe, the North-western United States and East Africa, where some resistant cultivars have retained their resistance over long periods of exposure to yellow rust (Line 1978; Van Dijk et al. 1988; Danial and Stubbs 1992). Such cultivars apparently carry yellow rust resistance of a sufficiently high level as shown by the seven Kenyan cultivars of undisputed durability (listed in Table 3). The ITs of such cultivars are invariably low to intermediate. They, therefore, do not represent PR.

Preliminary results of genetic studies of entries initially selected for PR (Table 1) and of Kenyan cultivars with durable resistance, suggest that in both cases the resistance is rather complex in nature.

Table 3. Disease severity (DS) on a 0 - 100 % scale and infection type (IT) on a 0 - 9 scale of seven wheat entries partially resistant to yellow rust and of seven wheat cultivars that have shown durable resistance to yellow rust.

Partially resistant			Durably resistant		
Entry	DS	IT[1]	Cultivar	DS[2]	IT[3]
PR-134	15	7.3	A.Mayo	1	2.5
PR-114	58	7.7	K.Kudu	1	2.5
PR-130	60	7.9	Enkoy	3	3.5
PR-91	61	7.9	K.Leopard	5	3.5
PR-124	67	7.0	Bounty	7	2.5
PR-115	72	7.8	Frontatch	7	2.5
PR-116	65	8.0	Bonny	10	2.5

[1] Mean value; [2] Source D.L. Danial and R.W. Stubbs 1992; [3] Average IT recorded in 1988-1991.

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Chapter 8

Response of different selection criteria on the type of resistance in wheat to yellow rust

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Summary

A highly heterozygous wheat population was created by mixing 40 F2's from CIMMYT, Mexico. The F2 was grown in Kenya and exposed to four selection criteria (S). **S1**=selecting the most resistant plants, **S2**=discarding the most susceptible and most resistant plants, **S3**=discarding the most susceptible plants and **S4**=selection for partial resistance (PR) i.e resistance characterized by a reduced epidemic build-up despite a susceptible infection type (IT).

In the first cycle selection for partial resistance started only in the F3 as in the F2 no partial resistance was observed. In the F4 of each of the four S-populations, 12 lines were selected to start a second cycle by intercrossing the twelve selected F4 lines within each of the four populations obtained. After two cycles of selection the selected populations were compared with each other and with various controls.

In the **S1** and the **S3** populations, the average level of resistance was markedly increased while the increase was moderate in the **S2**. Again, selection for PR (**S4**) was not successful because of the low level of resistance obtained when selecting for high IT's. Selection for partial resistance (**S4**) therefore does not lead to satisfactory levels of resistance, while (**S1**) leads to high levels of resistance probably of a non-durable nature. The (**S2**) approach, selecting against susceptibility and against complete resistance might therefore be the most advisable one at present leading to quantitative forms of resistance.

Introduction

Yellow rust of wheat caused by *Puccinia striiformis Westend* is one of the most widely distributed and regularly occurring rusts in different parts of the world. In many breeding programs, the use of the traditional breeding approach by selecting the most resistant plants or lines from the segregating populations, has resulted in many cases of breakdown of such resistance (Johnson *et al.*, 1969; Stubbs, 1972). In Kenya too break down of the high level of resistance to yellow rust in nearly all recently released cultivars and the build up of new more complex races were reported (Danial and Stubbs, 1992).

The effective resistance that appears so vulnerable to genetic adaptation of the pathogen is usually based on single, dominant genes that control a hypersensitive reaction which results in a low infection type. Another form of resistance which is assumed to be much more durable is the partial resistance (PR). Parlevliet and Van Ommeren (1975) defined PR to cereal rusts as resistance characterized by a reduced epidemic build-up despite a susceptible infection type. This form of resistance is often governed by minor genes with additive effects.

Parlevliet (1981, p 347) mentioned that the stronger one selects the more one selects for the major gene, non-durable type of resistance. It is therefore useful to compare various selection methods, the aim of the research reported here. Four selection methods, using the same heterogenous population as a basis, were followed over several cycles to study the result of the selection applied.

Materials and methods

The wheat population

A highly variable population was created by mixing F2 seed of 40 single crosses produced from 73 CIMMYT spring wheat parents. Each cross was represented by 500 seeds. Subsequently, the 20.000 seeds were divided into two parts; one for planting and one for storing at 5°C to be used as a control at a later stage.

In Kenya the main season runs from April to September. With additional irrigation the off season, October to March, is equally suitable for yellow rust resistance testing. At the test location, the experimental farm of the National Plant Breeding Research Centre, Njoro, the conditions are highly favourable for this pathogen the whole year around.

In the main season of 1989 F2 seeds were sown in one field, subdivided into four equally sized plots, in double rows 25 cm apart. Within the rows the

spacing was 15-20 cm. The double rows were alternated by a spreader row of the highly susceptible 'Morocco' at a distance of 20 cm.

The Pathogen

Since racial mixtures of the pathogen tend to reduce the possibilities to discern the low infection type resistance from the partial resistance (Parlevliet, 1983), only one race of the yellow rust with a wide virulence spectrum was used during all selection and evaluation procedures. This race is predominant in Kenya and virulent on the known major resistance genes *Yr*2, *Yr*2+, *Yr*6, *Yr*6+, *Yr*7, *Yr*7+, *Yr*8, *Yr*9, *Yr*9+ and A in 'Anza'. This race was usually introduced into the experimental field by dusting urediospores over the spreader plants of the susceptible cultivar Morocco at the tillering stage. Yellow rust epidemics developed very well throughout all cycles of the selection and good disease assessments were always possible.

During the selection and evaluation procedures, infected leaves were sampled from the field and sent to Wageningen, The Netherlands for race analyses under standard growth chamber conditions as described by Stubbs (1988) using the World and European differential sets (Johnson *et al.*, 1972).

Selection methods

In each of the four plots one of the following selection criteria (S) was applied (adopted from Broers, 1993).

S1. Only the most resistant plants with a disease severity (DS) between 0-5 % were selected. This method is representative for what breeders normally do when selecting for resistanc2/

S2. The most resistant and most susceptible plants were discarded and only those with a DS between 10-40 % were selected.

S3. The most susceptible plants were discarded and only those with a DS between 0-40 % were selected.

S4. Only plants with a high infection type (IT of 7-9) and as low a DS as possible were selected (selection for partial resistance).

To minimize differences in the development stage and to avoid under or over-estimation of the resistance level of the selected plants, the very early and very late plants were discarded before starting the selections.

Selection according to S1, S2, S3 and S4 and for other characteristics such as good tillering capacity and good general appearance were carried out when 50 % of the heads had emerged.

In the F2 there were no plants with a truly susceptible infection type (IT). Therefore plants were selected with as high an intermediate IT as possible in the

S4 plot. From the F2 a total of 150, 175, 259 and 185 plants (769 in total) were selected from the S1, S2, S3 and S4 plots respectively. Approximately 100 individual plants were taken at random from each plot and the seed harvested as bulk to represent a control for each selection criterion. These control populations were advanced every season to the next generation without carrying out any selection.

F3 lines of the 769 selected plants were sown in small plots consisting of one row of 4 m. Per plot 150-200 seeds were sown. The row distance was 30 cm. The selection was as in the F2. The number of F3 lines selected in the S1, S2, S3 were 36, 18 and 41 respectively. The F3 lines from the selected S4 plants very clearly segregated for IT and in many lines plants with high IT's were observed. Selection therefore was done on an individual plant bases within F3 lines with on average a fairly high IT and a moderate DS. Of each of the 58 selected lines five ears were taken from tillers with a high IT.

The F4 lines were grown as in the F3 in single row plots of 3 m long. The selection was as in the F3. From each of the S1, S2, S3 and S4, 12 F4 lines were selected. To start the second cycle of the recurrent selection program, the 12 lines were intercrossed in various combinations within its S population and all 12 lines occurred four times as a parent to produce 24 single crosses. F1 seeds were subsequently sown to produce F2 seeds and within each S-population equal amounts of seed of each of the 24 crosses were taken together to form the start of the second cycle.

In the main season of 1991, the four F2's of the second cycle were exposed to the same four selection criteria respectively. The number of plants selected in the S1, S2, S3 and S4 populations were 151, 111, 164 and 124 respectively.

In the subsequent off season, the 550 corresponding F3 lines were planted in the same way as in 1989/90 and 12 lines were selected from each S-population. From each selected line five ears were taken at random and harvested individually for re-testing in the F4. The 48 (4x12) individual F4 lines from the first cycle, used for crossing, had been advanced to the F6 without further selection. From each F6 line, five ears were selected at random and re-sown to produce the F7. In this way the 12 lines of each *S*-population, first cycle, were represented by 60 lines in the F8.

Response to selection

In 1992, an evaluation trial was carried out to measure the response of the four selection criteria after one and after two cycles of selection. The trial comprised of:

1) F8 lines (240) obtained from the F4 lines selected in the first cycle. Each

selection criterion was represented by 60 lines and each F8 line originated from one F7 line through random ear selection.
2) F4 lines (240), second cycle of the S1, S2, S3 and S4 populations whereby each S-population was represented by 60 lines, these 60 lines being derived from 12 selected F3 lines (five ear progenies per F3 line).
3) Original parents (73).
4) F8 control lines (40). These F8 lines originated from the randomly taken plants from the initial F2 population (approximately 100 plants of each S plot) which were advanced in bulk to the F6. From each of these four F6 bulks, ten ears were taken at random and advanced to the F8.
5) Reserve seed of the F2 initial population, which was divided into 20 seed lots and each seed lot was planted in a separate plot.
6) Reserve seed of the F2 second cycle representing each of the four S-populations. Seed of each of the four groups was divided into 20 seed lots and each seed lot was planted in a separate plot.
7) The susceptible cultivar Morocco was used as a check in 20 replicates.

All these entries were planted at two dates (4th april and 8th may 1992) and the entries were fully randomized at each date. Each plot measured two rows of 2 m. The row spacing was 20 cm. Spores of the yellow rust race were mixed with talc powder and dusted over all plots at tillering stage (DC 29 on the scale of Zadoks *et al.*, 1974) for 3-4 consecutive days. DS and IT were recorded three times with a weekly interval. DS was recorded by estimating the percentage of affected leaf area on the upper three leaves according to the Peterson 0-100% scale (Peterson *et al.*, 1948). IT was assessed by using the 0-9 scale of McNeal *et al.* (1971).

Results and discussion

Virulence of yellow rust populations between 1989-1991
The race analyses of isolates collected from the experimental fields at Njoro between 1989 and 1991 are shown in Table 1. The results revealed a fair variation in the racial composition. Apart from the race with ten virulence factors which was introduced every year, an additional five races were detected in 1989 showing five to twelve virulence factors. In 1990 and 1991 races with 11 to 12 virulence factors were detected.

Table 1. Yellow rust races detected at Njoro between 1989-1991 with their virulence factors to Yr resistance genes.

