Genetic variation between and within Ethiopian barley landraces with emphasis on durable disease resistance

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Abstract

Landraces are known to be variable. Their resistance to diseases can be assumed to be durable. The durability of resistance in landraces can be due to the multiline principle or due to genetic durable resistance. To investigate the degree of variation both between and within landraces and what type of resistance is present 1800 single plant derived lines of 18 Ethiopian barley landraces were studied for six traits among which resistance to two pathogens, *Puccinia hordei*, representing biotrophic fungi, and *Rhynchosporium secalis*, representing the hemi-biotrophic fungi.

The 1800 landrace lines were grown in 1991 and 1993 under field conditions at Holetta Research Centre, Ethiopia and evaluated for scald (*Rhynchosporium secalis*) disease severity (DS) after infection from the naturally occurring inoculum. Earliness, plant height, leafiness and 1000 grain weight were also measured. All five characters varied greatly both between and within the landraces. The degree of association between DS and the other characters was investigated and earliness had an important effect on DS. The frequency of resistant genotypes within the landraces increased markedly with altitude. Complete resistance to scald occurred frequently. Lines fully resistant in one year could be fully susceptible in the other year indicating that the resistance of these lines was race-specific. It means, that for leaf scald at least a considerable part of the resistance found was race-specific. In this pathosystem the multiline principle seems to operate to give durable resistance.

In 1990 over 1200 landrace lines, raised in the greenhouse, and each represented by five plants, were assessed at the young flag leaf stage for infection type (IT) and latent period (LP), the main component of partial resistance, after infection with barley leaf rust, race 1.2.1. This race was used because it carries virulence factors which can neutralize six of the nine known Pa-genes. Nearly all lines showed a high IT, which varied between 7 and 9 on the 0-9 scoring scale, indicating the absence of major genes for adult plant resistance in the landraces studied. For partial resistance the landraces showed a considerable variation both between and within the landraces. All landraces had at least some partial resistance.

In 1992 over 1700 landrace lines from the 18 landraces were grown in the greenhouse and evaluated for IT at the seedling stage after exposure to two barley leaf rust races (1.2.1 and A). Race A is virulent to fewer Pa-genes than race 1.2.1. Nearly all lines assessed showed a high IT (8-9 on the 0-9 scale) to the two races. This again confirms the absence of hypersensitive major resistance genes in the landraces studied. Moreover, four Ethiopian and one Dutch barley leaf rust race were analyzed for their virulence patterns on the seedlings of the differential series of 11 barley cultivars together carrying nine Pa-genes and on 21 barley entries, 19 of which representing individual lines derived from 14 Ethiopian barley landraces. The Ethiopian isolates showed patterns of virulence/avirulence similar to those of European isolates. Again there was no evidence of the presence of effective major genes in the Ethiopian barley landraces and the multiline principle that might give these landraces durable resistance to barley leaf rust does not operate. The durable resistance to this pathogen is based on genetically durable resistance genes.

The inheritance of the partial resistance to leaf rust in the landraces was studied using 10 landrace lines and their F1, F2 and F3 or F4 progenies. At the F1, most crosses showed intermediate or recessive inheritance while a few crosses showed dominance. From the generation mean analysis some epistasis was also observed. At the F2, crosses segregated and distributed continuously ranging from the low to the high parent and in most crosses transgressive segregation was observed which was confirmed by the F3 or F4 data. The partial resistance in the eight landrace lines is based on some to several minor genes.

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Statements (stellingen)

1. Ideology, insufficient agricultural technology and traditional agriculture are the greatest obstacles for sustainable prosperity in Ethiopia.

2. Landraces can still be very useful in the marginal areas of the country.

3. In Ethiopia the bottle neck to introduce improved varieties does not lie with the farmer.

4. Ethiopia is not a centre of origin for barley.

5. Gene banks when evaluating landraces generally overlook the abundantly present quantitative resistance.

6. For evaluating landraces properly the services of a well equiped phytopathological laboratory are essential.

7. In Ethiopia shortage of food is not because of drought or high population growth.

8. In Ethiopia it is possible to produce three barley crops per year but this is not advisable.

9. Wherever possible Ethiopian farmers tend to give some degree of priority to grow barley even when they can grow crops that bring in more cash.

10. A large part of the genetic diversity of barley in Ethiopia is not yet sampled and maintained by gene banks.

11. The collected and preserved barley landraces have been overlooked for utilization by breeding programs and not only in Ethiopia.

12. It is not the river Nile that washes away millions of fertile soil from the Ethiopian highlands.

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Contents

Chapter 1

General Introduction

Landraces, even of self-fertilizing crops, are often considered heterogeneous mixtures of lines and thus are interesting sources of variation for breeding purposes.

Landraces are assumed to carry resistance to the more important pathogens, and since they have been grown there for a long time exposed to the endemic pathogens the resistance still measurable must be assumed to be durable resistance. Durable resistance in landraces can in principle be based on two quite different principles:

1) On genetically durable resistance, such as the partial resistance in barley to barley leaf rust (Habgood and Clifford, 1981; Parlevliet, 1983);

2) On the multiline principle, where non-durable resistance genes together could give a lasting resistance (Jensen, 1965; Borlaug, 1958; Marshall, 1977).

The Ethiopian landraces form an ideal object to study these aspects. Barley is a major food crop in this country and has been so for several thousands of years, and even at present the majority of the 900,000 ha of barley are planted yearly with landraces. Barley is grown in Ethiopia in the extensive highlands at altitudes from about 1800 to over 3000 m. Due to the topography the growing conditions tend to vary from field to field. The highlands of Ethiopia are not only a suitable region for barley, it is also conducive to many diseases.

For this investigation two diseases were chosen, barley leaf rust, *Puccini hordei*, and leaf scald, *Rhynchosporium secalis*. In barley non-durable, race-specific major gene resistance and polygenically based partial resistance to the two pathogens are known to occur. The two pathogens represent two different groups of fungal pathogens, the biotrophs (*Puccinia hordei*) and hemi-biotrophs (*Rhynchosporium secalis*). The barley leaf rust is important at the lower altitudes of the barley growing regions, while leaf scald is especially severe at the higher altitudes.

The aims of the investigation were:

i) To study the variation for several agronomic traits both between and within landraces.

ii) To evaluate the presence and variation of resistance to both pathogens between and

within landraces.

iii) To evaluate the type and principles of resistance found in the landraces.

iv) To analyze genetically the partial resistance of barley to the barley leaf rust.

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Chapter 2

Aspects of Durable Resistance in Barley Landraces

Landraces are known to vary for a wide range of traits, among them disease resistance to the pathogens present in the region. The highlands of Ethiopia are known to be good sources of such variation as far as barley landraces are concerned. The barley landraces found in the region developed over several thousands of years and are considered genetically adapted to the existing pathogen populations to give fairly good and stable yields (Simmonds, 1979). This long time adaptation and their ability to give fair and stable yields despite of disease pressure suggest that landraces must carry some kind of durable resistance. Otherwise, the resistance would not be noticeable. Parlevliet (1983) pointed out that before the advent of modern breeding techniques crops did not show much disease, because they had reasonable levels of durable resistance accumulated over large spans of time. Johnson (1978; 1979) defined durable resistance as a resistance that lasts a long time when exposed to the parasite on a sufficiently large scale. Durable resistance in landraces has not been investigated but it can be related to two known principles.

1) The multiline principle. Non-durable, race-specific major genes can have a much longer effective life if they occur in a multiline or variety mixture, see below.

2) Resistance genes that are durable themselves. Johnson (1983) and Parlevliet (1983) gave various examples of individual major resistance genes that lasted for a long time. The polygenic partial resistance in barley to *Puccinia hordei* also appeared highly durable (Parlevliet, 1983).

The multiline principle. In self-fertilizing crops multilines and variety mixtures reduce the disease severity considerably when exposed to air borne pathogens (Browning and Frey, 1981; Wolfe, 1985) in comparison with monocultures. It is assumed that complex races do not easily build up due to stabilizing selection (SS) in the sense of Van der Plank (1963, 1968). This stabilizing selection is based on the assumption that races with a more complex character i.e. with more virulences, are less fit. Some researchers assume this to be a fact (Browning and Frey, 1981). Others do not agree with this assumption because they think that the multiline is a good breeding ground for new, more complex races

(Parlevliet, 1981). Parlevliet (1981) also stated that in commercial cultivars the number of components with different race-specific, non-durable major genes must be kept relatively small for practical purposes. In order to prevent the development of more complex races the SS must be fairly high in that situation. SS of that magnitude does not seem to occur. The studies of Marshall and Pryor (1978) showed that the higher the number of components of a multiline the smaller the SS can be to keep the development of complex races at bay, giving a much more durable resistance to these genes that are individually non-durable. This conclusion could mean that in the case of landraces with a high internal variation, i.e with a large number of components, that only a small SS is required in order to give durable resistance to the major-race-specific resistance genes that would be non-durable when used individually. In such landraces the build up of more complex races could be prevented provided the race-specific major genes are present in fairly large numbers distributed over the various genotypes (components).

There is another factor that can play a role not mentioned by Marshall and Pryor; the rate at which more complex races spread after their formation. With air borne pathogens like cereal rusts the rate of spread is very high; with splash borne pathogens such as *Rhynchosporium secalis* the rate is much lower as Habgood (1974) mentioned, when he discussed the use of race-specific major genes in commercial barley cultivars.

This would mean that in the case of leaf scald the multiline principle would have a better chance to be effective than in the case of leaf rust. The SS in order to keep major-race-specific resistance genes effective for a long time could be quite low in landraces that are highly variable due to the large number of components that might be present. Due to the low rate of spread between fields the multiline principle would be much more effective for resistance to leaf scald than for resistance to leaf rust seen on a regional level.

Genetically durable resistance: Parlevliet (1993) classified pathogens into three groups. Group 1 was characterized by pathogens that could easily adapt to cultivars with introduced major resistance genes. The crops carry high numbers of race-specific resistance genes, while the pathogen populations show many races. Against such pathogens these major resistance genes are usually of the non-durable type when used individually. The leaf scald and leaf rust both belong to this group.

Besides these race-specific, non-durable major genes resistance of a more durable nature is generally found. Usually this resistance is of a quantitative type such as the partial resistance of maize to *Puccinia sorghi* (Kim and Brewbaker, 1977) and of wheat to *Puccinia recondita* (Broers and Jacobs, 1989), the field resistance of potato to *Phytophthora infestans* (Black, 1970, Turkesteen, 1993), the quantitative resistance of maize to *Cochliobolus heterostrophus* and *Setosphaeria turcica* (Leonard, 1993) and of barley to *Rhynchosporium secalis* (Habgood, 1974), the partial resistance of barley to *Puccinia hordei* (Parlevliet, 1978a; Parlevliet and Kuiper, 1985), and the partial resistance of rice to *Magnaporthe grisea* (Roumen, 1994). The first two are oligogenically, the other six polygenically inherited. The six polygenically controlled pathosystems are not race-non-specific, as small race-specific effects have been reported in each case (Caten, 1974; Habgood, 1976; Leonard, 1993; Parlevliet, 1978b; Roumen, 1992). In a few cases monogenic resistance appeared durable, such as the resistance in wheat to stem rust by *Sr-2* (Van Ginkel and Rajaram, 1993), and to leaf rust by *Lr-34* (Drijepondt and Pretorius, 1989), and in barley to powdery mildew by *Ml-o* (Jorgensen, 1993). This led Parlevliet (in press) to the conclusion that not the race-specificity of the resistance, nor the number of genes are instrumental in the durability of resistance, but that the durability of the resistance is primarily caused by the resistance mechanism.

In barley a range of race-specific, non-durable resistance genes has been described for both leaf scald and leaf rust, as well as polygenic partial resistance (see chapters 4 and 6). In the Ethiopian landraces these resistances can be expected to occur, when they contribute to a durable protection of the landraces.

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Chapter 3

Variation Between and Within Ethiopian Barley Landraces

Summary

Eighteen barley landraces collected from 18 localities of 6 barley growing regions of Ethiopia were studied for two years at Holetta, Ethiopia for variation in scald severity, earliness, measured in days from planting to heading, plant height, 1000 grain weight and leafiness.

The observed variation between as well as within landraces was very large for all traits. They also varied in the degree of variation. Some landraces, 1726 and 3288 for instance, were more variable for all five traits than landraces such as 3432 and 3441. Days to heading and altitude were positively and highly significantly associated (r_s= 0.60).

It was also observed that when landraces were grouped according to their mean scald severity the other trait means of the landraces appeared to be inversely associated with scald severity indicating that landraces carrying higher frequencies of genes for earliness, shorter plant length, and less leaf canopy were more affected by scald severity.

Introduction

Landraces comprise the major genetic resources of cultivated barley in Ethiopia. Since Vavilovian times Ethiopia has been recognised as a centre of diversity for barley. The large diversity in the Ethiopian landraces could be due to the diversity in soils, climate, altitude and topography together with geographical isolation for longer periods (Harlan, 1968). During the last two decades extensive collections have been made by the Plant Genetics Resources Centre of Ethiopia (PGRC/E) to conserve this genetic diversity. However, most collected and preserved landraces at the Gene Centre are not yet studied for their genetic diversity. In recent years some studies were undertaken on some of these landraces and results showed that genetic variation was large for most characters studied (Endashaw, 1983; Engels, 1991; Mulugeta, 1985; Zemede, 1988, 1990). There is a clear feeling that more has to be done in this area so that more insight into their population

structure can be obtained. This information is important for the future use, maintenance, and exploitation of such landraces. This paper presents the results obtained from the assessment of the variation patterns in 18 barley landraces for certain plant characters.

Materials and Methods

Eighteen barley landraces, supplied by the Plant Genetics Resources Centre of Ethiopia (PGRC/E) and represented by 100 single plant derived lines each, were used in this study. The landraces evaluated with their origin of collection are shown in table 1.

Table 1. Barley landraces evaluated in this study.

Region	Locality	Altitude(m)	Acc.no[1]	Line no.	Entries[2]
ARSI	Gedeb	2580	1726	501 - 600	100
	Tiyo	2700	21895	1301 - 1400	100
BALE	Adaba	2630	3292	701 - 800	100
	Dinsho	2840	3252	1 - 100	100
	Dodola	2730	212845	901 - 1000	100
	Goba	2820	3288	601 - 700	100
	Goba	2820	212840	101 - 200	100
GAMOGOFA	--	--	218850	1201 - 1300	100
	Bonke	2600	212959	1601 - 1700	100
ILUBABOR	Bedele	1990	208925	801 - 900	100
SHEWA	Ambo	2430	1829	1001 - 1100	100
	AddisAlem	2580	3432	401 - 500	100
	BitaBelew	2250	208038	1401 - 1500	100
	BitaBelew	2250	208040	1501 - 1600	100
	Dendi	2900	3441	1701 - 800	100
	Jeldu	2850	3448	301 - 400	100
	Limu	2280	212938	201 - 300	100
SIDAMO	AletaWondo	1960	208852	1101 - 1200	100

[1] As supplied by the Plant Genetic Resources Centre of Ethiopia (PGRC/E).
[2] Of each landrace 100 single plant derived lines were produced.

The 1800 lines of the 18 landraces were grown at Holetta, Ethiopia in the 1991 and 1993 rainy seasons. Each line was sown on a three row plot of 1.5m length and with a row distance of 20cm. Two improved pure line barley cultivars, Holkr (a two-row cultivar) and Ardu 60b (six-row) were included for comparison. The plots were fertilized at sowing time at the rate of 30/30 N/P_2O_5 kg/ha

The following characters were measured on each plot: 1) scald severity was assessed on the 0-9 scoring scale of Saari and Prescott (1975). As a general indication: 0 = no visible scald lesions; 1 to 3 = resistant; 4 to 6 = moderately resistant and 7 to 9 = susceptible. The scald severity was measured on 10 to 15 plants taken from each plot. Three disease readings were taken each year and for the various calculations the third observation values were used; 2) Earliness was recorded as the number of days from planting to heading; 3) Plant height of a plant was measured in cm as the distance from plant base to the top of the ear of the tallest tiller excluding awns; 4) Leafiness was scored on a scale of 1 to 5 , where 1 was used to indicate a low degree of leafiness and 5 a high level of leafiness; 5) Thousand grain weight was measured on 200 barley grains adjusted at 12.5% moisture and the result obtained was multiplied by 5 to give the weight of 1000 grains.

For all characters studied means and standard deviations were used to compare and classify the observed variation in the landraces.

Results

Scald severity varied from 0.5 in landrace 3441 from Dendi, Shewa Region to 9.0 in landrace 218850 from an unknown locality in the Gamogofa Region with an overall mean of 5.2 (Table 2). The results of this character are discussed in more detail in chapter 6.

The overall mean for days to heading was 83 days. The earliest landrace (208950) headed on average after 62 days, while the latest (3441) came into heading after 97 days, giving a spread of over 30 days between landraces. Days to heading and altitude were positively and highly significantly associated (r_s= 0.60). Genetic variation within landraces for this character appeared considerable and is shown in table 3. Landrace 218850 was the least variable and quite uniform for earliness, while landrace 3288 from Jeldu, Shewa Region was extremely variable.

The overall average height of plants in the landraces was 88cm. The range in mean height was 70.5cm in landrace 212840 from Goba area, Bale Region to 112.2cm in landrace 1829 from Ambo area, Shewa Region. The variation within landraces for plant height too appeared large (Table 4) and varied with landraces, being moderate for a landrace like 212938 and large for a landrace like 3288 with both having about the same mean plant height.

The degree of leafiness in the landraces varied from 1.7 scale units to 5.0 scale units with an overall mean of 3.3 (Table 2). The variation within landraces was found to be very large (Table 5). Landraces 1726 was more variable for this character than the others.

The overall mean for 1000 grain weight in the landraces was 36.2g. The range in mean 1000 grain weight was from 21.2g in landrace 218850 to 52.7g in landrace 3441. The variation within landraces again was found to be high (Table 6).

Discussion

The results show that there was a very large variation between landraces in the characters studied (scald severity, earliness, plant height, leafiness and 1000 grain weight). The variation within landraces too was large for all the characters but the degree of variation varied greatly with landraces being small for scald severity in landrace 3432 and for days to heading in landraces 218850 and 208038 for instance. Some landraces were more variable than others. Landraces 1726 and 3288 for instance were more variable for all five traits than landraces 3432 and 3441 (Table 2). This indicates that landraces of barley vary in degree of variation as a whole or even per character in this centre of diversity. The results of this study agree with those reported by Engels (1991) from the characterization work of 3765 accessions of barley carried out for four years since 1982 at Holetta, Ethiopia. The variation he reported was the variation between accessions collected from different regions of Ethiopia and by comparing the accessions region wise. His study, however, did not analyze the variation or heterogeneity within individual landraces (accessions).

Another interesting point to note is that when the landraces are grouped according to their mean scald severity the other trait means of the landraces appeared to be inversely associated with this scald severity (Table 7). The inverse effect on 1000 grain weight can be seen as a direct (damaging) effect by scald. The inverse association with earliness and plant height is also reported from other leaf pathogens with a similar dispersal mechanism.

The large genetic variation reported here both between and within landraces is good evidence that most if not all Ethiopian barley landraces are mixtures of many different lines (component genotypes). The high variation observed in this study must be viewed

together with the variation reported previously (Endashaw, 1983; Engels, 1991; and Zemede, 1988 & 1990) despite the fact that their studies focused on the general aspect of variation. The results reported here will be an additional source of information for planning future collection, characterization and evaluation of landraces.

There are some views about the causes of wide variation in the Ethiopian barley landraces. The high diversity is due to hybridization and natural selection and diversified environments (Harlan,, 1968), simple mutations caused by temperature shock and intense ultra-violet light prevalent in the mountain areas (Schiemann, 1951). But, later Mulugeta (1985) proposed that disruptive selection would be appropriate to explain the variation in the Ethiopian landraces.

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Table 2. Mean and standard deviation (SD) of 18 barley landraces for five traits[1)]

Landrace	SS		DHD		PLHT		LFN[2]		TGW[2]		N
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
1726	5.8	3.0	83	7.8	86.8	10.7	3.6	1.3	33.6	6.6	84
1829	2.0	1.9	90	4.2	112.2	8.3	3.9	0.5	52.1	6.5	95
3252	4.1	1.6	89	7.5	75.0	7.4	2.6	0.7	33.4	5.0	44
3288	4.6	3.3	83	8.4	89.0	11.2	3.4	0.8	35.1	5.8	71
3292	7.5	1.7	84	5.4	80.1	6.2	3.0	0.9	34.3	2.3	79
3432	2.6	1.5	92	3.6	108.2	7.7	5.0	0.1	47.9	3.9	85
3441	0.5	1.1	97	5.3	97.8	5.9	5.0	0.1	52.7	6.8	50
3448	3.1	1.7	90	4.1	97.6	7.6	3.8	0.5	42.0	4.6	95
208038	5.5	2.9	78	1.8	89.3	8.3	3.1	0.7	33.8	5.0	95
208040	7.7	1.6	81	3.3	84.4	6.0	2.9	0.6	29.5	4.6	97
208852	7.2	2.5	82	2.8	86.5	7.6	3.6	0.7	28.7	7.7	97
208925	6.9	1.4	62	2.6	94.4	5.8	1.9	0.3	39.2	4.5	95
212840	4.2	2.8	81	7.0	70.5	7.6	1.7	0.8	30.4	4.2	71
212845	2.2	2.3	94	6.9	81.3	11.3	3.9	0.7	40.8	7.0	91
212938	8.2	1.1	71	2.1	88.3	5.1	2.2	0.5	32.5	4.9	79
212959	4.3	2.6	79	2.2	84.7	5.5	3.6	0.8	26.6	4.6	91
218850	9.0	0.0	69	1.8	81.2	7.8	2.7	0.9	21.2	3.2	95
218957	4.2	2.4	79	3.1	79.7	5.7	3.8	0.4	37.3	4.3	93
Mean	5.2	3.2	83	9.1	88.0	11.1	3.3	0.9	36.2	8.5	

[1)] SS = scald severity; DHD = days to heading; PLHT = Plant height; LFN = leafiness; TGW = thousand grain weight; N = number of lines evaluated.

[2)] Mean values of one season observations.

Table 3. Variation within 18 barley landraces for earliness (in days) in seven classes.