Year	Virulence factors to[1]	No. of virulence factors
1989	Yr2,Yr6,Yr7,Yr8,A	5
1989	Yr6,Yr7,Yr8,A,SD,SU	6
1989	Yr2,Yr6,Yr7,Yr7+,Yr8,Yr10,A,SU	8
1989,1990,1991	Yr2,Yr2+,Yr6,Yr6+,Yr7,Yr7+,Yr8,Yr9,Yr9+,A	10
1989,1990,1991	Yr2,Yr2+,Yr6,Yr6+,Yr7,Yr7+,Yr8,Yr9,Yr9+,A,SU	11
1990,1991	Yr2,Yr2+,Yr6,Yr6+,Yr7,Yr7+,Yr8,Yr9,Yr9+,A,Sd	11
1989,1991	Yr2,Yr2+,Yr6,Yr6+,Yr7,Yr7+,Yr8,Yr9,Yr9+,A,SU,SD	12
1990,1991	Yr2,Yr2+,Yr6,Yr6+,Yr7,Yr7+,Yr8,Yr9,Yr9+,A,SD,3N	12

[1] refers to resistance genes in the differential cultivar: Yr2 in Kalyansona, Yr2+ in Heines VII, Yr3N in Nord Desprez, Yr6 in Heines Kolben, Yr6+ in Heines Peko, Yr7 in Lee, Yr7+ in Reichersberg 42, Yr8 in Compair, Yr9 in Federation 4X/Kavkaz and Yr9+ in Clement. A, SD and SU refer to resistance factors not yet designated in the cultivars Anza, Strubes Dickkopf and Suwon 92/Omar
In x+ the + sign means additional virulence besides virulence against x.

Selection in cycle 1
The starting population had on average a fair level of resistance. The IT of the F2 plants ranged from 0 to 6-7. The DS varied between 0-90 %. Table 2 shows the number and percentage of plants selected according to the S1, S2 and S3 criteria respectively. Selection according to the S4, however, was problematic as plants with a truly susceptible IT did not occur. The 185 plants selected were plants with as high an IT as were present. These plants were characterized by a fairly high DS (40-90%) and, initially, an intermediate IT (4 to 7) at heading and a low to intermediate IT (2 to 4) when the flowering had been completed.

Among the F3 lines, selection according to the S1, S2 and S3 methods were quite possible. Selection for increased levels of resistance was effective in the S1, S2 and S3 populations. Many F3 lines of S4 showed single plant segregation for a high IT (7-9) and such plants were selected. However, those plants were nearly all characterized by a high DS, ranging from 60 to 90%, suggesting a positive and strong association between IT and DS.

The F4 showed the same tendency as the F3; high IT and high DS again were associated while selection towards higher levels of resistance regardless the IT in S1, S2 and S3 was quite effective, despite the fair level of resistance in the starting population.

Selection in cycle 2.
Table 2 shows the selection intensity applied. For the S1, S2 and S3, the selection proceeded as in the first cycle. In the S4, selection for a high IT was possible from the F2 onward. Selected F2 plants were characterized by IT's of 7 to 9 and a high DS, ranging between 60-90%. There were hardly if any, plants with true partial resistance, i.e. a high IT and a low DS.

Response to selection in the evaluation trial
The germination of the F2 control was very poor and was therefore excluded from the evaluation. Due to large differences in the development stage between individual plants of the F2, 2nd cycle, DS and IT were only measured on the third assessment date when all plants had fully developed.

The results of the evaluation trial are summarized in Tables 3 and 4. Compared with the controls (F8 control and parents) the response to selection was very clear in the S1, S3 and S4 (Table 3). The S1 gave always by far the best response, which was expected as S1 represents the strongest possible selection pressure. For instance, DS was reduced some 3-4 fold in F4 lines after the second selection cycle. At the end of the selection most lines had a complete or near complete resistance (Table 4).

Table 2. Number of individual plants selected from F2, first cycle and F2 second cycle in the S1, S2, S3 and S4 populations.

Selection criterion	F2, first cycle		F2, second cycle	
	no. of plants selected	selection intensity, %	no. of plants selected	selection intensity, %
S1	150	12.4	151	16.0
S2	175	14.3	111	13.0
S3	259	16.2	164	20.0
S4	185	8.9	124	7.4
Total	769	12.6	550	14.1

Table 3. Mean yellow rust disease severity (DS) and mean infection Type (IT) at the third assessment date of two plantings for several groups of wheat genotypes. DS and IT were assessed on the upper three leaves.

group	1st planting DS	2nd planting DS	Mean DS	1st planting IT	2nd planting IT	Mean IT
Cycle 1						
F8 S1	7.2	2.7	5.0	1.5	1.0	1.3
S2	22.1	9.4	15.8	2.9	2.8	2.9
S3	19.6	7.4	13.5	2.2	2.0	2.1
S4	62.2	38.2	50.2	5.2	5.2	5.2
F8 control	28.1	12.7	20.4	3.4	3.4	3.4
Parents	31.9	13.1	22.5	3.3	3.3	3.3
Cycle 2						
F2 S1	7.3	4.0	5.7	1.6	3.0	2.3
S2	18.7	17.6	18.2	2.7	3.0	2.9
S3	12.9	8.7	10.8	2.0	1.8	1.9
S4	46.6	60.3	53.5	5.3	6.2	5.8
F4 S1	2.2	0.7	1.5	0.9	0.4	0.7
S2	31.8	16.7	24.3	3.7	3.7	3.7
S3	10.2	6.4	8.3	1.7	1.9	1.8
S4	52.2	43.9	48.2	6.2	5.6	5.9

Table 4. Frequency distribution of yellow rust disease severity (DS) in seven classes of the F2 starting population, F8-control, Parents, F8 S-populations in the first cycle and F4 S-populations in the second cycle.

DS class	First cycle							Second cycle			
	F2-start[1]	F8-control	Parents	F8 S1	S2	S3	S4	F4 S1	S2	S3	S4
0-2	5	0	5	29	6	19	0	42	1	31	1
3-5	5	2	6	14	16	4	2	11	3	4	1
6-10	4	7	2	6	6	7	2	5	4	5	1
11-20	13	13	17	6	14	11	2	2	10	12	4
21-40	13	11	26	4	8	10	8	0	33	6	18
41-60	1	4	6	0	7	5	14	0	8	0	15
>60	2	3	9	1	3	4	32	0	1	2	20

[1] germination of F2 population was very poor.

S3 too gave a considerable improvement of the resistance level, which is interesting as only the most susceptible entries were removed. For instance, after the second cycle, DS was reduced by 61% in the F4 lines in comparison with the F8 lines.

The response of S2 was seemingly small, but it should be realized that the S2 ultimately consisted of a much higher proportion of genotypes with quantitative resistance than the starting population (Table 4). The much better response of S3 compared to S2 is caused by the much higher proportion of entries selected with a DS of 0-10% (Table 4).

S4 gave populations with a DS above that of the control. This has two causes. In the controls, the partial resistance was not or hardly expressed. They therefore do not represent good controls to assess the selection efficiency for PR. A second cause is the fact that it was not possible to combine a high IT (consistently over the years) and a low DS. Apparently DS and IT are strongly associated with each other. Spearman's correlation coefficient between mean DS and mean IT of the groups from Table 3 was high ($r=0.97$) and significant at $P=0.001$. This was observed also in other experiments (Broers, 1993; Danial, 1993). It indicates that selection for true PR in spring wheat to yellow rust is not possible at least under Kenyan conditions.

The aim of this experiment was to find out whether a relaxed selection pressure (S2) or selection for partial resistance (S4) would be the better approach to obtain a more durable resistance. As true partial resistance does not seem to exist in this pathosystem the S4 approach is not a realistic possibility. The S2 approach can lead to acceptable levels of quantitative resistance, but whether this resistance is of a more durable type cannot be answered yet. However, cultivars that have shown durability are nearly always cultivars with a low level of disease, suggesting that they carry quantitative resistance. Selection according to the S2 criterium therefore seems the most advisable. S1 is a very efficient approach, but that was already known as it represent the standard way of selecting yellow rust resistant wheats and the resistance selected in this way is certainly not durable as Danial and Kirigwi, 1994, clearly showed.

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Chapter 9

Stability of resistance to yellow rust in spring bread wheat: field observations at three highland locations

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Summary

Sixty nine genotypes with different levels of yellow rust resistance were tested in Mexico, Ecuador and Kenya. The genotypes were classified into four groups according to their origin and performance: 1) MEQR, 29 genotypes selected for quantitative resistance (QR) in Mexico and Ecuador, 2) KQR, nine genotypes selected for QR in Kenya, 3) DR, 13 genotypes with durable resistance in different wheat growing areas of the world, 4) CR, five genotypes with complete or near complete resistance in Kenya. Another four entries were added, two as highly susceptible checks and two carrying the overall resistance genes *Yr2* and *Yr9*.

Genotype x location interactions for qualitative resistance were very frequent. Genotype x location interactions for QR occurred fairly often. There was even a group x location interaction. The entries selected in Kenya for QR had in Kenya a significant higher disease severity than in Ecuador. The cultivars which were classified by experience as having durable resistance showed hardly any genotype x location interaction.

Introduction

Yellow rust of wheat is a major threat in many wheat growing areas (Stubbs, 1988). Genetic resistance is probably the easiest and cheapest approach to protect commercial cultivars against this disease. However, resistance often succumbed because of genetic adaptation in the pathogen population. Recently, successive breakdowns of resistance were reported such as 'Dashen' in Ethiopia and 'Cotopaxi' in Ecuador. The cultivar Pak 81, which is grown on about 80% of the acreage in Pakistan, is expected to become susceptible soon due the *Yr9* virulence which is approaching from Iran (E.E. Saari, pers. comm.). These and

other cases of breakdown (Stubbs, 1985; Danial and Stubbs, 1992) of resistance urged breeders to concentrate their breeding efforts on more durable resistance.

As Johnson (1984) points out, resistance can be considered durable after widespread use over a long period in an environment which is conducive to the disease. Practically, this means that only commercial cultivars are exposed to this test of durability and that testing for durability of resistance in breeding programs cannot be realized. Multi-location testing as often implemented by international breeding programs will not test the durability of resistance as changes in the virulence of the pathogen can not be predicted. However, multi-location testing will test abiotic stability and biotic stability against existing pathogen populations.

Based on experience, several cultivars have been identified with durable yellow rust resistance in different wheat growing areas of the world. In addition, genotypes have been selected for quantitative resistance (QR) in Mexico, Ecuador and Kenya. The main objective of this study is to assess the stability of various types of resistance of such cultivars and genotypes across three environments conducive for yellow rust and carrying geographically isolated yellow rust populations.

Materials and Methods

Genotypes

Sixty spring wheat genotypes and cultivars were used in this study. Fifty six of them can be grouped as follows:

MEQR: Twenty nine genotypes, selected for (QR) under Mexican and Ecuadorian conditions. All genotypes had a high infection type in the seedling stage with the Mexican isolate 89009 of race 14E14 (Johnson, *et al.*, 1972).

KQR: Nine genotypes, selected for QR under Kenyan conditions, characterized by relatively high infection types in the field;

DR: Thirteen genotypes with durable resistance (DR) from different regions;

CR: Five genotypes with complete to near complete resistance under Kenyan conditions (qualitative resistance);

In addition 'Taichung 23' and 'Jupateco 73S' were used as highly susceptible checks (SUSC) and 'Kalyansona' (*Yr2)* and 'Fed*4/Kav' (*Yr9*) were used as differentials (DIFF).

Some of the other genotypes have also known race-specific genes. For

instance, 'Anza' possesses *YrA* (Wellings, *et al.*, 1988) and 'Pavon 76' carries *Yr6* and *Yr7* (Badebo, *et al.*, 1990).

Locations

Three locations with conducive environments to yellow rust were selected:

1) The experimental station of the Njoro Plant Breeding Research Center (NPBRC), Njoro, Kenya at an altitude of 2160 m;
2) The experimental station Sta. Catalina of INIAP (Instituto Nacional de Investigaciones Agropecuarias), Quito, Ecuador at an altitude of 3050m;
3) The experimental station Atizapan, Mexico, at an altitude of 2650 m.