Landrace	Earliness class							N	Mean
	50.0[1] 66.9[2]	67.0 74.9	75.0 82.9	83.0 90.9	91.0 98.9	99.0 106.9	>106.9		
	Number of landrace lines								
208925	94	0	1	0	0	0	0	95	62
218850	2	92	1	0	0	0	0	95	69
212938	0	73	6	0	0	0	0	79	71
208038	0	6	86	3	0	0	0	95	78
218957	0	12	74	7	0	0	0	93	79
212959	0	8	76	7	0	0	0	91	79
212840	2	1	50	8	10	0	0	71	80
208040	0	0	72	23	2	0	0	97	81
208852	0	0	55	40	2	0	0	97	82
1726	0	17	26	25	1	0	0	84	83
3288	0	17	12	33	8	1	0	71	83
3292	0	7	15	51	5	1	0	79	84
3252	0	1	8	17	13	5	0	44	89
1829	0	0	4	60	26	3	3	96	90
3448	0	1	1	58	29	6	3	95	90
3432	0	0	1	42	38	4	0	85	92
212845	0	0	3	25	33	26	4	91	94
3441	0	0	0	8	19	20	3	50	97
Total	98	235	491	407	200	67	10	1508	

[1] low and [2] high boundaries of a class

Table 4. Variation within 18 barley landraces for plant height (in cm) in eight classes.

Landrace	Plant height class								N	Mean
	42.3[1] 54.2[2]	54.3 66.2	66.3 78.2	78.3 90.2	90.3 102.2	102.3 114.2	114.3 126.2	126.3 138.2		
	Number of landrace lines									
212840	1	17	39	14	0	0	0	0	71	70.5
3252	0	5	25	14	0	0	0	0	44	75.0
218957	0	2	26	63	16	0	0	0	93	79.9
3292	0	1	29	47	1	1	0	0	79	80.1
218850	0	1	29	60	5	0	0	0	95	81.2
212845	0	6	34	31	17	3	0	0	91	81.3
212959	0	1	11	63	16	0	0	0	91	84.7
208040	0	0	12	70	15	0	0	0	97	84.8
208852	0	0	14	46	35	2	0	0	97	86.5
1726	0	0	19	35	23	7	0	0	84	86.8
212938	0	0	5	45	29	0	0	0	79	88.3
3288	0	2	11	25	25	7	1	0	71	89.0
208038	0	0	10	34	47	4	0	0	95	89.3
208925	0	0	1	20	62	12	0	0	95	94.4
3448	0	0	1	20	52	22	0	0	95	96.6
3441	0	0	0	4	35	11	0	0	50	97.8
3432	0	1	0	0	10	60	14	0	85	108.2
1829	0	0	0	2	7	47	37	3	96	112.2
Total	1	36	266	593	381	176	52	3	1508	

[1] low and [2] high boundaries of a class.

Table 5. Variation within 18 barley landraces for the degree of leafiness on a 1 to 5 scoring scale.

Landrace	1	2	3	4	5	N	Mean
				Number of landrace lines			
212840	32	26	13	0	0	71	1.7
208925	9	85	1	0	0	95	1.9
212938	4	55	20	0	0	79	2.2
3252	3	17	21	3	0	44	2.6
218850	6	42	26	19	2	95	2.7
208040	0	25	57	15	0	97	2.9
3292	2	18	40	7	12	79	3.0
208038	0	18	50	27	0	95	3.1
3288	0	15	14	42	0	71	3.4
208852	0	2	44	40	11	97	3.6
1726	2	23	18	8	33	84	3.6
212959	0	8	36	35	12	91	3.6
3448	2	1	16	71	5	95	3.8
218957	0	23	70	0	0	93	3.8
1829	0	0	17	68	11	96	3.9
212845	0	2	22	49	18	91	3.9
3432	0	0	0	1	84	85	5.0
3441	0	0	0	1	49	50	5.0
Total	60	360	465	386	237	1508	

Table 6. Variation within 18 barley landraces for 1000 grain weight (in g) in five classes

Landrace	Thousand grain weight class					N	Mean
	14.9[1] 24.8[2]	24.9 34.8	34.9 44.8	44.9 54.9	54.9 64.9		
	Number of landrace lines						
218850	84	10	1	0	0	95	21.2
212959	45	40	6	0	0	91	26.6
208852	31	50	9	7	0	97	28.7
208040	14	72	10	1	0	96	29.5
212840	5	55	11	0	0	71	30.4
212938	9	40	30	0	0	79	32.5
3252	3	24	16	1	0	44	33.4
1726	8	38	35	3	0	84	33.6
208038	1	55	38	1	0	95	33.8
3292	0	43	34	2	0	79	34.3
3288	1	39	26	5	0	71	35.1
218957	1	27	64	1	0	93	37.3
208925	0	14	78	3	0	95	39.2
212845	1	15	45	30	0	91	40.8
3448	0	6	61	28	0	95	42.0
3432	0	0	15	66	4	85	47.9
1829	0	3	7	50	36	96	52.1
3441	0	2	4	24	20	50	52.7
Total	203	533	490	222	60	1508	

[1] low and [2] high boundaries of a class

Table 7. Barley landraces grouped according to their scald severity and the corresponding means of earliness, plant height, leafiness and 1000 grain weight (TGW).

Group	Severity Range	Severity Mean	Earliness	Plant height	Leafiness	TGW
1	0.0-1.9	0.7	91	92.6	3.9	44.0
2	2.0-3.9	2.7	87	93.4	3.9	40.3
3	4.0-5.9	4.7	81	86.9	3.2	35.9
4	6.0-7.9	6.7	79	87.8	3.2	37.9
5	8.0-9.9	8.7	75	84.6	2.7	29.1

Chapter 4

The Barley-Barley Leaf Scald Pathosystem

Summary

Rhynchosporium secalis is a very important pathogen of barley, especially in areas where the weather is cool and semi-humid. When severe epidemics occur the pathogen can cause considerable yield losses. *R. secalis* is a highly variable pathogen, despite the fact that it has no known perfect state nor sexual recombination. Conidia are important for infection and dispersal of the pathogen.

A number of studies showed that *R. secalis* can be controlled by the resistance present in barley. The two types of resistance reported in barley to *R. secalis* are race-specific resistance and partial resistance. The former type of resistance is major genic while the latter is polygenic in nature.

Introduction

Scald is a common disease of barley, especially in the cooler and semi-humid areas (Dickson, 1962; Skoropad & Kao, 1965). It is widespread in Europe and North America and has also been reported from South America, Africa, the Middle East, Japan, Korea, and Australia (Mathre, 1987).

Yield losses as high as 35-40% have been estimated to occur when severe epidemics strike (Jenkins & Jemmett, 1967; James et al., 1968). From a more recent study in Ethiopia losses as high as 23-67% have been reported (Eshetu Bekele, 1985). However, losses of 1-10% are probably much more common (Jenkins & Jemment, 1967; Evans, 1969). Yield losses occur mainly through reduced 1000 grain weights, although other above ground parts may be reduced as well (James et al., 1968).

The pathogen

Rhynchosporium secalis (Oud.) J. J. Davis is the causal organism of scald of barley (*Hordeum vulgare* L.). The fungus has no known sexual state (Owen, 1963). The

mycelium is hyaline to light grey and develops as a compact stroma under the cuticle of the host plant. Sessile conidia (2-4 x 12-20 μ) are borne on cells of the fertile stroma. They are hyaline and cylindric to ovate, mostly with an apical beak (Ayesu-Offei & Clare, 1970).

Although, *R. secalis* has no known perfect state and so no sexual recombination, it is a highly variable pathogen (Kline, 1960; Skoropad, 1960; Ayesu-Offei & Clare, 1971; Ali and Boyd, 1974; Owen, 1963). In California, numerous pathogenic races have been identified on 14 barley cultivars (Jackson & Webster, 1976). The pathogen species does not appear to be highly specialized as to host range, because several grass species are susceptible to some isolates from cultivated barley (Schein, 1957, 1960; Kajiwara and Iwata, 1963; Ali and Boyd, 1974). However, some researchers do not agree with this idea because they reported strict host specialization in some locations (Caldwell, 1931, 1937; Sprague, 1950; Owen, 1958).

Conidia are produced under cooler and humid conditions only on wet lesions after leaf tissue has become necrotic. Alternate wetting and drying cycles deplete the reserves of the fungus and it will cease to sporulate after some time. Conidia do not seem to overwinter. Survival in crop residues up to 12 months was demonstrated. There is no evidence that the fungus survives saprophytically in the soil outside the debris (Shipton et al., 1974).

Conidia may be carried by wind but only for relatively short distances. Water-splash dispersal within the crop field seems very important. A long distance dispersal of the conidia seems possible through infected plant debris and infected grains, but in most cases disease development depends on local inoculum (Shipton et al., 1974).

It is not clearly known whether seedborne inoculum has any importance here. But some researchers believe that primary inoculum of *R. secalis* can exist as mycelium in the pericarp and hull of infected seed. In a seed lot with 36% infection, a transmission rate from seed to seedling of 26% was noted (Jackson & Webster, 1976). However, most investigators believe that infected host residue is the principal source of primary inoculum (Shipton et al., 1974).

Conidia require a relative humidity of over 92% and optimum temperatures between 12 and 18°C for germination and infection (Shipton et al., 1974). A 24 hour dark, moist period may be sufficient for spores to infect leaves. Lesions appear in 14 days (Mathre, 1987).

Conidia and isolates may show interactions with temperature. At high temperatures some isolates could very well infect hosts while others are successful only at low temperatures (Mathre, 1987).

Most infections in the field occur on the lower leaves, which become visible about two weeks after the initiating rains. Infection of the leaves may be facilitated by direct contact with the inoculum on the plant debris (Skoropad, 1960). Details of the infection process have been described by Ayesu-Offei and Clare (1970). Invading hyphae initially establish a sub-cuticular stroma without showing any visual symptoms. Toxic metabolites (rhynchosporiosides), produced from such stroma, then can lead to cell collapse of the underlying epidermal cells ahead of hyphae penetration into them (Ayesu-Offei and Clare, 1971; Auriol et al., 1978). The collapse of these cells becomes visible as water soaked areas, which later develop into lenticular shaped lesions characteristic of the disease. The above sequence of events takes time, the actual duration varying with host genotype, isolate and environment (Fowler and Owen, 1971; Ali and Boyd, 1974).

Host resistance

Scald, caused by *R. secalis,* may be controlled in several ways such as by fungicides, integrated disease management practices and the use of resistant cultivars. Of these, resistant cultivars represent a relatively cheap and effective control. Habgood & Hayes (1971) studied the genetics of resistance in barley seedlings and reported that the resistance found was effective and controlled by one or two major genes; in some genotypes the resistance was race-specific, in the others race-specificity could not be clearly identified with the races used. Habgood (1972) identified another form of resistance which was much less effective at the seedling stage but appeared to be monogenically inherited and potentially race-specific. The race-specific resistance has been suggested to be fairly appropriate for the control of scald in barley (Habgood, 1974) as the scald pathogen is not readily disseminated between crops reducing the chances for the emergence of new races as well as the spread of established races.

The race-specific resistance and its lack of durability is shown by cultivar Atlas 46 in California. It was released in 1947 and after six years scald was found on it and by 1956

it was extremely susceptible (Houston & Ashwarth, 1957).