At the three locations the 60 genotypes were planted as an non-randomized block design with two replicates. Plots consisted of two rows of 1 m with a row distance of 25 cm in Kenya and Ecuador. In Mexico, plots were planted on beds. On each bed two rows were planted. Beds were 75 cm apart. Perpendicular to the plots, a spreader row of "Morocco" was planted. In the case of Kenya and Ecuador, natural infection started the epidemic. In Mexico, the epidemic was started by injecting a spore/water suspension of Mexican isolate 89009 of race 14E14 in tillers of "Morocco" in the spreader row.

Disease severity (DS) was assessed on a 0-100 scale (Peterson, *et al.*, 1948). In Kenya, DS was assessed at stage DC70 (Zadoks, *et al.*, 1974). In Ecuador DS was assessed at stage DC68 and in Mexico at stage DC65.

All analyses were performed with logit-transformed DS (Logit(DS) (Zadoks and Schein, 1979). Though the experiments were non-randomized, an analysis of variance was performed using a randomized complete block design combined over locations.

Results and discussion

The three locations differed considerably in DS. Taking all the genotypes into account, Mexico had by far the lowest average DS. A large part of the difference between Mexico and the other locations is assumed to be caused by overall resistance genes effective in Mexico (resulting in qualitative resistance there) but not effective at the other locations. Apparently, the range in virulence factors in Kenya and Ecuador is wider than the one in Mexico. This can be exemplified by the *Yr9* differential "Fed*4/Kav", which indicated presence of virulence for this gene in Kenya and Ecuador and absence of virulence in Mexico. It is therefore difficult to compare Mexico with the other two locations.

In order to analyse the QR results one has to disregard the qualitative

resistance data. Disease severities of less than 5% were considered to indicate qualitative resistance. This type of resistance occurred very frequently (40 out of the 60 entries) at the Mexico location. At the same time all entries with a qualitative resistance expressed in Ecuador or Kenya showed a qualitative resistance in Mexico (Table 1). To analyse the QR those entries were used, that had a DS of 5% or more at both the Ecuador and the Kenya locations. Table 1 presents the data where the entries are grouped as mentioned in "materials and methods". On these 51 entries an anova was carried out. This resulted in some interesting observations:

1) The DS for all groups was higher in Ecuador than in Kenya, except for the KQR group, which had a higher DS in Kenya, the reversal being highly significant.
2) There were some significant genotype x location interactions in the MEQR and KQR group but not in the DR group.
   When Mexico was included in the analysis it was observed that:
3) Several entries gave an interaction for QR in Mexico compared to the QR of the other two locations (Table 1).
4) A further observation was that a large number of entries showed a genotype x location interaction for qualitative resistance; 32 for Mexico versus the other two locations and 5 between Ecuador and Kenya. This indicates that many entries are carrying race-specific resistance genes.

Host pathogen interactions apparantly do occur fairly frequently within QR in wheat to yellow rust. The too high DS in Kenya of the KQR group might have a similar cause. These entries were selected several years ago for their quantitative resistance (Danial, 1993) in Kenya. It is tempting to explain the observations by an erosion of the resistance in Kenya. Exposed to another yellow rust population, that of Ecuador, the full quantitative resistance became expressed again. There are, however, two objections to this explanation. In Kenya no erosion over the years was observed of these entries, although they were tested almost every season, and these entries were never commercially grown in Kenya.

The genotypes, that showed by far the least interactions with locations were those belonging to the DR group. Even Africa Mayo and Altar 82, with qualitative resistance, did not show a genotype x location interaction.

Table 1. Yellow rust disease severities of a range of wheat genotypes at three highland locations. The genotypes are arranged in four groups with quantitative resistance (QR) at the Ecuador and Kenya locations (MEQR, KQR, DR and other entries) and a rest group.

Genotype	Location			Genotype	Location		
	Mex	Ecua	Kenya		Mex	Ecua	Kenya
MEQR				**DR**			
Parula	0	20	32.5	Kenya Kudu	0	12.5	10
INIA 66****	12.5	80	75	K. Leopard	5	20	15
Jupateco 73R****	7.5	70	27.5	Amazonas 6	0	20	20
Opata 85*,****	25	82.5	27.5	Pavon 76	2	25	30
Frontana	2	17.5	12.5	Napo 63	0.5	50	27.5
Thatcher	30	50	40	Crespo 63	0	50	12.5
Thatcher-L34	15	32.5	12.5	Fan Lui	0	30	17.5
Tobari 6	2	65	25	Enkoy	0	20	8.5
Trap #1	1	32.5	7.5	Anza****	10	70	35
Tonichi 81	1	20	5	Israel	2	35	10
Esmeralda 86*	25	80	27.5	Bonza 63	0	30	30
Papago 86	20	47.5	35				
Siren****	5	72.5	22.5	**Mean DR**	**1.6**	**33.0**	**19.6**
Pfau/Vee#5	1.5	45	50				
Sonoita 81	0	52.5	20				
665	0	60	35	**Other entries**			
Blueskye	0	45	55	**CR**, RS-19****	5	50	20
Rabe	0	55	22.5	**CR**, RS-47****	5	80	60
CNO 79	20	55	35	Kalyansona	25	82.5	40
Turaco	0	32.5	15	Fed 4/KVZ	0	40	20
Liz*	2	8.5	22.5	Jupateco 73S	55	95	80
Pionero inta	1	20	17.5	Taichung 29	75	100	90
Spica****	5	32.5	30				
Cucurpe 86	5	52.5	27.5	**Mean Others**	**27.5**	**74.6**	**51.7**
Tepoca****	10	72.5	40				
Sha 5	0	8.5	5				
YMI#6	1.0	30.5	27.5	**Entries without QR at Ecuador and/or Kenya.**			
Mean MEQR	**7.1**	**30.8**	**18.6**	**DR**, Afr. Mayo	0	1.5	0
				DR, Altar 82	0	7.5	3.5
KQR				**MEQR**, 3-2	0	0.1	2.5
Pr-105	0.5	20	60	**MEQR**, Yaco***	0	1.5	22.5
Pr-2	0	27.5	85	**KQR**, Pr-7**	0	0	22.5
Pr-6	0	8.5	40	**KQR**, Pr-134***	0	1	45
Pr-124	0	17.5	50	**CR**, RS-27***	0	1.5	35
Pr-31	0	32.5	65	**CR**, RS-10***	0	1	7.5
Pr-46	0	15	25	**CR**, RS-15	0	1	2.5
P3-91*	5	70	50				
Mean KQR	**0.8**	**27.3**	**54.3****				

*) Significant (P=0.05%, LSD test) genotype x location interaction for QR between Ecuador and Kenya.
**) Significant (P=0.01%, LSD test) genotype group x location interaction for QR between Ecuador and Kenya.
***) Significant (P=0.05%, LSD test) genotype x location interaction for qualitative resistance between Ecuador and Kenya.
****) Significant (P=0.05%, LSD test) genotype x location interaction for QR between Mexico and either Ecuador or Kenya.

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IV. Genetic analysis of yellow rust resistance

Introduction

Various types of resistance which are considered to be durable to the cereal rusts and to other diseases were reported. Van der Plank (1963) stressed breeding for durable resistance and used the terms vertical and horizontal resistance which are identical with race-specific and race-non-specific resistance respectively. Race non-specific resistance he assumed to be polygenic and durable. Sharp and Volin (1970) studying resistance in wheat to yellow rust described temperature sensitive genes with minor effects and concluded that the genes studied were of a race-non-specific nature. Milus and Line (1986) reported a temperature-sensitive resistance in the cultivars Gaines, Nugaines and Luke which have been shown to be durably resistant to yellow rust. Parlevliet and Van Ommeren (1975) in their work in barley to barley leaf rust, introduced the concept of partial resistance which is a form of quantitative resistance. This partial resistance was shown to be typically polygenic and appears to be of a durable nature (Parlevliet, 1981). In FAO projects, Robinson (1976) proposed to exploit horizontal resistance in breeding programs through a strategy based on transgressive segregation for higher levels of resistance after crossing susceptible cultivars with each other.

Durability of resistance

Durable resistance is defined as "resistance that remains effective in a cultivar that is widely grown for a long period of time in an environment favourable to the disease" (Johnson, 1983).

In the wheat-yellow rust system breeding for resistance can be achieved by single genes or by the combined effect of several genes, each of small effect, and the resistance may be either complete or incomplete (partial or quantitative). Despite failure of resistance due to major race-specific resistance genes in many cultivars (Johnson *et al.*, 1969; Stubbs, 1972; Stubbs, 1985; Danial *et al.*, 1993), other cultivars remained resistant for relatively long periods (Johnson, 1988; Van Dijk *et al.*, 1988; Milus and line, 1986; Danial, 1993). Such cultivars are considered to be durably resistant and have been identified in many wheat growing areas.

Race specificity

Race non-specific resistance in wheat to the cereal rusts and to diseases in other crops has often been suggested by various authors to be associated with minor genes or polygenes, with adult plant resistance, quantitative resistance, partial resistance or incomplete resistance that reduce the infection rate (e.g. Lewellen *et al.*, 1967; Robinson, 1976; Van der Plank, 1963, 1968). However, Parlevliet (1977), and Parlevliet and Van Ommeren, 1985) showed small race specific effects amongst genes that have minor effects in reducing the rate of development of leaf rust on barley. It can not be assumed, therefore, that either genes with minor effects or resistance that reduce the infection rate are truly race non-specific.

The number of genes involved in partial resistance

The genetics of partial resistance has been investigated in some details for other cereal-rust systems and the results were summarized by Parlevliet (1993). The number of genes involved tends to be restricted in most cases, two in maize to *Puccinia sorghi* (Kim and Brewbaker, 1977), two to three in wheat to *P. recondita* (Broers and Jacobs, 1989; Jacobs and Broers, 1989), three to five in wheat to *P. gramminis* (Knott, 1988), up to five or six minor genes in barley to *P. hordei* (Parlevliet, 1978).

The data suggest that partial resistance is the result of the cumulative effects of several genes with small to intermediate effects.

Inheritance of quantitative and of durable resistance

The approach of selection for partial resistance may vary with the type of pathogen. Selection in wheat for partial resistance to yellow rust, characterized by a reduced disease severity together with a high infection type, was found to be very difficult and did not seem a suitable approach in this pathosystem (Danial, 1993; Broers, 1993). But there are many wheat lines with a low disease severity and an intermediate infection type. This resistance can not be described as partial resistance, a better description is quantitative resistance. Despite the apparent difficulties of obtaining true partial resistance, a survey of cultivars grown in the past in Kenya identified a number of wheat cultivars with high levels of resistance which were kept over at least 25 years. They had a low infection type and can not be considered to be quantitatively resistant, but they

must be considered as durably resistant (Danial *et al.*, 1993).

The main objectives of this part are :

1. To postulate the resistance genes of nine spring wheat genotypes selected for their quantitative resistance at the seedling stage to eight races of *P.striiformis*.
2. To study the genetic background of five spring wheat genotypes with a quantitative resistance under Kenyan environments.
3. To study the inheritance of durably resistant Kenyan wheat cultivars.

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Chapter 10

Postulation of *Yr*-resistance genes in nine wheat genotypes to *Puccinia striiformis*

D.L. Danial

Summary

The seedling reaction of nine spring wheat genotypes was assessed to eight yellow rust races with known virulence factors. The genotype Pr91 was suggested to carry *Yr2*, while Pr31, Pr105, Pr134 were assumed to carry a combination of *Yr2* and *Yr9*. Pr7, Pr124, Pr46 and Pr2 were postulated to have *Yr6* and *Yr9* or Yr6 + an additional unknown gene, while Pr6 is assumed to carry *Yr7* and *Yr9*.