Besides the race-specific, major gene resistance barley cultivars may carry different levels of partial resistance against the pathogen. The most important characteristics of this resistance type are discussed in chapter 6. Habgood (1974) reported the presence of partial resistance to leaf scald in several West European barley cultivars (Proctor, Ruby, Zephyr, Cambrinus, Inis and Old Cornish). Quite recently Kari and Griffiths (1993) studied 11 barley cultivars in a series of trials at the seedling stage for components of partial resistance to *Rhynchosporium secalis* in order to predict field resistance from these components but the differences between the cultivars in the seedling stage were too small for a reliable prediction.

Inheritance of Resistance

The race-specific resistance in most cases is controlled by **major resistance genes.** A number of genetic studies on host resistance have been carried out by several workers. These studies have generally emphasized simple mendelian inheritance involving linkage, multiple allelism, a number of recessive genes for resistance and complementary gene actions (Riddle and Briggs, 1950; Dyck & Schaller, 1961; Wells & Skoropad, 1963; Starling et al., 1971; Habgood & Hayes, 1971; McDonald et al., 1989). These reports, however, do not fully agree with one another. A whole series of genes reported from literature conditioning resistance to *R.secalis* are shown in Table 1 with the barley cultivars in which they were identified.

Partial resistance in barley appeared **polygenically inherited.** Habgood (1974) studied the inheritance of partial resistance in barley to *R.secalis* using a diallel crosses between six European spring barley cultivars (Proctor, Ruby, Zephyr, Cambrinus, Inis and Old Cornish). F2 and part of the F3 material were studied with their parents. It was found that resistance was complex in inheritance. From the F2 data it was concluded that both dominant and recessive inheritance were important in conferring resistance, additivity being very important. The F3 material suggested that these additive alleles were not completely concentrated in the most resistant cultivar, Proctor, due to the high frequency of transgressive segregation that occurred in all cross combinations. Habgood (1976) also reported small race-specific effects of this polygenic, partial resistance.

Selection in the F2 did not seem very efficient (low h^2), due to uneven distribution of the inoculum from the spreader rows.

Table 1. Genes for resistance to *Rhynchosporium secalis* in barley.

Gene symbol	Cultivars in which gene was found
Rh	Turk CI 5611-2 (c, f)*
Rh2	Atlas CI 4118 (c)
Rh3	Wisconsin Winter x Glabron CI 8162 (d)
Rh3, Rh	Brier CI 7157 (b)
Rh4	Lamesita CI 7565 (c)
Rh4	Osiris CI 1622 (d)
$Rh^2$4, Rh^{2**}	Modoc CI 7566 (c, d)
Rh5	Turk CI 5611-2 (c)
rh6	Jet CI 967 (a)
rh7, rh	Jet CI 967 (a, d)
rh8	Nigrinudum CI 2222 (g)
Rh9	Abyssinian CI 668 (a)
Rh10	Osiris CI 1622 (d)
rh11	CI 4364 (d)
Rhx	Trebi CI 936 (e)

* Gene symbols represented by a letter or letters in parenthesis were identified (a) by Baker and Larter (1963); (b) by Bryner (1957); (c) by Dyck and Schaller (1961); (d) by Habgood and Hayes (1971); (e) Riddle and Briggs (1950); (f) by Riddle and Suneson (1948) and (g) by Wells and Skoropad (1963).

** Rh^2 refer to alleles at that Rh locus.

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Chapter 5

Variation of Resistance to *Rhynchosporium Secalis* in Ethiopian Barley Landraces.

Summary

Eighteen barley landraces originally collected from localities differing in altitude (1960-2900m) in six regions of Ethiopia (Arsi, Bale, Gamogofa, Ilubabor, Shewa and Sidamo) were studied for two years (1991 and 1993) under field conditions at Holetta, Ethiopia, for variation of scald resistance between and within landraces. Between landraces a very wide variation was observed, ranging from a mean scale value of 0.5 for landrace 3441 to a mean of 9.0 for landrace 218850 in 1991. A similar pattern was also observed in 1993. Variation within landraces also was high. Landraces such as 1726, 1829, 3288, and 3448 were among those that showed a large variation within themselves. However, not all of the variation observed within landraces was considered true genetic variation. Only the variation due to genetic effects was considered real variation in the landraces.

In this study the relationship between scald severity and altitude was negative and significant. The resistance level of a landrace tended to increase the higher the elevation and so the higher the disease pressure. Race-specific resistance effects were observed. Ethiopian barley landraces are heterogeneous mixtures of lines and the durability of their resistance seems at least partly due to the multiline effect.

Introduction

Rhynchosporium secalis (Oud.) J. Davis is the pathogen that causes the scald of barley. It is a common disease of barley, especially in the cooler and semi-humid barley growing areas (Dickson, 1962; Skoropad & Kao, 1965). It is widespread in Europe and North America and has also been reported from South America, Africa, The Middle East, Japan, Korea, and Australia (Mathre, 1987).

The disease causes considerable yield losses in several countries. For instance, Jenkins and Jemmett (1967) reported losses as high as 35-40% in the UK, Schaller (1951) up to 35% in California, Khan (1986) up to 47% in Western Australia.

In Ethiopia, scald is also common wherever barley is grown but the severity increases with altitude as the weather become cooler and more humid (Hailu Gebre 1981). Here, scald can cause yield losses up to 67% (Eshetu, 1985). Although the disease is so damaging, the Ethiopian barley landraces seem to withstand the disease pressure to a certain extent and give some to fair yields. As these landraces are considered genetically heterogeneous, consisting of mixtures of many different lines, it is assumed that each individual line has an effect on the level of this disease. This chapter studies the variation in scald resistance within and between eighteen Ethiopian barley landraces.

Materials and Methods

Eighteen barley landraces, supplied by the Plant Genetics Resources Centre of Ethiopia (PGRC/E), and represented by 100 single plant derived lines each, were used in this study. The landraces with their scald severities are presented in table 1.

In the 1991 and 1993 main rainy seasons all 1800 lines of the 18 landraces were planted and assessed for scald severity and certain agronomic characters (see below) at Holetta, Ethiopia. Sowing occurred on 22 June in 1991 and on 27 June in 1993. Each line was sown on a three row plot of 1.50m length and with a row distance of 20cm. However, not all lines in each landrace were evaluated in this study due to shortage of seed of these lines. Two improved pure line barley cultivars, Holkr (a two-row) and Ardu 60b (a six-row) with a susceptible and an intermediate resistance to scald respectively, were planted as controls alternatingly every 30 plots. The plots were fertilized at the rate of 30/30, N/P_2O_5 kg/ha.

The Holetta Research Centre location is considered very conducive to scald. In the 1991 trial the epidemic originated from naturally occurring inoculum supplemented with some infected straw stubble of barley. In the 1993 field trial the epidemic originated from naturally occurring inoculum only.

Per plot scald severity, days to heading, plant height, and leafiness were assessed. Scald severity was assessed on the 0 - 9 scoring scale of Saari and Prescott (1975). As a general indication: 0 is considered immune with no visible scald lesions; 1 to 3 as resistant; 4 to 6 as moderately resistant; and 7 to 9 as susceptible. Severity was assessed on 10 to 15 plants taken from each plot. As heading varied considerably among entries

the disease assessments were taken at three dates (30/8, 13/9 and 2/10 in 1991, and 25/8, 18/9 and 7/10 in 1993) on all plots. For the various calculations, however, only the assessments obtained from the third observation date were used.

Earliness was recorded as the number of days from planting to heading. Plant height of a plant was measured in cm as the distance from plant base to the top of the ear of the tallest tiller excluding awns. Leafiness was scored on a scale of 1 to 5, where 1 was used to indicate a low degree of leafiness and 5 a high level of leafiness. For all traits evaluated means and standard deviations were used as parameters for measuring the variation of that trait in the landraces studied. Rank correlation coefficients (r_s) were calculated to understand the average association over landraces. Multiple regressions were calculated based on the idea that the association between scald severity and the other traits may differ between landraces. Four sets of data (scald severity, earliness, plant height and leafiness) were subject to multiple regression analysis on a PC/computer using MSTAT-1 statistical package (Freed et al., 1986). The analysis was applied taking disease severity as dependent and the other traits as independent variables. The analysis was carried out for the individual landraces.

Results

The range, means and standard deviations of the scald severities of both 1991 and 1993 are presented in table 1. In 1991 the mean severity among landraces ranged from 0.5 for landrace 3441 to 9.0 for landraces 208925 and 218850 and the standard deviation within landraces varied from 0.0 in landraces 208925 and 218850 to 3.5 in landrace 3288. In 1993 the severity showed a similar range among landraces from 0.4 for landrace 3441 and 9.0 for landrace 218850 and the standard deviation within landraces ran from 0.0 in 218850 to 4.2 in landrace 1726. This clearly shows that great differences between as well as within landraces occurred.

Table 1. Range, mean and standard deviation (SD) of scald severity (on the 0 - 9 scale) of 18 Ethiopian barley landraces exposed to scald in 1991 and 1993.

Landrace	Scald severity						Over all mean	No. of lines assessed
	1991			1993				
	Range	Mean	SD	Range	Mean	SD		
3441	0-5	0.5	0.9	0-9	0.4	1.5	0.4	50
1829	0-8	3.2	2.6	0-8	0.8	2.0	2.0	96
212845	0-8	2.7	2.5	0-9	1.5	3.0	2.1	91
3432	1-7	3.9	1.4	0-9	1.3	2.6	2.6	84
3448	0-9	4.6	2.0	0-9	1.6	2.3	3.1	95
212840	0-9	5.9	2.9	0-9	2.2	3.3	4.0	71
218957	1-9	4.8	2.2	0-9	3.7	3.9	4.2	93
3252	2-9	6.4	1.3	0-9	2.2	2.1	4.3	44
212959	0-8	5.1	2.6	0-9	3.5	3.9	4.3	91
3288	0-9	5.0	3.5	0-9	4.1	4.0	4.5	71
208038	0-9	6.1	3.1	0-9	4.9	4.0	5.5	96
1726	1-9	6.5	2.6	0-9	5.0	4.2	5.7	84
208925	9-9	9.0	0.0	1-9	4.7	2.8	6.8	95
3292	2-9	7.6	1.1	0-9	7.1	2.8	7.3	79
208040	6-9	7.8	0.8	1-9	7.6	2.9	7.7	97
208852	0-9	7.7	2.3	0-9	7.9	2.8	7.8	97
212938	8-9	8.9	0.1	1-9	7.6	1.6	8.2	79
218850	9-9	9.0	0.0	9-9	9.0	0.0	9.0	95
Holkr[1]	4-9	7.6	1.0	0.8	2.5	2.9	5.1	29[2]
Ardu60b[1]	0-8	4.0	2.8	0-8	3.2	2.9	3.6	20[2]
Mean		5.9	3.0		4.3	4.0	4.9	

[1] Holkr and Ardu6b, improved barley cultivars intered as control.
[2] The number of observations taken on that control cultivar.