In field tests, disease severity (DS) of the genotypes remained constant over the years and ranged widely between the genotypes (from 15% to 100% DS). This quantitative resistance must be based on different genes as both DS and the IT varied greatly. This means that it should be possible to accumulate this type of resistance.

Introduction

Partial resistance is characterized by a slow epidemic build up despite a susceptible infection type (Parlevliet and van Ommeren, 1975). Among a large number of wheat entries (Chapter 7) nine spring wheat genotypes were selected that had a low disease severity (DS) and a high infection type (IT). The genotypes were therefore assumed to be partially resistant. However, over the years IT was found to be a rather unstable and so unsuitable parameter to select for partial resistance (Danial, 1993). Despite the instability of the IT, the selected genotypes differed in their level of resistance and were assumed to be quantitatively resistant.

As the Kenyan yellow rust population carries a large number of virulence factors, often 10 or more (Chapter 1) it would be useful to know whether these genotypes carried defeated major overall genes along with their quantitaive resistance.

Material and Methods.

Seedling test

Nine spring wheat genotypes, originating from CIMMYT and selected in Kenya (Table 1) were used. The extremely susceptible cv. Morocco was included as a check. The experiment was carried out at the Research Institute for Plant Protection (IPO-DLO), Wageningen, The Netherlands. Seedling tests were conducted in growth cabinets as described by Stubbs (1988). Two consecutive tests were carried out and each consisted of three replications. Ten to 15 seeds of each genotype were grown in plastic pots at 15°C with 16 hours light (ca. 20.000 lux) and were inoculated at the seedling stage (DC=10, Zadoks *et al.*, 1974) with urediospores suspended in mineral oil. The plants were then incubated at 9°C for 24 hours in a dew chamber and afterwards transferred to a growth chamber with 16 h of light at 18°C with ca. 28.000 lux and 8 h dark at 15°C. Eight races with known virulence patterns were used for inoculations (Table 2).

Seven days after inoculation, the second leaves were removed and fertilizer solution was added to the plants (N:P:K=15:20:25). Sixteen days after inoculation, IT's were recorded on the 0-9 scale of McNeal *et al.* (1971), with a 1 to 3 indicating resistance or avirulence, a 4-6 an intermediate reaction and a 7-9 susceptibility or virulence. From the virulence/avirulence patterns on the seedlings, the identity of the resistance genes was postulated.

Adult plant test

The nine genotypes were tested for their adult plant resistance between 1988-1991. The experiments were carried out at the experimental fields of the National Plant Breeding Research Centre at Njoro, Kenya. The genotypes were planted in two replicates in plots of two rows of 2m length. The cv. Morocco was planted as a spreader row perpendicular to the rows in the plots. Inoculation of the spreader rows took place at tillering stage with a race carrying virulence to *Yr2, Yr2+, Yr6, Yr6+, Yr7, Yr7+, Yr8, Yr9, Yr9+* and Anza. DS and IT were recorded three times with a weekly interval on the upper three leaves. DS was assessed using the 0-100 Peterson scale, (Peterson *et al.*, 1948) and IT using the 0-9 scale (McNeal *et al.*, 1971). In each growing season, infected leaves were sampled from the field and sent to Wageningen, The Netherlands for race analysis as described by Stubbs (1988) using the world and European differential sets (Johnson *et al.*, 1972).

Table 1. Infection types (Resistant, R=0-3, Susceptible, S=7-9) of nine wheat genotypes and of the susceptible cv. Morocco to eight yellow rust races with known virulence factors and the postulated overall resistance genes.

Race	Origin	Virulence on *Yr* genes[1]	Genotype[2]									
			1	2	3	4	5	6	7	8	9	10
1	Zambia	2,3N,6,9,A	S	S	S	S	S	S	S	S	R	S
2	Kenya	2,2+,6,6+,7,7+,8,9,9+,A	S	S	S	S	S	S	S	S	S	S
3	Kenya	2,6,7,8,A	S	R	R	R	R	R	R	R	R	S
4	Ethiopia	7,9,10,SD	R	R	R	R	R	R	R	R	S	S
5	Nepal	1,2,2+,6,6+,7,7+,8,A	S	R	R	R	R	R	R	R	R	S
6	The Netherlands	2,2+,3V,3N,4+,7,9,9+,SU	S	S	S	S	R	R	R	R	S	S
7	The Nertherlands	2,2+,3V,3N,4+,7,7+,9,9+,SD,SU	S	S	S	S	R	R	R	R	S	S
8	The Netherlands	1,2,2+,3V,3N,4+,6,6+,9,9+,SD,SU	S	S	S	S	S	S	S	S	R	S
Postulated *Yr* genes			2	2 and 9			6 and 9				7 and 9	

[1] refers to resistance genes in the differential cultivars: *Yr1* in Chinese 166, *Yr2* in Kalyansona, *Yr2+* in Heines VII, *Yr3*(V) in Vilmorin 23 and *Yr3*(N) in Nord Desprez, *Yr4+* in Hybrid 46, *Yr5* in *Triticum speltum album*, *Yr6* in Heines Kolben, *Yr6+* in Heines Peko, *Yr7* in Lee, *Yr7+* in Reichersberg 42, *Yr8* in Compair, *Yr9* in Federation 4*/Kavkaz, *Yr9+* in Clement and *Yr10* in Moro. A, SD, SU, CV and SP refer to resistance factors not yet designated in the cultivars Anza, Strubes Dickkopf, Suwon 92/Omar, Carstens V and Spaldings Prolific. X+ (2+ 6+ etc.) means additional unknown resistance factor besides *Yrx*.

[2] 1= Pr91, 2=Pr31, 3=Pr105, 4=Pr134, 5=Pr7, 6=Pr124, 7=Pr46, 8=Pr2, 9=Pr6, 10=Morocco.

Table 2. Mean disease severity (DS) and infection type (IT) of ten wheat genotypes in the field at the adult plant stage. Means over the years 1989-1991.

Genotype	DS	IT
Morocco	90	9.0
Pr2	75	6.8
Pr91	61	7.9
Pr31	52	5.0
Pr124	51	4.5
Pr6	35	5.8
Pr105	29	6.8
Pr46	29	4.9
Pr134	15	7.3
Pr7	15	5.5

Results

Seedling test

The identification of known resistance genes is based on the IT's for a range of races. Seedling IT's given by each genotype are presented in Table 2 and four groups of genotypes were identified.

Group I, represented by Pr91, showed a high IT (7-9) to all the races that possess virulence to *Yr2* and a low IT with race 82E0 which lacks virulence to *Yr2*. This indicates the presence of *Yr2*.

Group II, Pr31, Pr105 and Pr134, were observed to have a high IT (7-9) to five races having virulence to both *Yr2* and *Yr9* and a low IT when one or both virulences were absent. This indicated the presence of *Yr2 and Yr9*.

Group III, Pr7, Pr124, Pr46 and Pr2 had a low IT to races 3, 4, 5, 6, 7 and 8 and a high IT to races 1 and 2. This indicates the presence of *Yr6* and *Yr9*

Group IV, Pr6, showed a high IT with the races 2, 4, 6 and 7 and a low IT with the races avirulent for *Yr7* and *Yr9*, indicating the presence of *Yr7* and *Yr9*.

The cv. Morocco was susceptible to all races suggesting absence of effective resistance genes in this cultivar.

Adult plant test

At the adult plant stage, the levels of resistance between 1988 to 1991 varied among the genotypes from moderately resistant to quite susceptible compared to the cv. Morocco. (Table 1). This indicates the presence of quantitative resistance ranging from fairly high (Pr134 and Pr7) to low (Pr2). Race analyses revealed a fair variation in the racial composition in the field between 1988-1991. Apart from race 2 which was introduced every year in the plots, an additional five races carrying up to twelve virulence factors were detected.

Discussion

The postulation of genes following inoculation with different known races is based on the gene-for-gene relationship (Zadoks, 1961). This approach is not a fool-proof way of determining the genetic constitution of genotypes but is a fast method to identify with reasonable certainty which known genes are present, effective or not.

Wheat is grown on the Kenyan highlands throughout the year between 1600-2800 m and a continuous movement of the inoculum from one place to another usually takes place. Consequently a high inoculum pressure is available throughout the year and severe infection already in the seedlings takes place especially at elevations between 2200 to 2800 m. Effective seedling resistance at these elevations is required and the results obtained from this study indicate the absence of effective seedling resistance genes in all genotypes to race 2 a predominant race in Kenya and shows the importance and the need for adequate protection in the long run.

With the exception of Pr2, the genotypes studied in this experiment seem to carry *Yr9* in combination with *Yr2*, *Yr6* or *Yr7*. In CIMMYT derived germplasm *Yr9* is widely present and introduced through the IB/IR wheat-rye translocation from russian winter wheat. *Yr2* was introduced through Kalyansona which is used as parent in CIMMYT crosses (Rajaram *et al.*, 1983).

Four known yellow rust resistance genes (*Yr2*, *Yr6*, *Yr7*, *Yr9* or combinations of these) were detected from IT data in the examined lines. Although the genotypes have shown race specificity to some races and ineffective seedling resistance genes to race 134E150, an acceptable resistance in the field in some genotypes was observed. This quantitative resistance must be based on several genes as the genotypes differ significantly in DS and IT. This opens the possibility to accumulate this quantitative resistance through crosses between moderately susceptible wheat genotypes. Pope (1965) and Sharp

(1972) indicated that increased resistance to yellow rust was obtained through the accumulation of minor resistance genes in progenies from crosses between wheat cultivars classified as susceptible to the pathogen. Such forms of resistance is likely to be durable but breeders should keep in mind that only time and exposure will determine how durable such a resistance is.

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Chapter 11

Inheritance of resistance to yellow rust in five quantitatively resistant spring wheat genotypes

D.L. Danial

Summary

Five quantitatively resistant wheat genotypes (Pr2, Pr7, Pr46, Pr105 and Pr134), characterized by different levels of resistance to yellow rust were crossed among each other and with the highly susceptible cv Morocco. Disease severity (DS) and infection type (IT) of yellow rust were assessed for the parents, F2 and F4 progenies at the adult plant stage in the field. The crosses with Morocco suggested that Pr2 carries one or two, Pr46, Pr105 and Pr134 two, and Pr7 at least three resistance factors.

Transgressive segregation occurred in all crosses between the quantitatively resistant genotypes but to a limited extend. Thus the loci in the various resistant genotypes seem partly identical and/or linked.

Introduction

In various cereal-rust pathosystems partial resistance has been described and studied (Parlevliet, 1979). In wheat partial resistance as defined by Parlevliet and van Ommeren (1975) against yellow rust (*Puccinia striiformis*) is difficult to discern. Despite an extensive effort no entries with a high infection type (IT) and a low disease severity (DS) were found (Danial, 1993). Entries with a reduced DS and intermediate IT, however, were frequently observed.

To study the inheritance of this quantitative resistance, five entries with varying levels of quantitative resistance were intercrossed and crossed with the highly susceptible cultivar Morocco.

Materials and Methods.

Production of F1 seed

Five spring wheat genotypes (Pr2, Pr7, Pr46, Pr105 and Pr134), originating

from CIMMYT, were used. The genotypes were selected in Kenya and varied in their level of resistance from fairly resistant to quite susceptible. The cv. Morocco was used in the crosses as a universal susceptible. In a wire-screen-protected net house, fifteen crosses were made in a half diallel set. F1 plants were bagged at flowering time to prevent outcrossing and seed was harvested per cross. In all crosses the ears were enclosed in cellophane bags at flowering time to prevent any possible outcrossing and seed was harvested per cross.

F2-F4 generations

The F2 seeds together with their respective parents were planted in rows measuring 20 m long and 20 cm between seeds. Each cross was represented by approximately 200-300 seeds. At maturity 60 plants per cross were selected at random, harvested and threshed by hand.

Each F3 line was planted in a single row of 4 m long and with a plant distance of approximately 20 cm. The parents of each cross were planted in the same way. Within each cross the lines with the lowest and with the highest DS were identified and individual plants with low and high DS were selected respectively. Of clearly segregating lines the least and most affected plants were sampled. The F4 single plant progenies were planted as single rows, 2m long. The parents of each cross were planted in the same way alongside with their F4 progeny.

Of the crosses with cv Morocco no F3 and F4 was analyzed as the F2 plants with a susceptibility similar to that of the cv Morocco did not produce seed.

Inoculation and disease assessment

Race 134E150 (race designation: Johnson et. al, 1972) was used as it is predominant in Kenya. Inoculations of parents and progenies was usually carried out at tillering stage. DS was recorded according to the 0-100% scale of Peterson et al.(1948). Assessment of DS was carried out on the upper three leaves between heading and flowering

Results and discussion

Mean DS and IT of the parents of observations from six growing seasons is given in Table 1. Pr2 showed a low level of resistance while Pr7 was fairly resistant when compared with the highly susceptible cv. Morocco. The genotypes showed an intermediate IT ranging from 5.8 in Pr2 to 4.2 in Pr46.

Table 1. Mean yellow rust disease severity (DS) and infection type (IT) of five wheat genotypes and the cultivar Morocco assessed in six growing seasons.

Genotype	DS	IT
Morocco	90	9.0
Pr2	60	5.8
Pr105	35	5.0
Pr46	30	4.2
Pr134	20	5.3
Pr7	15	4.8

In the crosses with Morocco a variable proportion of the F2 plants showed a necrotic reaction. The severity of the necrosis varied from moderate to severe. Often such plants died and in none of these plants a proper DS assessment was possible. Of these crosses DS scores were taken from the non-necrotic F2 plants only. Frequency distributions for DS of all crosses are presented Table 2.

Crosses with Morocco

The classification of the F2 plants into DS classes carries an error of unknown magnitude since the plants vary in earliness and because assessments of single plants cannot be considered very accurate. Clear cut segregation ratios are therefore not expected. Nevertheless some conclusions can be drawn from the data shown in Table 2.

Pr2 x Morocco

The high number (105) of F2 plants with a DS similar to that of the susceptible parent Morocco, and the remainder considered of having some resistance coming from Pr2, could be explained by either a 1:3 or 3:13 ratio. The latter fitting better than the former.

Pr7 x Morocco

The distribution suggests intermediate inheritance. There were no F2 plants with a DS similar to that of Morocco. This indicates three or more genes with an additive effect between them as the chance of an F2 plant with the same phenotype for susceptibility as the parent Morocco is $(1/4)^n$, with n being the number of independent genes. Thus for two genes the chance that no plants as susceptible as Morocco are found among 81 F2 plants is 0.005 and with three genes it is 0.23, indicating at least three genes.

Table 2. Number of F2 plants or F4 lines in eight Yellow rust disease severity (DS) classes of 15 crosses between six wheat genotypes and DS of the parents.

Cross	DS progenies								DS parents					
	0	5	10	20	30/40	50/60	70/80	90	Total	Pr2	pr7	Pr46	pr105	Pr134	Morocco
Pr2 x Mo															
F2	2		1	2	5	9	10	105	134	35					90/100
Pr7 x Mo															
F2	4		16	10	28	12	11		81		5				90/100
Pr46 x Mo															
F2	1	7	9	14	36	20	21	27	135			20			90/100
Pr105 x Mo															
F2	2		7	7	11	10	12	7	56				15		90/100
Pr134 x Mo															
F2	8		15	8	31	14	12	7	95					10	90/100
Pr2 x Pr7															
F2	1		21	29	27	3	2		83	30	5				
F4			1	2	10	8	14	1	36	65	25				
Pr2 x Pr46															
F2		52	56	20	1	1			130	30		25			
F4			6	5	26	14	5		56	65		30			
Pr2 x Pr105															
F2	1	7	12	44	49	9			122	30			10		
F4			1	4	32	13	9		59	65			40		
Pr2 x Pr134															
F2			6	39	84	14	5		148	30				10	
F4			1	6	29	18	4		58	75				25	

Table 2. Continued.

Cross	DS progenies									DS parents					
	0	5	10	20	30/40	50/60	70/80	90	Total	Pr2	pr7	Pr46	pr105	Pr134	Morocco
Pr7 x Pr46															
F2	6		141	13	2				162		10	30			
F4				10	32	15	2		59		25	40			
Pr7 x Pr105															
F2			100	53	11	3			167		5		15		
F4		3	19	15	14	7	1		59		25		25		
Pr7 x Pr134															
F2			61	58	32	8	7	3	169		5			10	
F4		3	19	15	14	7	1		59		25			25	
Pr46 x Pr105															
F2		96	59	17	2	1			175			25	15		
F4		2	4	24	12	13	2		57			30	40		
Pr46 x Pr134															
F2	102		20	13	9	2	1		147			25		10	
F4		23	24	11	2				60			30		25	
Pr105 Pr134															
F2	1		38	57	49	7	2		154				15	10	
F4				1	11	27	19		58				40	25	

Pr46 x Morocco, Pr105 x Morocco and Pr134 x Morocco
The F2 distributions suggest intermediate inheritance with a restricted number of additive genes, as the Morocco phenotype for DS occurred clearly at a higher frequency than in the Pr7 x Morocco cross. The number of genes could be one or two for Pr46 and Pr105 and probably two for Pr134, assuming independent segregation. In case of linkage more factors could be involved.

Crosses with Pr2
In the four crosses with Pr2 transgression beyond the parents occurred indicating the segregation of genes. However, the frequency of transgression was low to very low. This suggests that either part of the resistance is in common or is linked. If Pr2 carries one resistance gene it must be fairly closely linked to a resistance gene in the four other resistant genotypes. If Pr2 carries two genes one must be in common with a resistance gene in the four other entries.

Crosses with Pr7
The frequency of transgression varied from some (with Pr2 and Pr46) to fair with (Pr105 and Pr134) indicating that Pr2 and Pr46 have a higher proportion of their resistance in common with the resistance of Pr7 than Pr105 and Pr134. In the cross with Pr134 even near Morocco types occurred.

Other crosses
The cross Pr46 x Pr105 showed some transgression. The crosses Pr46 x Pr134 and Pr105 x Pr134 showed transgression predominantly to one side, resistant and susceptible respectively.

The quantitative resistance does seem to be located on relatively few loci. Only Pr7 may carry resistance alleles on three loci or more. Some of these loci in the resistant genotypes are identical and/or linked. This latter conclusion is derived from the observation that Morocco type of plants were hardly observed. Only in the cross Pr105 x Pr46 two F4 lines came close to the susceptibility of Morocco and in the cross Pr134 x Pr7 three such plants were observed in the F2. With independent assortment of all loci involved a much higher frequency of F2 plants and F4 lines with a susceptibility like that of Morocco should have been found.

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Chapter 12

Inheritance of resistance to yellow rust in five durably resistant spring wheat cultivars.

D.L. Danial

Summary

Five durably resistant wheat cultivars (Enkoy, Africa Mayo, Kenya Leopard, Kenya Kudu and Frontatch) and the highly susceptible cultivar Morocco were intercrossed in a half diallel.

From the F1 and F2 data Enkoy, Africa Mayo and Kenya Kudu seem to carry one dominant factor for resistance, Kenya Leopard one recessive factor and Frontatch two recessive factors.

The F2 to F5 progenies of all crosses between the resistant cultivars showed restricted segregation. The amount of segregation varied from very little to moderate. This indicates that the resistance factors in these cultivars are located on one piece of chromosome with probably several factors for resistance closely linked. The degree of linkage between these resistance factors seems to vary from very strong to fair. Such closely linked factors may explain the durability of the resistance of these cultivars.

Introduction

Durably resistant (DR) cultivars are cultivars that remain resistant when widely grown for a long period of time in an environment favourable to the disease (Johnson, 1983, 1988). Such resistance can be considered as an important resource for further use by the breeders. In Kenya, despite failures of resistance in wheat to yellow rust, due to race specificity, a number of wheat cultivars has remained resistant for long periods and are assumed to be durably resistant (Danial and Stubbs, 1992). Resistance in these cultivars is varied from near complete to incomplete.

There is no information available about the genetic background for yellow rust resistance in these Kenyan cultivars. This study was therefore directed at analyzing the inheritance of this durable resistance.

Materials and Methods

The host plant

Five cultivars (Table 1) and the universally susceptible cultivar Morocco were used. Crosses were made in october 1990 in a half diallel set among the six cultivars to produce 15 crosses. Crosses were carried out at Njoro, Kenya in a field protected from birds with a wire mesh. The F1 plants were harvested per cross. Crosses were evaluated in the F2 and F5 generations in one row plots of 1 m. The F2 seed was planted in June 1992 in five rows of 20 m long and 50 cm apart and with a distance between the plants of 15 to 20 cm. Approximately 100 plants were harvested at random from each cross to obtain F3 lines. The F3's were planted in January 1992 and the 20 most susceptible and 20 most resistant lines from each DR x DR cross were selected and segregating plants within each line were harvested individually. Each F3 line was in the F4 represented by the progenies of four single F3 heads which were planted in one row of 1 m each. Planting of the F4 took place in May 1992. The selection for the most resistant and most susceptible lines and plants was continued in this F4 generation. The F5 seed was planted in October 1992. In each testing cycle, the lines of each cross were planted between their respective parents.

Table 1. Name, cross and year of release of five Kenyan wheat cultivars used in the genetic analysis

Cultivar	Cross[a]	Year of release
ENKOY[b]	[HERBRAND SEL/WIS245xSUP51)] x[(FR-FN/Y)^2.A][c]	----
AFRICA MAYO	AFRICA/MAYO 48	1960
FRONTATCH	FRONTANA/K58/NEWTHATCH	1963
KENYA LEOPARD	LAGAGEDINHO/3* KENYA 381P// CI 12632/3* 354P	1966
KENYA KUDU	KENYA 131/KENYA 184P	1966

[a] Source: National Plant Breeding Research Centre, Njoro.
[b] Originated from Kenya and released in Ethiopia in 1974 as Enkoy.
[c] Source: Hailu Gebre-Mariam et al., 1991.

The pathogen
The F2's were not inoculated because a natural epidemic of yellow rust developed very well at the seedling stage already. Inoculation of the F3 plants was carried out at the tillering stage with yellow rust urediospores from a race with a wide virulence spectrum. This race is predominant in Kenya and virulent on the known yellow rust major resistance genes *Yr2, Yr2+, Yr6, Yr6+, Yr7, Yr7+, Yr8, Yr9, Yr9+* and *A* in Anza. The subsequent generations (F4 and F5) were inoculated with the same race collected from the previous cycle.

Disease assessment
Disease severity (DS) was recorded on the upper three leaves after heading had been completed. DS was recorded according to the 0-100 % scale (Peterson *et al.*, 1948).

Results

The resistance levels of the parents
Mean DS and infection type (IT) at the adult plant stage of assessments over the years are summarized in Table 2. The DS varied between 2.6 to 8.7% and the IT ranged between 0.5 to 3.0. The ranking order for DS between the five resistant cultivars varied little between the years.

Table 2. Disease severity (DS) and infection type (IT) of five durably resistant wheat cultivars and the susceptible cv Morocco averaged over four years.

	1989-1992	
Cultivar	DS	IT[1]
Enkoy	8.7	2.7
A.Mayo	0.8	0.5
K.Leopard	8.5	3.0
K.Kudu	2.6	1.2
Frontatch	4.8	1.2
Morocco	90.0	9.0

[1] scored according to the scale of McNeal *et al.*, 1971.