There was a good agreement between the two years. The disease severity between the two years was highly and significantly correlated (r_s = 0.87). The landraces at the extremes such as the resistant landrace 3441 and the extremely susceptible landrace 218850 showed little or no variation within them. But even the landraces that were severely affected in 1991, such as landraces 208925 and 212938 showed in 1993, when the disease pressure was lower, a clear variation within the landraces. All other landraces showed at least a fair amount of variation within landraces. Most landraces showed a

significant and similar variation patterns within themselves in both years (Tables 2a and 3a). Within a landrace lines can be found that are classified as resistant as well as lines that are classified as susceptible. In several landraces the lines ranged from a severity of 1 up to a severity of 9. In total there were 112 lines from 9 landraces in 1991 and 529 lines from 16 landraces in 1993 that had an immune type of reaction (disease severity of 0), while a total of 257 lines from 16 landraces in 1991 and 211 lines in 1993 gave a resistant reaction of 1-3. On the other hand, of all landrace lines tested 693 in 1991 and 649 lines in 1993 showed a susceptible reaction (7-9) (Tables 2a and 3a). Some landraces showed a considerably higher disease severity than Holkr, a susceptible, improved barley cultivar, and other landraces showed a clearly lower severity than Ardu60b, a moderately resistant, improved barley cultivar (Table 1).

Disease severity was correlated with certain plant characters such as earliness, plant height and leafiness and altitude of origin of the landrace (Table 4). A strong and highly significant ($p < 0.01$) negative association ($r_s = -0.72$) was found with both earliness and leafiness. A significant ($p < 0.05$) negative association ($r_s = -0.60$) was also found with altitude (Table 4, Table 5). Severity was positively correlated with plant height but this was not significant. The relationship between earliness and plant height was positive but also was not significant. A positive and a highly significant association ($p < 0.01$) was found between earliness and leafiness ($r_s = 0.76$). Earliness and altitude are positively and significantly associated, i.e. the higher the altitude the later the landrace.

Despite the high correlation in scald severity between the two years large differences in severity could occur for individual lines. Table 6 shows 21 lines from 9 landraces that had an immune type of reaction in one year and a significantly higher reaction, often extremely susceptible in the other year. These "differential interactions" occurred between and within landraces (1726, 3288).

Results of the multiple regression analyses of disease severity on earliness, plant height and leafiness are shown in table 7. Results showed that the association of scald severity with earliness was more important than its association with the other traits. The slopes of landraces could differ significantly from zero and from each other ($p < 0.05$) (Table 7). for instance the b of landrace 208852 was significantly steeper than the b of landrace 1726, while both differed significantly from zero.

Table 2a. Distribution of landrace lines according to their reaction to scald of barley in Ethiopia in 1991.

Landrace	Reaction (0-9 scale)											
	0	1	2	3	4	5	6	7	8	9	N	Mean[1]
3441	35	10	3	1	--	1	--	--	--	--	50	0.5
212845	13	24	21	7	4	9	2	2	8	1	91	2.7
1829	20	13	13	6	11	11	9	8	5	--	96	3.2
3432	--	5	10	13	25	22	9	1	--	--	85	3.9
3448	3	7	7	4	15	23	22	12	1	1	95	4.6
218957	--	5	15	10	14	12	14	7	13	3	93	4.8
3288	18	--	1	6	3	7	6	5	7	18	71	5.0
212959	5	5	10	7	12	10	6	6	30	--	91	5.1
212840	2	4	7	3	10	5	7	3	5	25	71	5.9
208038	11	5	3	1	2	9	5	4	41	14	95	6.1
3252	--	--	7	3	3	3	7	4	9	8	44	6.4
1726	--	3	6	5	8	10	9	2	6	35	84	6.5
3292	--	--	1	--	--	4	5	8	52	9	79	7.6
208852	5	1	--	3	--	1	4	4	33	46	97	7.7
208040	--	--	--	1	--	1	6	5	75	9	97	7.8
212938	--	--	1	--	--	--	--	--	--	78	79	8.9
218850	--	--	--	--	--	--	--	--	--	95	95	9.0
208925	--	--	--	--	--	--	--	--	--	95	95	9.0
Total	112	82	105	70	107	128	111	71	285	437	1508	

Table 2b. Landrace lines classified according to their predicted reaction to scald of barley in 1991.

Landrace	Reaction (0-9 scale)											
	0	1	2	3	4	5	6	7	8	9	N	Mean[1]
3441	50	--	--	--	--	--	--	--	--	--	50	0.5
212845	5	11	19	35	17	4	--	--	--	--	91	2.7
1829	4	2	18	34	34	4	--	--	--	--	96	3.2
3432	--	--	--	--	85	--	--	--	--	--	85	3.9
3448	--	--	1	15	18	56	4	1	--	--	95	4.6
218957	1	--	--	--	26	66	--	--	--	--	93	4.8
3288	1	--	4	4	24	11	14	13	--	--	71	5.0
212959	--	--	--	3	10	64	14	--	--	--	91	5.1
212840	--	--	--	--	--	12	56	3	--	--	71	5.9
208038	--	--	--	--	3	23	37	32	--	--	95	6.1
3252	--	--	3	4	10	1	5	10	7	4	44	6.4
1726	--	1	--	1	12	18	10	10	22	10	84	6.5
3292	--	--	--	--	--	--	1	26	51	1	79	7.6
208852	1	--	--	--	--	7	8	19	39	23	97	7.7
208040	--	--	--	--	--	--	6	18	73	--	97	7.8
212938	--	--	--	--	--	--	--	--	14	65	79	8.9
208925	--	--	--	--	--	--	--	--	--	95	95	9.0
218850	--	--	--	--	--	--	--	--	--	95	95	9.0
Total	62	14	45	96	239	266	155	132	206	293	1508	

[1] Mean scald severity of the landraces.

Table 3a. Distribution of landrace lines according to their reaction to scald of barley in Ethiopia in 1993.

Landrace	Reaction (0-9 scale)											
	0	1	2	3	4	5	6	7	8	9	N	Mean[1]
3441	45	1	1	--	2	--	--	--	--	1	50	0.4
1829	79	3	3	1	3	2	2	1	2	--	9	0.8
3432	60	6	4	2	3	1	--	2	4	3	85	1.3
212845	69	2	1	2	2	1	--	4	2	8	91	1.5
3448	44	21	9	2	4	4	6	2	2	1	95	1.6
3252	9	11	9	4	6	1	2	1	--	1	44	2.2
212840	38	10	2	3	4	1	--	1	2	10	71	2.2
212959	44	3	2	1	6	2	3	4	3	23	91	3.5
218957	37	7	4	4	7	1	2	2	--	29	93	3.9
3288	27	2	3	2	4	1	4	2	3	23	71	4.1
208925	--	13	14	18	7	4	2	6	30	1	95	4.7
208038	29	8	1	1	1	3	8	3	4	37	95	4.9
1726	28	3	4	1	2	2	--	1	2	41	84	5.0
3292	4	2	4	1	3	3	5	7	4	46	79	7.1
208040	6	5	1	3	--	--	3	2	1	76	97	7.6
212938	1	2	1	2	1	--	--	4	62	6	79	7.6
208852	9	1	1	--	--	1	--	--	3	82	97	7.9
218850	--	--	--	--	--	--	--	--	--	95	95	9.0
Total	529	100	64	47	55	27	37	42	124	483	1508	

Table 3b. Landrace lines classified according to their predicted reaction value to scald of barley in 1993.

Landrace	Reaction (0-9 scale)											
	0	1	2	3	4	5	6	7	8	9	N	Mean[1]
3441	32	17	1	--	--	--	--	--	--	--	50	0.4
1829	33	46	17	--	--	--	--	--	--	--	96	0.8
3432	2	55	28	--	--	--	--	--	--	--	85	1.3
212845	26	20	28	11	6	--	--	--	--	--	91	1.5
3448	14	20	55	4	1	1	--	--	--	--	95	1.6
3252	--	--	38	6	--	--	--	--	--	--	44	2.2
212840	9	20	7	15	11	6	--	3	--	--	71	2.2
212959	--	1	11	34	37	8	--	--	--	--	91	3.5
218957	--	6	16	13	39	11	7	1	--	--	93	3.7
3288	--	--	38	4	--	6	9	--	8	6	71	4.1
208925	--	1	--	10	47	21	6	3	4	3	95	4.7
208038	1	--	1	3	30	39	18	--	3	--	95	4.9
1726	5	13	8	4	10	3	9	14	7	11	84	5.0
3292	--	--	--	--	--	--	4	69	6	--	79	7.1
208040	--	--	--	2	2	3	16	24	20	30	97	7.6
212938	--	--	--	--	--	1	2	36	40	--	79	7.6
208852	--	1	--	1	1	7	11	15	16	45	97	7.9
218850	--	--	--	--	--	--	--	--	--	--	95	9.0
Total	122	200	248	107	184	106	82	165	104	190	1508	

[1] Mean scald severity of the landraces.

Table 4. Rank correlation coefficients (r_s) between scald severity (SS), earliness (ER), plant height (HT), leafiness (LF) and altitude (AT)

Character	SS	ER	HT	LF	AT
SS		-0.72**	0.31	-0.72**	-0.60*
ER			0.31	0.76**	0.60*
HT				0.45	-0.20
LF					0.20

*p < 0.05; **p < 0.01

Table 5. Percentage barley lines resistant to scald relative to the altitude from which the landraces were collected.

Altitude range (m)	Resistant lines (No)	Landraces tested (No)	Total lines tested (No)	Percentage of lines resistant
< 2000	8	2	192	4.2
2100-2300	18	3	272	6.6
2400-2600	104	4	355	29.3
2610-2750	84	3	263	31.9
2800-2900	111	5	331	33.5

Table 6. The reaction of a number of lines to scald in the two years of study in Ethiopia.

		Reaction (0 - 9) scale	
Landrace	Line	1991	1993
3252	70	9.0	0.0
3252	71	7.0	0.0
1726	509	9.0	0.0
1726	516	0.0	9.0
1726	518	8.0	0.0
1726	519	5.0	0.0
1726	522	9.0	0.0
1726	526	9.0	0.0
3288	601	0.0	9.0
3288	637	0.0	9.0
3288	651	0.0	9.0
3288	695	9.0	0.0
3292	742	8.0	0.0
3292	798	8.0	0.0
1829	1069	0.0	4.0
208852	1152	0.0	9.0
208852	1184	9.0	0.0
208038	1423	8.0	0.0
208038	1442	8.0	0.0
208040	1514	8.0	0.0
3441	1780	0.0	4.0

Table 7. Relationships of resistance between Scald Severity (Y) and Earliness (x_1), Plant height (x_2) and leafiness (x_3) in eighteen barley landraces. *, ** indicate significant differences ($p < 0.05$, $p < 0.01$) between slopes of x_1, x_2 and x_3.