Performance of F1 and F2 generations of the crosses with 'Morocco'.

The classification of the F2 plants into either resistant or susceptible was not easy. Plants with a DS of 20 to 60% were considered to be intermediate and so difficult to classify. Below or above these values the plants were considered resistant and susceptible respectively.

Enkoy x Morocco
The F1 was as susceptible as 'Morocco' indicating a recessive inheritance. However, the F2 segregated in a ratio of 3(R):1(S) indicating that Enkoy carries one dominant factor (Table 3). This change in expression from recessiveness towards dominance might be caused by a different race as the F1 and F2 were not tested in the same season.

Africa Mayo x Morocco.
The F1 showed a dominant inheritance and the F2 segregated in the ratio of 3(R):1(S) indicating that Africa Mayo carries one dominant factor.

Kenya Leopard x Morocco
The F1 showed a recessive inheritance. The F2 segregated towards susceptibility with 5% resistant, 28% intermediate and 67% susceptible suggesting one recessive factor in K.Leopard assuming that the intermediate F2 plants are mostly resistant ones. A two recessive gene model does explain the 5% resistant but not the 28% intermediate ones.

Kenya Kudu x Morocco
The F1 showed dominance. The F2 segregated in the ratio of 3(R):1(S) indicating that K.Kudu carries one dominant factor.

Frontatch x Morocco
The F1 showed a recessive inheritance. The F2 segregated in the ratio of 3 (R): 13 (Intermediate + Susceptible) suggesting that Frontatch carries one recessive factor and one dominant factor. The latter factor only being expressed in the presence of the homozygous recessive condition of the first factor

Table 3. Frequency distribution of yellow rust disease severity (DS) in nine classes for the progenies of fifteen crosses at the adult plant stage and the DS of the six parents. Enkoy=EN; Africa Mayo= AM; Kenya Leopard=KL, Kenya Kudu=KK; Frontatch=FR and Morocco=MO.

Cross	DS progenies										Parents					
	0	1	5	10	20	30/40	50/60	70/80	90/100	Total	EN	AM	KL	KK	FR	MO
EN X MO																
F1									11	11	5					90/100
F2	259	3	49	4	1	13	2	11	84	427	10					90/100
AM X MO																
F1	9									9		0				90/100
F2	244		90	5	3	8	6	12	89	457		0				90/100
KL X MO																
F1								4	1	5			5			90/100
F2	1		6	2	14	16	18	17	101	175			10			90/100
KK X MO																
F1	8									8				1		90/100
F2	256	2	31	1	7	26	2	47	71	441				1		90/100
FR X MO																
F1								8	2	10					5	90/100
F2	5		70	8	40	56	16	59	185	439					5	90/100
EN X AM																
F1	13									13	5	0				
F2	310	19	60	17	11	6	1			429	10	0				
F5	25		19	25	21	15	4	3		112	15	0				

Table 3. continued.

Cross	DS progenies										Parents					
	0	1	5	10	20	30/40	50/60	70/80	90/100	Total	EN	AM	KL	KK	FR	MO
EN X KL																
F1			3		1						5		5			
F2	202	32	116	43	24	5	1		1	424	10		10			
F5	16		25	18	8		1			68	15		15			
EN X KK																
F1	14									14	5			1		
F2	363		58							421	10			0		
F5	17		60	8	2	1				88	15			5		
EN X FR																
F1				1	2					3	5				5	
F2	283	5	97	29	51	33	2		1	501	10				5	
F5	27		16	25	31	17	4			120	15				1	
AM X KL																
F1	5									5		0	5			
F2	292		117	23	23	5				460		0	10			
F5	15		16	8	6	3				48		0	15			
AM X KK																
F1	15									15		0		1		
F2	446	3	2	4	4	6				465		0		0		
F5	23		12	7	4	19	9	10		84		0		5		

Table 3. continued

Cross	DS progenies										Parents					
	0	1	5	10	20	30/40	50/60	70/80	90/100	Total	EN	AM	KL	KK	FR	MO
AM X FR																
F1	7									7		0			5	
F2	353	6	25	21	30	12	3	4	14	468		0			5	
F5	54		20	6	19	26	14	5		144		0			1	
KL X KK																
F1	12									12			5	1		
F2	312		67	17	25	2				424			10	0		
F5	55	13	6	4	6					84			15	5		
KL X FR																
F1	2		4		1					7			5		5	
F2	182	28	126	26	47	12			2	423			10		5	
F5	17		11	4	1	3				15			15		1	
KK X FR																
F1	13									13				1	5	
F2	319		46	21	26	13				425				0	5	
F5	43		29	7			1			80				5	1	

Performance of F1, F2 and F5 generations of the crosses between the resistant parents

Each cross showed only a restricted segregation beyond the parental values, varying from very little to a fair amount. In no cross the amount of segregation approached the amount one would expect if the resistance of the cultivars was controlled by genes that differed with the cultivars and which were not linked. This indicates, that the genes for resistance in the five cultivars are located at the same chromosomal region (Table 3).

Enkoy x Africa Mayo
The F1 showed dominance. The F2 and F5 segregated beyond the parent Enkoy. Little segregation towards susceptibility was observed in the F2 while in the F5, despite selection for the most resistant and most susceptible genotypes, the segregation was only slightly more.

Enkoy x Kenya Leopard
The F1 showed semi-dominance. Transgressive segregation beyond both parents in the F2 and the F5 was observed. The number of plants segregating beyond the parental values in the F2 was fairly large while a limited number of plants segregated in the F5. One plant resembling 'Morocco' was found in the F2 which could be the result of contamination.

Enkoy x Kenya Kudu
The F1 showed dominance. The F2 showed no segregation and no Morocco types were observed. The F5 showed very little segregation.

Enkoy x Frontatch
The F1 showed semi-dominance. Both The F2 and the F5 showed some segregation.

Africa Mayo x Kenya Leopard
The F1 showed dominance. There was very little segregation in the F2 and F5.

Africa Mayo x Kenya Kudu
The F1 showed dominance. There was a slight segregation in the F2 and F5.

Africa Mayo x Frontatch
The F1 showed dominance. There was a fair amount of segregation in the F2 and somewhat less in the F5. The lesser segregation in the F5 was due to the fact that the Morocco type of segregating plants did not produce seed (too

severely diseased).

Kenya Leopard x Kenya Kudu
The F1 showed dominance. The F2 and F5 showed only a little segregation beyond the least resistant parent.

Kenya Leopard x Frontatch
The F1 showed semi-dominance. Two susceptible plants were found in the F2 (probably volunteers) and only a slight transgressive segregation was observed in the F2 and F5.

Kenya Kudu x Frontatch
The F1 showed dominance. The F2 and F5 showed only little segregation.

Discussion

The F1, F2 and F5 were field tested in different years. Consequently, environmental conditions such as temperature and light could influence the expression of the resistance factors.

The reversal of dominance which was observed in the cross Enkoy x Morocco could be the results of exposure to different pathogen races. Similar shifts in dominance have been reported before (Lupton and Macer, 1962; Chen and Line, 1992).

The durably resistant cultivars used in this study were different from each other in DS and IT. Based on the F2 data in the crosses between the susceptible cv. Morocco and the resistant parents, Enkoy, Africa Mayo and Kenya Kudu seem to carry one dominant factor for resistance. The resistance of Kenya Leopard seems conferred by one recessive factor and Frontatch might carry two factors, one epistatic over the other.

In nine of the ten crosses between the resistant cultivars no clearly susceptible plants or lines were found. Only in the cross between A. Mayo x Frontatch several highly susceptible plants were observed, but even in this cross the amount of segregation was restricted. If it is assumed that the resistant cultivars carry one resistance factor, which is the same for all cultivars the lack of highly susceptible plants or lines in the progenies is explainable. But the fact that in some cultivars the resistance is recessive and in others dominant and the fact that this resistance appeared to be very durable are difficult to explain in this way. The simple inheritance, the difference in type of inheritance and the

durability could be explained by assuming that all five resistant parents carry a piece of chromosome on which several loci for resistance reside. Each cultivar may carry a few, but not necessarily the same resistance factors on that chromosome region, which, due to the close linkage, inherit as a single factor. In the case of A. Mayo and Frontatch the resistance factor(s) on that chromosome region might be separated sufficiently to get some segregation and so some susceptible plants.

The little to slight segregation beyond the resistant parents either towards more or towards less resistance could be explained by resistance factors with small effect (quantitative resistance) not located on or near the chromosome region with the major resistance effects. This quantitative resistance could be of the same type of resistance as the residual resistance described in Chapter 1.

That these cultivars carry the same region of chromosome with partly different resistance alleles is probably primarily due to the fact that these cultivars were selected in the same period (late fifties to early sixties) i.e. under a similar breeding system and yellow rust population and only secondarily to a possibly similar origin. Of this latter the restricted information about the pedigrees does not allow any clear conclusion. But different resistance alleles on the same chromosome region do in fact indicate a different genetic origin rather than the same.

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V. General discussion

Virulence patterns of the yellow rust populations and breeding for complete resistance

The yellow rust populations in Kenya showed a wide variation and a rapid increase in the virulence factors varied from seven to twelve (Danial *et al.*, 1993. Such increase in virulence factors was also reported in the United kingdom (Priestly, 1978) and in the Netherlands (Stubbs, 1985).

Most of the races identified in Kenya were characterized by a virulence to *Yr9*. This major resistance gene is widely used in CIMMYT germplasm and is usually utilized by many national breeding program such as in Kenya and Ethiopia. As a result of uitilizing such major gene in the breeding programs there has been a long history of cultivars that were initially resistant and became susceptible as a new race of the pathogen evolved. Among the cultivars which possess *Yr9* and became rapidly susceptible in Kenya and Ethiopia are Paa and Dashen.

Because of the pressure of yellow rust in kenya, seedling resistance to this pathogen is required especially for late planting at high altitudes. Therefore, it is important to monitor the development of new races of yellow rust with increased virulence for adult plant resistance and seedling resistance, especially in areas where yellow rust cause a substantial damage.

Selection for complete to near complete resistance to yellow rust and other rust diseases is easy in the field and is therefore very attractive to the breeder because of the high heritability of the resistance genes. However, breeders should keep in mind that by adopting such an approach, the erosion of resistance genes is very rapid and the build up of new, more complex races is likely to occur. Therefore, selection for complete resistance especially from crosses where the history of the parents is unknown should be avoided. It should be pointed out that most of the sixteen major resistance genes which have been identified and listed by McIntosh (1988), were unfortunately overcome by one or more of the yellow rust races (Stubbs, 1985)

How to assess quantitative resistance

Quantitative resistance (QR) is resistance that shows a continuous range of variation in resistance from extremely susceptible to fairly resistant. From the data obtained in Chapter 5, DS and AUDPC proved to be suitable parameters to measure QR. It should be realized that AUDPC requires more assessments and is too laborious to carry out in a breeding program. IT appeared too

unstable trait to rely on, it showed fluctuations from one season to another and appeared poorly associated with DS (Chapter 4, 5 and 6). Apparently, genotypes with intermediate IT's (QR) seem to fluctuate for their IT's while those showing a low IT (0-1) and/or a high IT (8-9) appear to be more stable, suggesting that the use of IT as a parameter to measure QR can not be recommended.

Based on the results obtained in Part II, there are some other factors which should be considered during the assessments of resistance in the field such as:

1) Interplot interference
2) Earliness, observation date and leaf layer
3) Nitrogen level

Ad 1) Interplot interference operating especially with air borne pathogens, may underestimate the level of QR. This type of underestimation varies greatly with the pathosystem, from very large in barley to leaf rust, *Puccinia hordei* (Parlevliet and van Ommeren, 1975, 1985) to moderate in barley to powdery mildew, *Erysiphe graminis* f.sp. *hordei* (Norgaard kundsen *et al.*, 1986). In case of wheat-yellow rust no interplot interference was observed (Chapter 3) and there was no indication of underestimation of resistance in small adjacent plots as compared to the isolated plots (Danial *et al.*, 1993). The genotypes showed the same ranking order irrespective of the plot situation or year. It cannot be generalized, therefore that interplot interference does operate in the same magnitude for all wind borne pathogens. This means that a satisfactory and economical assessment of QR in wheat to yellow rust can be carried out in small plots.

Ad 2) During the screening and selection in the field, the breeder should consider the disturbing effect of differences in earliness. This effect can be large if earliness shows extreme differences (Danial, 1994). To avoid misinterpretation of the data collected, the breeder is advised to classify the genotypes into groups of similar earliness for comparison.

The ranking order for DS of the genotypes varied with the observation date and was most pronounced in the flag leaves and least in the third leaves. The data obtained in Chapter 5 indicate that an accurate assessment of DS can be easily carried out on either the flag leaf or the second leaf at a not too early observation date.

Ad 3) The effect of nitrogen level on the QR was studied in the field. The data reported in Chapter 4 showed that DS and IT increased moderately with increased N rates (Danial and Parlevliet, 1993). The magnitude of increase in DS and IT was not the same for all genotypes. Moderately resistant genotypes responded more to nitrogen than the most resistant and the most susceptible

genotypes. The ranking order for DS of the genotypes was affected by the N-treatments and consequently a wrong estimate of the level of the resistance could occur. Therefore selection by the breeder for QR should be done at N-levels similar to those used in the area for which he is breeding for.

Taking the above discussed factors into account, a breeder should be able to carry out an accurate assessment for QR of his material in the field.

What is durable resistance

Disease resistance in a cultivar plant is described as durable if it remains effective while being extensively used in agriculture for a long period in an environment favourable to the disease (Johnson, 1981, 1983, 1988).

In wheat to the cereal rusts, despite the ability of the pathogen to overcome resistance in many cultivars early in their commercial life, some cultivars have remained effectively resistant for many years while being widely grown. Such durable resistance is very valuable to the breeder.

In part III different selection criteria were examined to select for a higher levels of resistance. Selection for partial resistance in wheat to yellow rust as defined by Parlevliet and Van Ommeren (1975) appeared very difficult (Broers, 1993; Danial, 1993). Apparently true partial resistance does not seem to exist because of the instability of IT and because of the systemic growth pattern of this pathogen as compared with the non-systemic growth habit of the other cereal rusts. It should be noted that each infection point of *P. striiformis* develops into a long stripe which may be several centimeters long whereas in the infection of *P. hordei* on barley each infection point develops in the form of a tiny, round pustule. However, there is increasing evidence and information about durable forms of resistance. For example, the cultivars Africa Mayo, Kenya Kudu, Enkoy, Kenya Leopard, Bounty, Frontatch, Trophy, Bonny and Kenya Plume seem to be durable in Kenya. This resistance cannot be described as partial resistance, and some not even as QR. Similarly, other durably resistant cultivars have been identified in different regions such as Europe (Van Dijk *et al.*, 1988) and the Pacific Northwest USA (line, 1978). In addition, some cultivars of CIMMYT origin or derived from CIMMYT germplasm have been suggested to possess durable resistance such as Anza (Broers, pers.comm.)

When comparing cultivars with their major gene resistance being overcome by new races of yellow rust, considerable differences in the level of residual resistance were observed. The data presented in Chapter 1 indicates the existence of fair levels of residual resistance in the cultivars Kenya Popo and

Kenya Kulungu. Their relatively high resistance as compared to the very susceptible cultivar Paa indicates the presence of this residual, quantitative resistance which may be controlled by minor genes. Such cultivars, therefore are may be durably resistant. By using such cultivars in the breeding programs it is hoped that lines selected from such crosses carry increased levels of this resistance. However, breeders should keep in mind that the durability of QR is not yet proven.

Temperature sensitive resistance seems also to be durable and should be further investigated. The cultivars Nugaines and Crest carrying temperature-sensitive resistance genes, have been grown in the NW of USA for more than twenty years and are still resistant (Milus and Line, 1986, Qayoum and Line, 1985). The resistance of such cultivars are reported to be expressed at high temperature and controlled by a minimum of two to three genes (Milus and Line, 1986).

The data in Chapter 11 indicate that the number of resistance factors in the quantitatively resistant wheat genotypes is restricted and ranging between one to three or four. In Chapter 12 the durably resistance wheat cultivars seemed to carry resistance factors which seems to be closely linked. The five durably resistant cultivars seem to carry a piece of chromosome with several loci for resistance. Each cultivars might carry a few resistance alleles that differ with the cultivars. On top of this some minor genes for QR might be present as well. The durability of this resistance is then coming from the combined effect of two or more strongly linked resistance alleles. To produce two or more virulence factors to neutralize such a resistance in a single step is apparently very difficult for the pathogen.

How to select for durable and/or quantitative resistance

Usually, durable resistance cannot be easily identified during the normal procedures of selection and breeding. One of the most essential elements in the definition of durable resistance is that the cultivar should be exposed and tested over a long period in an environment favourable to the disease. Cultivars with such a durable resistance should be used as genetic basis for its resistance in the breeding programs. This can be done by crossing the moderately susceptible cultivars (carrying QR) with the durably resistant cultivars or crossing the durably resistant cultivars with each other. If a breeder wants to breed for high levels of QR he should start with parents which are carrying reasonable levels of QR and preferably not related to each other. In the progenies he should remove consistently all the lines that are relatively susceptible and those lines

that are completely resistant. These latter ones carry a combination of defeated major genes that as a combination is still effective.

Transgressive segregation to higher levels of resistance is a good approach to obtain QR. This can be detected in progeny of crosses between cultivars that exhibit intermediate levels of QR. Such transgression is reported in Chapter 12 and has been documented (Wallwork and Johnson, 1984; Krupinsky and Sharp, 1979). When such QR could be combined with resistance of durably resistant cultivars, high levels of very durable resistance could be achieved.

Practical implications for the breeding programs

For durable resistance to be transferred to new cultivars in a breeding program, it is recommended to use cultivars or parents that have shown durable resistance in the region in which the breeding program is to be carried out. If breeding material is introduced from elsewhere, it is possible that race-specific major genes, effective in this area, are introduced. It is therefore important that material introduced from other regions is tested thoroughly and not used in the breeding program if they appear to carry such resistance genes. Only imported material with QR or resistance proven to be durably in the area from which the entry is derived should be introduced into the breeding program.

If breeder desires to go for QR, the use of QR parents and selection against the more susceptible plants and lines throughout the program from the F2 onward is a simple and effective approach as Parlevliet and Van Ommeren (1988) showed for barley to barley leaf rust

If breeder wishes to base the resistance on cultivars with proven durable resistance, he could cross such cultivars and select for high levels of resistance, a simple and straight forward approach, but with a certain risk. Through recombination new genotypes may appear and be selected, that carry a resistance gene or a combination of genes that can be neutralized by the pathogen.

Identification of resistant cultivars as durable does not necessarily mean absolute durability. The cultivar Aton which has been grown for more than twenty years in the U.K became susceptible in 1992 (Johnson, 1993).

Stability of resistance is different from durability. Stability reflects the expression of a resistance of a given cultivar under a given range of environments. Resistance selected in a given environment does not necessarily exhibit the same level of resistance elsewhere as described in Chapter 9.

At Njoro, weather conditions are very favourable to grow wheat throughout the year. Although supplemental irrigation may be required during the short rainy season, economical and fast breeding of cultivars can be easily achieved by growing five generation in two years. This means that the advanced lines can be tested for yield and quality after three to four years from crossing.

Because of the rapid increase and the variation of the rust populations, serious consideration should be given to develop facilities in the region for handling isolates of the rust pathogens. For instance, all rust isolates in the past were collected and tested at a few places such as IPO, Wageningen, The Netherlands and the cereal rust laboratory in the USA. At present, IPO has discontinued with such activities which are important for the East African region. In Kenya where infrastructure and political stability is an advantage, Njoro for instance, could be a good centre for this region.

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Summary

In Kenya, yellow rust, caused by *Puccinia striiformis* Westend, is one of the major threats of the bread wheat crop. Inoculum is air-borne and infection may take place at any plant stage. The symptoms consist of narrow, yellow, linear stripes mainly on the leaves and spikelets. Effective chemical control is available but expensive, especially in developing countries. Breeding of resistant cultivars based on major genes is an easy approach but unfortunately many cultivars with such a resistance became susceptible some time after their release as a new race of the pathogen evolved. However, some cultivars remained resistant over a long period of time and are considered to be durably resistant.
The objectives of this thesis were to characterize the durable resistance in wheat to yellow rust and to develop guidelines for its assessment and its use in breeding programs.

Breeding for complete resistance and virulence factors of the yellow rust population

The yellow rust races in Kenya showed a clear increase in the virulence factors. Before 1976, the number of virulence factors varied from 0 to 7 or 8, whereas the races after 1986 had up to 12 virulence factors.

A selection program based on a population derived from 21 wheat genotypes with complete to near complete resistance to yellow rust and where the selection again was for (near) complete resistance, lead to the conclusion that such an approach can not be recommended. The selection program ran over a period of five years. In this period the resistance of over 50% of the parents broke down and several of the F7 lines too appeared susceptible while their F6 parental lines were still resistant. Apparently a build up of more complex yellow rust races is inevitable for the wheat-yellow rust pathosystem even when resistant parents are selected and tested carefully.

Assessments of quantitative resistance

Quantitative resistance can be assessed best by using the parameter disease severity (DS) as it is strongly associated with the area under the disease progress curve (AUDPC), a parameter describing the accumulated amount of disease. Infection type (IT) was poorly associated with the AUDPC and seemed

an unsuitable parameter for assessing the level of resistance.

The importance of interplot interference in the screening of yellow rust in wheat was studied in Kenya and Mexico. In Kenya there was no indication whatsoever of interplot interference, whereas in Mexico there was a very slight underestimation of the level of resistance in adjacent plots. The ranking order was always the same irrespective of the test plot situation. It was concluded that screening of wheat to yellow rust in small plots gives results that are very representative for the farmers fields both in level and ranking order.

Earliness, observation date and leaf position are factors that should be considered by the breeder during the assessment of resistance. The effect of heading date can be large if the genotypes show extreme differences in earliness in the field and this disturbing effect can be avoided by classifying the genotypes into earliness groups for comparison. Based on the assessment of yellow rust of 20 wheat genotypes on different observation dates and on different leaf positions in the field, it was concluded that an accurate assessment of DS can best be made on either the flag leaf or the second leaf at a not too early observation date.

The nitrogen level (N) is another factor that affects the assessment of quantitative resistance. DS increased moderately with increased nitrogen rates and the ranking order for quantitative resistance of the genotypes was clearly affected by the N-treatments.

Selection for partial or for quantitative resistance

Based on the screening of over 15.000 spring wheat entries to select for partial resistance to yellow rust, it was concluded that selection for partial resistance is rather difficult and does not seem to be a promising approach because the combination of a strongly reduced DS and a high IT did not seem to occur. However, the selected genotypes varied greatly in their levels of resistance and may be considered as representing quantitative resistance.