Landrace	Y	=	a	+	bx_1	+	cx_2	+	dx_3	Slopes
1726	Y_1*	=	27.9	−	$0.20x_1$	−	$0.06x_2$			**
	Y_2	=	26.6	−	$0.14x_1$	−	$0.07x_2$	−	$1.02x_3$	**
1829	Y_1	=	22.0	−	$0.15x_1$	−	$0.05x_2$			**
	Y_2	=	7.6	−	$0.02x_1$	−	$0.001x_2$	−	$1.40x_3$	**
3252	Y_1	=	21.7	−	$0.18x_1$	+	$0.008x_2$			**
	Y_2	=	5.5	−	$0.007x_1$	−	$0.04x_2$	−	$0.30x_3$	NS
3288	Y_1	=	25.6	−	$0.21x_1$	−	$0.03x_2$			**
	Y_2	=	13.8	−	$0.04x_1$	−	$0.01x_2$	−	$3.50x_3$	**
3292	Y_1	=	16.3	−	$0.09x_1$	−	$0.01x_2$			**
	Y_2	=	13.5	−	$0.06x_1$	−	$0.02x_2$	+	$0.20x_3$	NS
3432	Y_1	=	3.2	−	$0.000x_1$	+	$0.006x_2$			NS
	Y_2	=	4.9	−	$0.14x_1$	−	$0.001x_2$	+	$1.67x_3$	*
3441	Y_1	=	0.6	−	$0.001x_1$	−	$0.000x_2$			NS
	Y_2	=	16.2	−	$0.09x_1$	−	$0.07x_2$	+	$0.06x_3$	*
3448	Y_1	=	22.3	−	$0.17x_1$	−	$0.02x_2$			**
	Y_2	=	17.2	−	$0.17x_1$	−	$0.02x_2$	+	$0.51x_3$	**
208038	Y_1	=	35.2	−	$0.32x_1$	−	$0.05x_2$			*
	Y_2	=	22.9	−	$0.17x_1$	−	$0.004x_2$	−	$1.19x_3$	*
208040	Y_1	=	21.9	−	$0.20x_1$	−	$0.005x_2$			**
	Y_2	=	28.2	−	$0.32x_1$	+	$0.82x_2$	+	$0.07x_3$	**
208852	Y_1	=	51.0	−	$0.47x_1$	−	$0.06x_2$			**
	Y_2	=	44.7	−	$0.43x_1$	−	$0.044x_2$	+	$0.88x_3$	**
208925	Y_1	=	9.0	+	$0.00x_1$	+	$0.00x_2$			0
	Y_2	=	6.6	+	$0.36x_1$	−	$0.06x_2$	−	$3.10x_3$	*
212840	Y_1	=	10.5	−	$0.07x_1$	+	$0.01x_2$			NS
	Y_2	=	19.4	−	$0.27x_1$	+	$0.02x_2$	+	$1.90x_3$	**
212845	Y_1	=	19.0	−	$0.14x_1$	−	$0.03x_2$			**
	Y_2	=	17.7	−	$0.16x_1$	−	$0.04x_2$	+	$0.71x_3$	**
212938	Y_1	=	17.9	−	$0.11x_1$	−	$0.01x_2$			**
	Y_2	=	-0.1	+	$0.02x_1$	+	$0.08x_2$	−	$0.45x_3$	*
212959	Y_1	=	38.3	−	$0.37x_1$	−	$0.06x_2$			*
	Y_2	=	10.4	−	$0.01x_1$	−	$0.03x_2$	−	$1.02x_3$	*
218850	Y_1	=	9.0	+	$0.00x_1$	+	$0.00x_2$			0
	Y_2	=	9.0	+	$0.00x_1$	+	$0.00x_2$	+	$0.00x_3$	0
218957	Y_1	=	21.2	−	$0.21x_1$	−	$0.004x_2$			*
	Y_2	=	5.3	−	$0.17x_1$	+	$0.06x_2$	+	$2.12x_3$	*

* Y_1 and Y_2 relate to year one (1991) and year two (1993) respectivelly.

Discussion

Landraces with low, intermediate or high disease severity showed a variable degree of variation. Even landraces that showed uniformly a 9.0 in 1991 (such as 208925) were not uniformly susceptible in 1993 or vice versa (Table 2a and 3a). The observed increase in resistance at higher altitudes (Table 5) is best explained as an adaptation to the rapidly increasing disease pressure with increasing altitude. This relationship with altitude in the landraces does confirm the observations of Harlan (1976) who showed earlier that the Ethiopian highlands are good sources for resistances to leaf pathogens of barley. When the landraces were compared individually with the two improved barley cultivars they showed a good level of resistance over the control cultivars (Table 1). Cultivar Ardu 60b appeared more resistant than Holkr and some landraces showed an average resistance even far better than that of Ardu 60b.

The results of the multiple regression analysis showed that the three plant characters, earliness, leafiness and plant height in that order had affected the scald severity. Part of the observed variation in scald severity therefore is due to the variation in these other traits. Tables 2b and 3b show the variation in scald severity after removing the effects of the other traits, leaving the true genotypic variation for scald severity. Although the variation for scald severity decreased the pattern remained the same, a large variation between and within landraces.

Assuming a certain durability of the scald resistance in these landraces the question is what causes this durability. Is it due to a genetically durable form of resistance such as the partial resistance in the barley-leaf rust pathosystem (Parlevliet, 1993) or is it due to the so called multiline effect (Browning and Frey, 1969; McDonald et al., 1988) or due to a combination of both? The data shown in table 6 cannot be explained by partial resistance, but are compatible with the presence of race-specific major genes. Although not investigated it can be assumed that the *Rhynchosporium secalis* population in Ethiopia is quite variable as it appeared variable everywhere when it was analyzed (Ali and Boyd, 1974; Jackson and Webster, 1976; Skoropad, 1960). The presence of race-specific major resistance genes in a genetically heterogeneous host population and a genetically variable pathogen population indicate clearly that the multiline principle is operating in the landraces studied and that the durability of the scald resistance is at least partly derived

from this principle.

Whether there is also partial resistance present cannot be concluded with certainty because of the presence of apparent race-specific major genes. However, partial resistance is usually present in comparable pathosystems (Parlevliet, 1993). And here too there are indications of its presence. If no partial resistance is present the level of susceptibility, after a race-specific major gene looses it effectiveness, would become that of the most susceptible genotype, a 9 in Table 6. If the level of susceptibility is lower it means there is some other resistance left. Parlevliet (1993) named this resistance residual resistance. He showed that this residual resistance occurs widespread and here too it seems present as many lines in this study showed a differential change not from 0 to 9 but from 0 to 4, 5, 6 or 7 (Table 6) or from a 1 or 2 to a 5, 6, or 7 (not shown in Table 6). This is completely in line with what one would expect if partial resistance is present alongside the race-specific major gene resistance. This partial resistance reinforces the durability of the major genes within the multiline strategy.

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Chapter 6

The Barley-Barley Leaf Rust Pathosystem

Summary

The importance of barley leaf rust appears to be limited to the Andes region of South America and North Africa. In other areas it does not seem to cause severe yield losses.

The pathogen, *Puccinia hordei*, has both a sexual and asexual phase. The alternate host, *Ornithogalium* spp. completes the sexual cycle where barley is the primary host. *P. hordei* is a typical specialist with a very narrow host range, some species of *Hordeum*.

The resistance in barley to leaf rust is of two types. Hypersensitive resistance, which is expressed in a lower infection type, is inherited major genically, while partial resistance is inherited polygenically. The former is characterized by race-specificity and lack of durability while the latter is considered durable and characterized by a reduced epidemic build-up despite a susceptible infection type.

Introduction

Barley leaf rust is an important disease of barley, especially in the Andes Region of South America and North Africa. In other areas, where the disease develops late, mainly after ear emergence (Melvelle et al., 1976), it is not considered as destructive (Parlevliet, 1994). Losses can be great when the barley is affected early (King and Polley, 1976; Melville et al., 1976). Severe early infection causes shrivelled kernels and a slight decrease in grain number (Mathre, 1987). Like other leaf rust diseases barley leaf rust may also reduce vigour and plant growth by increasing transpiration, respiration, and reducing photosynthesis (Sapkal et al., 1992).

The Pathogen

Puccinia hordei is the causal agent of leaf rust in barley. It is a polycyclic pathogen with a sexual phase (basidiospores, aeciospores, and teliospores) and an asexual phase (aecidiospores and urediospores). The latter phase is responsible for the economic yield

losses (Alexopoulos and Mims, 1979). It is a heteroucious pathogen with a few *Hordeum* species as primary host and *Ornithogalium spp.* as alternate host (Wahl, 1972; Clifford, 1985). The alternate host is important for sexual recombination of the fungus and effective only in the Near East, in South East Australia and possibly in North Africa (Parlevliet, 1994). In all other areas the evolution of the pathogen must depend on mutation and parasexual mechanisms. The uredia often serve as sources of primary inoculum of this pathogen. Long-distance dispersal of the urediospores is by way of wind.

As to host range *P. hordei* is a typical specialist which is restricted only to some species of *Hordeum* (Anikster et al., 1971; Anikster, 1982; Parlevliet, 1995). The form that attacks the cultivated barley can only attack the wild barley *(H. spontaneum)* and none of the other *Hordeum* species. Forms that have other *Hordeum* species as a host cannot affect the cultivated and wild barley.

Host resistance

There are two kinds of resistance in barley to leaf rust; **hypersensitive resistance** and **partial resistance.**

The hypersensitive resistance is a form of resistance which results in the death of host cells at some stage during hyphae colonization and characterized by a lower infection type (IT). Partial resistance is a form of non-hypersensitive or quantitative resistance which is characterized by a reduced epidemic build-up, despite a susceptible infection type (IT) (Parlevliet, 1978).

Inheritance of Resistance

The **hypersensitive resistance** is governed by major genes (Pa-genes). So far, nine Pa-genes (Table 1, chapter 8) from cultivated barley have been described by different workers (Roane & Starling, 1967, 1970; Starling, 1956; Brückner, 1971; Clifford & Jones, 1981; Parlevliet, 1976, 1983a; Tan, 1976).

This resistance is characterised by race-specificity and lack of durability of resistance. Each Pa-gene is effective against some races of the pathogen only.

Histological studies showed that the hypersensitivity genes cause a collapse of the

invaded host cell and of neighbouring cells after a haustorium has been formed in the invaded host cell. This results in small necrotic flecks, which are described as a low or resistant infection type. In other words, this mechanism of resistance in barley to leaf rust operates post-haustorially (Niks, 1982; 1983).

In a susceptible cultivar no cell collapse occurs after penetration and formation of haustoria. Whitish specks become visible after 6-12 days which develop in one or a few days into orange brown pustules (up to 1mm) that are surrounded by light green to greenish yellow halos (Clifford, 1985).

Partial resistance shows a susceptible infection type in all plant stages (Parlevliet, 1975) and is characterized by fewer and smaller urediosori that appear later and sporulate over a shorter period (Parlevliet and Kuiper, 1977; Neervoort and Parlevliet, 1978).

The epidemic build-up is the collective result of these components, but the components do not contribute equally to this build-up. The reduced number of sori and especially the longer latent period determine the rate of reduced epidemic development (Parlevliet & Van Ommeren, 1975; Neervoort & Parlevliet, 1978; Parlevliet et al., 1985; Parlevliet, 1986).

Genetic studies have shown that partial resistance is polygenically inherited (Parlevliet, 1978; Parlevliet and Kuiper, 1985; Johnson & Wilcoxson, 1979). It has also been shown that the most important components of partial resistance (infection frequency and latent period) are controlled by the same polygenes indicating that partial resistance is predominantly governed by the genes controlling pleiotropically latent period and infection frequency (Parlevliet, 1986).

In partially resistant cultivars the development of the infection units up to the formation of haustorium mother cells is the same as in hypersensitivity resistance. But after this stage a fairly high proportion of the haustorium mother cells are unable to produce a haustorium in the host cells to be penetrated because the host cells formed a cell wall thickening preventing the penetration, pre-haustorial resistance (Niks, 1982, 1986). For this reason a considerable proportion of the host cell penetration attempts fail, the number of colonies that can form visible pustules will be reduced, while the time needed for such pustules to appear increases due to the reduced growth, causing longer latent periods (Niks, 1986; Parlevliet, 1995).