Similarly, when a large number of F2 populations were exposed to four selection criteria to select for higher levels of possibly durable resistance, selection for partial resistance did not lead to satisfactory levels of resistance because of the high correlation between DS and IT, whereas by discarding the most resistant and most susceptible plants, acceptable levels of quantitative resistance were obtained. This latter approach seems to be the most advisable.

Sources of durable resistance

The old wheat cultivars Africa Mayo, Kenya Kudu, Enkoy, Kenya Leopard and Frontatch remained resistant over a long period of time. Such cultivars are characterized by a low infection type and a high level of resistance and they are considered to be durably resistant.

Evaluation of the resistance level of Kenyan wheat cultivars before and after their break down of their major gene resistance in the past ten years revealed that many of these cultivars seem to carry moderate to good levels of residual resistance (quantitative resistance in fact) which could be of great importance in any breeding program.

Stability of resistance

Based on evaluation of durable resistant cultivars and genotypes which have shown quantitative resistance at Mexico, Kenya and Ecuador, genotype x location interactions were detected for Kenya, Ecuador and Mexico and it was concluded that durable sources of resistance selected in a given environment do not necessarily display the same levels of resistance elsewhere.

Genetic background of genotypes with quantitative and durable resistance

Seedling tests against eight yellow rust races with nine genotypes with various levels of quantitative resistance revealed the presence of several major resistance genes that are ineffective in the field situation.

Five quantitatively resistant genotypes and 'Morocco' were intercrossed in a half diallel. From the crosses with Morocco, the impression was gained that the resistant genotypes carried one to three or four factors for resistance. These factors were partly the same and partly different. There seemed linkage between some of these resistance factors.

The inheritance of the durable resistance of the cultivar Africa Mayo, Enkoy, Kenya leopard, Kenya Kudu and Frontatch was studied. In the crosses with highly susceptible 'Morocco', each resistant cultivar seemed to carry a single factor, dominant in Africa Mayo, Enkoy and Kenya Kudu, and recessive in Kenya Leopard. Only Frontatch seemed to carry two recessive factors. In all crosses between the resistant cultivars there was segregation that varied from little (most crosses) to fair (Africa Mayo x Frontatch). There was no independent segregation. As neither the IT nor the inheritance (recessive/-

dominance) of the parents were the same, while some segregation occurred, it was concluded that the resistance of the cultivars is based on resistance factors that are closely linked on the same chromosome part. Only for Frontatch one gene may occur independently.

Samenvatting

In Kenia is gele roest, veroorzaakt door *Puccinia striiformis* Westend, één van de grootste bedreigingen van de tarwe. Het inoculum is "air borne" en infectie vindt plaats in elk groei stadium. De symptomen bestaan uit smalle, gele strepen op het blad en op de aren. Effectieve chemische bestrijding is beschikbaar, maar duur, vooral in de ontwikkelingslanden. Veredeling van resistente rassen, gebaseerd op hoofdgenen, is een eenvoudig methode om toe te passen. Door het ontstaan van nieuwe fysio's, verloren vele van die rassen hun resistentie al snel na hun introductie. Niettemin zijn er rassen, die over een lange periode resistent bleven. Deze rassen worden als duurzaam resistent beschouwd.

De doelstellingen van dit proefschrift waren het karakteriseren van duurzame resistentie in tarwe tegen gele roest en het ontwikkelen van richtlijnen voor het evalueren en selecteren ervan in veredelingsprogramma's.

Veredeling voor volledige resistentie en virulentiefactoren van gele roest populaties

De gele roest populatie in Kenia vertoonde een duidelijke toename in de virulentiefactoren. In de fysio's, bestudeerd voor 1976, werden 0 tot 7 virulentiefactoren waargenomen, terwijl na 1986 de fysio's tot 12 virulentiefactoren vertoonden.

De resultaten van een selectie programma, gebaseerd op 21 tarwe genotypen met een volledige tot bijna-volledige resistentie tegen gele roest en waar opnieuw voor (bijna) volledige resistentie werd geselecteerd, leidden tot de conclusie dat zo'n benadering niet aanbevolen kan worden. Het selectieprogramma werd in een periode van vijf jaren uitgevoerd. Tijdens deze periode werd meer dan 50% van de resistente ouders vatbaar voor gele roest en werden ook verschillende F7 lijnen vatbaar, terwijl de lijnen van hun F6 ouders nog resistent waren. Veredeling voor (bijna) volledige resistentie leidt kennelijk in een snel tempo tot complexere fysio's ook al zijn de ouders zorgvuldig geselecteerd.

Meten van kwantitatieve resistentie

Kwantitatieve resistentie (KR) kan het best gemeten worden via de mate van aantasting (MA) die een zeer sterke associatie heeft met de oppervlakte onder

de curve van het ziekte verloop (OOKZV), een parameter die de geaccumuleerde hoeveelheid aantasting beschrijft. Infectietype (IT) vertoonde een zwakke associatie met de OOKZV en bleek een onbetrouwbare schatter van KR.

In Kenia en Mexico werd de betekenis van interplot interferentie bij het evalueren van gele roest in tarwe bestudeerd. In Kenia kon geen interplot interferentie worden aangetoond, terwijl in Mexico de mate van resistentie in aangrenzende veldjes in zeer geringe mate werd onderschat. De rassenvolgorde was steeds dezelfde ongeacht de veldtoetssituatie. Evalueren van tarwe tegen gele roest in kleine, naast elkaar liggende, veldjes is zeer representatief voor de situatie in commerciële velden, zowel voor de mate van resistentie als voor de volgorde van de rassen.

Vroegheid, waarnemingsdatum en bladlaag zijn factoren die de veredelaar in acht moet nemen tijdens het meten van KR.
Het effect van vroegheid op de evaluatie kan belangrijk zijn als de genotypen extreme verschillen vertonen. Deze verstoring kan gecorrigeerd worden door de genotypen in vroegheidsgroepen in te delen en de resistentie binnen die groepen te vergelijken.

Gebaseerd op het meten van de aantasting van 20 tarwegenotypen op verschillende waarnemingsdata en verschillende bladlagen mag er geconcludeerd worden dat een nauwkeurige schatting van de MA het best gedaan kan worden op het vlagblad of op de tweede bladlaag en dan op een waarnemingsdatum, die niet te vroeg is.

Het stikstof niveau (N) is een andere factor dat het meten van KR beïnvloedt. Een toename van de stikstofdoseringen gaf een duidelijke toename van de MA en de genotypenvolgorde voor KR veranderde bij verandering van het N-niveau.

Selecteren voor partiële of voor kwantitatieve resistentie

Meer dan 15.000 zomertarwelijnen werden getoetst op hun niveau van partiële resistentie. Selectie voor partiële resistentie bleek heel moeilijk te zijn. Het lijkt een weinig belovende methode te zijn, omdat een combinatie van een sterk gereduceerde aantasting en een hoog infectietype niet schijnt te bestaan. Er waren echter wel aanzienlijke verschillen in de KR (geringere aantasting en een wat lager infectie type).

Een zeer variabele populatie, afkomstig van een groot aantal kruisingen, werd aan vier selectieprocedures blootgesteld. De selectieprocedure, gericht op de selectie van partiële resistentie, leidde niet tot genotypen met een lage MA

en hoog IT. Een lage MA en een hoog IT leken niet te combineren. De beste selectieprocedure om hoge niveaus van KR te verkrijgen bestond uit het steeds verwijderen van de meest vatbare en de (bijna) volledig resistente typen.

Bronnen van mogelijk duurzame resistentie

De oude Keniaanse tarwerassen Africa Mayo, Kenya Kudu, Enkoy, Kenya Leopard en Frontatch bleken nog steeds resistent te zijn na een lange periode. Deze rassen hebben een laag IT en een hoge mate van resistentie en worden beschouwd als duurzaam resistent.

Bij een inventarisatie van de Keniaanse tarwerassen op hun resistentie voor en na de doorbraak van de hoofdgenen voor resistentie in de afgelopen tien jaar bleek, dat vele van deze rassen nog een middelmatig tot hoge mate van restresistentie bezaten (in feite KR), die van groot belang kan worden voor veredelingsprogramma's.

Stabiliteit van resistentie

Bij toetsing van o.a duurzaam resistente rassen en de KR genotypen in Mexico, Kenia en Ecuador werden vrij veel genotype x locatie interacties waargenomen voor KR en er mag geconcludeerd worden dat KR bronnen, die geselecteerd zijn op een locatie elders, niet hetzelfde resistentiepatroon hoeven te vertonen.

Overerving van kwantitatieve en duurzame resistentie

Negen genotypen met verschillende niveaus van KR werden in het zaailingstadium tegen acht gele roestfysio's getoetst. Er bleken verscheidene hoofdgenen voor resistentie, die in Kenia te velde niet effectief zijn, in deze genotypen voor te komen.

Vijf KR genotypen werden onderling en met "Morocco" gekruist. Uit de kruising met Morocco, werd afgeleid dat de resistente genotypen een tot drie resistentiefactoren bevatten afhankelijk van de mate van KR. Deze factoren waren deels hetzelfde en deels verschillend van elkaar. Tussen enkele van deze resistentie factoren leek een koppeling te bestaan.

De overerving van de resistentie van de duurzaam resistente rassen Africa Mayo, Enkoy, Kenya Leopard, Kenya Kudu and Frontatch werd bestudeerd. De kruisingen met het zeer vatbare ras Morocco duiden op de aanwezigheid van

één resistentie factor, recessief in K.Leopard en dominant in A.Mayo, K.Kudu en Enkoy. Frontatch zou twee recessieve factoren bevatten. In de kruisingen tussen de resistente rassen was er meestal heel weinig uitsplitsing, maar wel wat. In twee kruisingen met Frontatch was er wat meer uitsplitsing. Deze waarnemingen wijzen er op dat de vijf rassen een stuk chromosoom met meerdere resistentiefactoren gemeen hebben. Op dat stuk chromosoom kunnen de resistentie factoren met het ras verschillen. Frontatch zou daarnaast een tweede factor dragen dat of zwak of niet gekoppeld is met dat chromosoom stuk.

CURRICULUM VITAE

Daniel Lotfy Danial was born June 16, 1950 in Helwan, Cairo, Egypt. He began his study in plant production at Ain Shams University, Faculty of Agriculture, Cairo, Egypt in 1969. In June 1972, he completed his study and obtained the B.Sc.in Agriculture. From July 1972 to August 1974 he traveled extensively in Europe. In September 1974, he continued his study at the Wageningen Agricultural University. He completed the "propadeuse" level study in 1975 and the "kandidaats" level study in plant pathology in 1977. From september 1977 to March 1978 he was attached to the Research Institute for Plant Protection (IPO), Wageningen, The Netherlands. In March 1980, he completed his study and obtained the" Doctoraal" degree with specialization in plant pathology, virology and weed sciences. After his studies from March 1980 to December 1980 he was appointed as scientist at Unilever Research, Duiven, The Netherlands. From May 1981 to January 1983 he was employed by the Department of Phytopathology of the Wageningen Agricultural University for research on late blight in potato and powdery mildew in wheat. From June 1983 to December 1988 he was appointed as associate expert by the Netherlands Ministry of International Development Cooperation, and assigned as wheat breeder-pathologist for the International Maize and Wheat Improvement Centre (CIMMYT), Mexico, based in Kenya. From January 1989 to December 1993 he was employed by the Department of Plant Breeding of the Wageningen Agricultural University for research on durable resistance in wheat to yellow rust. This work, which resulted in this thesis, was carried out at the National Plant Breeding Research Centre in Njoro, of the Kenya Agricultural Research Institute (KARI) in Kenya under the auspices of a collaborative agreement between the Netherlands Minister for International Development Cooperation, the Agricultural University of Wageningen and KARI.