The partial resistance in barley to barley leaf rust is highly durable. Parlevliet (1985)

showed that several cultivars (such as Hasso, Julia and Vada) have been cultivated in Europe for many years without any erosion of the partial resistance they carry.

Although, the partial resistance in barley to barley leaf rust is polygenic and durable it can not be classified as non-race-specific, because Parlevliet (1977) showed that there are small differential interactions for partial resistance to barley leaf rust isolates. These small differential interactions are by no means restricted to this pathosystem. They seem to occur in many pathosystems (Parlevliet, 1985).

Breeding for partial resistance

Many plant breeders often think that selection for polygenic or partial resistance is difficult, time consuming and less attractive than monogenic resistance. Parlevliet and co-workers studied selection methods for partial resistance in barley to leaf rust. From these studies they concluded that selection for partial resistance at all plant stages was effective; in the seedling stage in the greenhouse, in the adult plant stage in the greenhouse and in the field. In the field single plant selection and selection in small plots were highly effective (Parlevliet et al., 1980; Parlevliet and Kuiper, 1985). Selection for a longer latent period in the greenhouse after crossing Vada with Cebada Capa, both with a considerable level of partial resistance, resulted in lines with a latent period and partial resistance far beyond that of Vada (Parlevliet et al., 1985; Parlevliet and Kuiper, 1985). Line 17-7-16 is one of those lines which gets hardly affected by barley leaf rust in the field (Parlevliet, 1995).

In the field selection for partial resistance appeared very successful. In two unrelated populations, that were genetically highly variable, selection was carried out first on single plants followed by selection among lines of the selected plants. The best lines were then intercrossed in all directions within the populations. Again F2 plant and F3 line selection was done. The best lines of each population were intercrossed between populations and again F2 plant and F3 line selection was carried out. At each stage the selection consisted of only removing the 30% most diseased plants or lines, a very mild selection (Parlevliet and Van Ommeren, 1988a). This was actually selection against susceptibility, rather than selection for resistance. This allows at the same time the selection for other agronomic characters. At the end of this selection programme several lines more resistant than Vada

were obtained (Parlevliet and Van Ommeren, 1988b). Parlevliet (1983b) also reported that selection for partial resistance depends on the host-pathosystem. If the heritability of partial resistance is fairly high (barley-*P. hordei*, oats-*P. coronata*, etc.) selection is not difficult. In other situations where the heritability of partial resistance is lower one cannot select efficiently on a single plant basis (eg. potato-leaf roll virus).

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Chapter 7

Variation of Resistance to *Puccinia Hordei* in Ethiopian Barley Landraces

Summary

In the spring of 1990 single plant derived lines of 18 Ethiopian barley landraces were evaluated in the greenhouse for infection type and latent period, the major component of partial resistance.

In the adult plant stage 1227 landrace lines and at the seedling stage 1722 landrace lines were assessed for infection type. In both plant stages no effective major resistance genes to barley leaf rust could be found and the multiline principle that might give these landraces durable resistance to barley leaf rust does not operate. On the other hand, the variation between and within the landraces for latent period was large. Some landraces such as landrace 212845 showed a highly significant and longer latent period than most other landraces. All landraces carry some partial resistance.

Resistance to barley leaf rust in Ethiopian barley landraces therefore seems predominantly if not fully of the partial resistance type that could give these landraces their durable resistance to barley leaf rust.

Introduction

Barley leaf rust, *Puccinia hordei,* is one of the important diseases of barley (*Hordeum vulgare)* in many areas of the world. Genetic resistance in the host has been found the best means to control this disease. Two types of resistance are recognised in barley to leaf rust; the major genic, hypersensitive type of resistance, which results in death of host cells at some stage during hyphae colonization and characterised by a lower infection type, and the polygenic, non-hypersensitive type of resistance, characterised by fewer and smaller urediosori of a susceptible type (Roane, 1962; Parlevliet, 1978). In the former several genes (Pa - Pa9) for barley leaf rust resistance have been identified but most of these genes have become ineffective, while the latter, partial resistance, provides a more durable resistance (Parlevliet, 1983). Many different genes are necessary for any

resistance breeding programme. One possibility to get these genes is from centres of high genetic diversity to augment the narrow genetic base of modern barley cultivars. Landraces have been studied as a good source of major resistance genes but hardly as a good source of partial resistance. Studying landraces also could provide a good chance of understanding whether the multiline (mixture) effect or partial resistance plays a role in the durable resistance of landraces to barley leaf rust.

Parlevliet and Moseman (1986) studied 244 Ethiopian barley landrace lines for partial resistance to barley leaf rust and reported a fairly high level of partial resistance in some lines under field and greenhouse conditions. These lines were not traceable to identifiable landraces and could not answer how landraces are protected against leaf rust. For this reason a set of Ethiopian barley landraces was studied at the WAU, the Netherlands, for resistance between 1990 and 1992 under greenhouse conditions.

Materials and Methods

Eighteen barley landraces, supplied by the Plant Genetics Resources Centre of Ethiopia (PGRC/E), and represented by up to 100 single plant derived lines each, were used in this study. These landraces were collected during the years from 1978 to 1985 from a range of altitudes (1960 - 2900 m.a.s.l.) in six barley growing regions of Ethiopia. In the spring of 1990 the 18 landraces were sown in the greenhouse for assessment of resistance.

Plants were sown in plastic pots and per line five plants were raised. L94, an extremely susceptible, and Vada, a partially resistant barley cultivar, were also planted at weekly intervals to ensure the availability of plants at approximately equal heading stage with the landrace lines to be studied. The barley leaf rust race 1.2.1 was used for this study. This race is virulent on the race-specific major genes Pa, Pa2, Pa4, Pa5, Pa6, and Pa8 and avirulent on the Pa3, Pa7 and Pa9 (Parlevliet, 1983). For each series fresh spores were used. After collection the spores of this race were kept overnight in an exsiccator before inoculation.

Plants in the young flag leaf stage (plants just heading), including L94 and Vada plants, were inoculated in 34 consecutive series and observations were taken on 25 tillers per line. Plants in each series were inoculated according to Parlevliet (1975) by dusting a mixture of urediospores and lycopodium spores over the plants. The inoculated plants

were incubated overnight at a relative humidity of 100% for about 12 hrs. During the period between inoculation and observation day temperatures in the greenhouses varied from 20-26°C and during the night from 10-12°C.

From one week after inoculation, the latent period, the major component of partial resistance, was measured according to Parlevliet (1975) by assessing the moment that 50% of the ultimate urediosori became visible. The actual latent period (LP) in days was converted into a relative latent period (RLP) taking the LP of L94 and Vada as 100% and 185 % respectively.

The infection type (IT) was recorded 2 to 3 days after the LP was determined, mostly from the flag leaves but in some cases also from leaves next to the flag leaves according to the 0-9 scale of McNeal et al. (1971), which is expressed as 0= no visible symptoms; 1-3= resistant (R); 4-5= moderately resistant (MR); 6-7= moderately susceptible (MS); 8-9= susceptible (S). Following the same procedure the 18 landraces were also assessed for seedling resistance using two barley leaf rust races, race 1.2.1 and race A, race A carrying fewer virulence factors than race 1.2.1.

Results

The ranges, means and standard deviations of the mean relative latent period of the 18 barley landraces are shown in Table 1. All landraces had some to fair levels of partial resistance as they had a mean LP highly significantly larger than L94. The landraces differed significantly among each other. All landraces, except 3441 were more resistant than landrace 208040 and landrace 212845 was significantly more resistant than all the other landraces with the exception of 3432. Table 2 shows that there was also considerable variation in the LP within landraces.

The IT of the 18 landraces at the seedling and adult plant stage are presented in Tables 3, 4 and 5. The majority of the landrace lines in the seedling as well as in the adult plant stage had a very high IT with race 1.2.1 (Tables 3 and 5). Only a very few lines had an IT lower than 7, and none had an IT lower than 5. To race A slightly more, but still less than 2%, had an IT below 7. Mean Infection types in the seedling stage varied from 8.7 for 212938 to 9.0 for all landraces (Table 3). In the adult plant stage the mean IT varied from 8.2 for 218850 to 9.0 (Table 5). With leaf rust race A the seedlings of the 18 barley landraces showed similar mean infection types ranging from 7.7 to 9.0 (Table 4).

Table 1. Range, mean and standard deviation (SD) of the mean latent period for barley leaf rust, race 1.2.1 on 18 barley landraces assessed at the flag leaf stage.

	Relative latent period			
Landrace	Range	Mean	SD of the mean	No. of lines
L94	--	100.0	0.00	81*
208040	99-142	113.7	1.04	78
3441	106-130	116.1	0.72	56
208038	103-146	117.9	1.11	76
212840	103-139	120.4	1.11	72
1829	109-133	120.6	0.90	56
3292	105-152	123.5	0.84	78
218957	108-136	125.1	0.54	79
212959	103-149	125.3	1.16	74
208852	98-159	125.3	1.32	72
208925	111-141	126.8	0.77	78
3288	106-188	127.6	1.71	63
3252	111-149	128.2	0.97	58
218850	110-159	128.6	1.05	78
1726	96-160	128.9	1.39	70
212938	105-163	129.4	1.09	77
3448	106-153	131.5	1.29	59
3432	122-161	139.7	1.29	50
212845	112-171	142.1	2.02	53

* Number of plants of L94 observed over the series.

Table 2. Distribution of the barley landrace lines in nine relative latent period classes to barley leaf rust, race 1.2.1, with a class interval of 10 units

Land race	Relative latent period									Mean
	95.5 105.5	105.6 115.5	115.6 125.5	125.6 135.5	135.6 145.5	145.6 155.5	155.6 165.5	>165.6	N	
208040	13	36	21	5	3	--	--	--	78	113.7
3441	--	28	25	3	--	--	--	--	56	116.1
208038	5	31	24	11	3	1	--	--	75	117.7
212840	7	14	23	24	4	--	--	--	72	120.4
1829	--	14	30	12	--	--	--	--	56	120.6
3292	1	7	47	16	6	1	--	--	78	123.5
212959	2	8	27	25	10	1	--	--	73	125.0
218957	--	1	37	40	1	--	--	--	79	125.1
208852	1	13	28	19	7	2	2	--	72	125.3
208925	--	2	29	37	10	--	--	--	78	126.8
3288	--	5	28	21	5	1	--	3	63	127.6
3252	--	2	19	25	11	1	--	--	58	128.2
218850	--	3	27	34	13	1	--	--	78	128.6
1726	1	7	16	34	7	1	4	--	70	128.9
212938	1	2	21	40	9	1	3	--	77	129.4
3448	--	2	16	21	17	3	--	--	59	131.5
3432	--	--	3	15	20	9	3	--	50	139.7
212845	--	1	6	12	13	11	6	4	53	142.1
Total	31	176	427	394	139	33	18	7	1225	

Table 3. Distribution of barley landrace lines according to their infection type to barley leaf rust, race 1.2.1 at the seedling stage in the greenhouse.

Land race	Infection Type										N	Mean
	0	1	2	3	4	5	6	7	8	9		
212938	--	--	--	--	--	1	--	12	--	87	100	8.7
212840	--	--	--	--	--	--	--	12	--	88	100	8.8
3432	--	--	--	--	--	--	--	1	--	98	99	8.9
1726	--	--	--	--	--	--	--	2	--	98	100	8.9
3288	--	--	--	--	--	--	--	2	--	98	100	8.9
3292	--	--	--	--	--	1	--	--	--	99	100	8.9
208038	--	--	--	--	--	--	--	--	3	97	100	8.9
218957	--	--	--	--	--	--	--	--	--	50	50	9.0
3252	--	--	--	--	--	--	--	--	--	100	100	9.0
3448	--	--	--	--	--	--	--	--	--	100	100	9.0
208925	--	--	--	--	--	--	--	--	--	100	100	9.0
212845	--	--	--	--	--	--	--	--	--	100	100	9.0
1829	--	--	--	--	--	--	--	--	--	100	100	9.0
208852	--	--	--	--	--	--	--	--	--	100	100	9.0
218850	--	--	--	--	--	--	--	--	--	100	100	9.0
208040	--	--	--	--	--	--	--	--	--	100	100	9.0
212959	--	--	--	--	--	--	--	--	--	100	100	9.0
3441	--	--	--	--	--	--	--	--	--	72	72	9.0
Total	--	--	--	--	--	2	--	29	3	1687	1721	
C.C.*												1.1
L94												9.0

* Cebada Capa

Table 4. Distribution of barley landrace lines according to their infection type to barley leaf rust, race 'A,'at the seedling stage in the greenhouse.

Land race	Infection Type										N	Mean
	0	1	2	3	4	5	6	7	8	9		
212938	--	--	--	--	--	--	--	11	10	79	100	7.7
3288	--	--	1	4	7	--	--	--	3	85	100	8.3
3252	--	--	--	1	--	9	--	--	--	90	100	8.5
3292	--	--	--	2	3	2	--	--	2	91	100	8.6
212840	--	--	--	--	--	--	--	3	12	85	100	8.8
218957	--	--	--	--	--	--	--	--	8	42	50	8.8
208038	--	--	--	--	--	--	--	--	2	98	100	8.9
3448	--	--	--	--	--	--	--	--	2	98	100	8.9
3432	--	--	--	--	--	--	--	--	4	96	100	8.9
208925	--	--	--	--	--	--	--	--	2	98	100	8.9
212845	--	--	--	--	--	--	--	--	4	96	100	8.9
1726	--	--	--	--	--	--	--	--	--	100	100	9.0
1829	--	--	--	--	--	--	--	--	3	97	100	8.9
208852	--	--	--	--	--	--	--	--	--	100	100	9.0
218850	--	--	--	--	--	--	--	--	--	100	100	9.0
208040	--	--	--	--	--	--	--	--	--	100	100	9.0
212959	--	--	--	--	--	--	--	--	--	100	100	9.0
3441	--	--	--	--	--	--	--	--	--	72	72	9.0
Total	--	--	1	7	10	11	--	14	52	1627	1722	
C.C.*												1.1
L94												9.0

* Cebada Capa

Table 5. Distribution of barley landrace lines according to their infection type to barley leaf rust, race 1.2.1, at the adult plant (flag leaf) stage in the greenhouse.

Land race	Infection Type											Mean
	0	1	2	3	4	5	6	7	8	9	N	
218850	--	--	--	--	--	--	8	9	17	44	78	8.2
208852	--	--	--	--	--	--	--	--	40	32	72	8.4
3252	--	--	--	--	--	--	--	--	19	39	58	8.7
218957	--	--	--	--	--	--	--	--	19	60	79	8.7
1726	--	--	--	--	--	--	3	--	4	63	70	8.8
1829	--	--	--	--	--	--	1	--	6	49	56	8.8
212938	--	--	--	--	--	--	--	1	11	65	77	8.8
3432	--	--	--	--	--	--	--	1	6	43	50	8.8
3292	--	--	--	--	--	--	--	--	12	66	78	8.8
208925	--	--	--	--	--	--	--	--	14	64	78	8.8
212845	--	--	--	--	--	--	--	--	4	49	53	8.9
212959	--	--	--	--	--	--	--	--	10	64	74	8.9
3441	--	--	--	--	--	--	--	--	7	49	56	8.9
3288	--	--	--	--	--	--	--	--	3	60	63	8.9
208038	--	--	--	--	--	--	--	1	1	74	76	8.9
3448	--	--	--	--	--	--	--	--	--	59	59	9.0
212840	--	--	--	--	--	--	--	--	--	72	72	9.0
208040	--	--	--	--	--	--	--	--	1	77	78	9.0
Total	--	--	--	--	--	--	12	12	174	1029	1227	

Discussion

Parlevliet and Van Ommeren (1975) and Parlevliet et al. (1985) showed that LP in the adult plant stage is very highly correlated with partial resistance in the field, r being 0.92 to 0.97. This means that the LP in the adult plant stage is a very good estimator of partial resistance.

The LP varied considerably between and within landraces and all landraces carried at least some partial resistance. Genotypes (landrace lines) without any partial resistance and so having a LP similar to that of L94 (=100%) were quite rare, only some 3% (Table 2).

And the resistance found in these landraces is nearly all of the partial resistance type as defined by Parlevliet and Van Ommeren (1975). They defined partial resistance as a reduced epidemic build up (longer LP) despite a high, susceptible IT. In this sense only 12, out of the 1227 (1%) could not be classified as being partially resistant (Table 5).

If major resistance genes were present, and effective, a much higher proportion of lines with low IT's such as Cebada Capa (Tables 3 and 4) would have been found. Resistance to barley leaf rust in Ethiopian barley landraces therefore seems to be predominantly if not fully of the partial resistance type. It is this partial resistance that appears to give these landraces their durable resistance to barley leaf rust.

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Chapter 8

Virulence of *Puccinia Hordei* on Barley in Ethiopia.

Summary

The virulence patterns of five barley leaf rust cultures were studied in 1992 on the seedlings of the differential series of 11 barley cultivars together carrying nine Pa-genes. Of 21 barley entries, most of which representing individual lines derived from 14 Ethiopian barley landraces the reaction to those five cultures was determined.

The five cultures of *Puccinia hordei* were not virulent on seedlings of barley cultivars carrying the resistance genes Pa3 and Pa7. Sudan and Armelle, both carrying the Pa gene, were resistant to Isolate 2. Gold, reportedly carrying Pa4, was susceptible to all isolates. Cultivars with Pa2, Pa2 + Pa5, Pa2 + Pa6, Pa8 and Pa9 showed an intermediate infection type to certain isolates and a susceptible one to others.

The virulence patterns of the Ethiopian leaf rust isolates seem similar to those in Europe.

All five cultures were virulent on the seedlings of the Ethiopian barleys indicating the absence of effective major gene resistance in these barleys against *Puccinia hordei*.

Introduction

Virulence in barley leaf rust, caused by *Puccinia hordei* Otth., its importance, and the genetics of host resistance have been studied in several countries (Moseman & Greeley, 1965; Johnson, 1968; Roane & Starling, 1970; Brückner, 1972; Clifford, 1974; Rintelen, 1975; Anikster et al., 1975, 1976; Parlevliet, 1976; Clifford & Udeogalanya, 1976; and Tan, 1976).

Barley leaf rust was first reported in Ethiopia by Stewart and Dagnachew (1967). It is prevalent especially in lower altitude areas of the country where it can cause economic losses. At higher altitudes the disease seems less important because disease epidemics occur late in the season (personal observation). Very little is known about its virulence.

In November 1992 four barley leaf rust cultures were collected from local barley

cultivars in Ethiopia. The purpose of this study was to determine the virulence spectra of these cultures and also to compare these cultures with the leaf rust race that is most frequently found in Europe and also elsewhere (Parlevliet, 1983).

Materials and Methods

Inoculum. The test cultures of *Puccinia hordei* were collections from four locations of Ethiopia (Asasa and Bekoji in the Arsi and Holeta and Sheno in the Shewa regions with altitudes 2350, 2670, 2400, and 2800m respectively). Not all leaf samples were studied for possible variation in the fungus within a location; but only single-spore isolates derived from a single leaf sample representing an individual location were used. The four single-spore isolates were maintained and increased at Wageningen on L98, a highly susceptible barley cultivar. The collections were done by Mr Yitbarek Semeane and Berhane Lakew of IAR, Ethiopia.

Barley leaf rust races from Europe were represented by race 1.2.1 which has a wide virulence spectrum, carrying virulence to the resistance genes Pa, Pa2, Pa4, Pa5, Pa6 and Pa8 (Parlevliet, 1983).

Hosts. Seed of the 11 differential cultivars (Table 1) carrying the currently known genes for resistance to barley leaf rust, was provided by the Department of Plant Breeding of the Wageningen Agricultural University (WAU), the Netherlands. Nineteen Ethiopian landrace lines selected from 1800 landrace lines and representing 14 landraces and L94 and Vada were used in this study as well.

Inoculation and evaluation. Five to seven seedlings per entry were raised in flats. Per flat 15-20 entries were sown. Inoculation was carried out by dusting fresh urediospores over the seedlings when the second leaf of the seedlings had fully emerged. The spores were diluted 10 times with lycopodium spores before inoculation. After inoculation seedlings were kept overnight in complete darkness and at 100% R.H. to allow spore germination and infection to occur. After this incubation the flats were transferred to greenhouse benches and kept at 18-22°C.

Seedlings were evaluated for their infection type to the five leaf rust cultures 10-14 days after inoculation and when urediosori had formed. Infection types (IT) were classi-

fied according to the scale of McNeal et al. (1971) where IT 0 = no visible symptoms; 1-3 = resistant; 4-5 = Moderately resistant; 6-7 = moderately susceptible and 8-9 = susceptible.

Results

Table 1 shows the reaction of all 32 barley entries to the five isolates. The cultivars, Ribari and Cebada Capa, with Pa3 and Pa7 respectively, were resistant to all isolates. This shows the effectiveness of these genes to these isolates. Sudan and Armelle were resistant to isolate 2 indicating that the Pa gene found in the two cultivars is effective. Gold, Sundance, L94, Vada and all landrace lines from Ethiopia showed a highly susceptible infection type to all isolates, except line 725 to isolate 4. Certain cultivars, Armelle, Bolivia, Peruvian, Quinn and CI 1243 showed intermediate resistance (MR) to one or more isolates used in this study. Cultivars Peruvian and Bolivia took 2 to 3 days more to sporulate with isolates 1.2.1 and 2 when compared with the other entries infected with the same isolates. The IT of the two cultivars for these two isolates was a susceptible one.

The IT's of the differential cultivars with the five isolates are shown separately in Table 2. The Ethiopian races had a virulence spectrum ranging from very similar to 1.2.1 (race 1) to a slightly less wide virulence spectrum (race 4) to a clearly more narrow virulence spectrum (races 2 and 3).

Table 1. Reaction of 32 barley cultivars/lines to five isolates of *Puccinia hordei*; 1-11 are differential cvs; 12-29 are Ethiopian landrace lines; 30-31 are control cvs. R= resistant, MR= moderately resistant, MS= moderately susceptible, S= susceptible.

Entry No.	cultivar/line	Isolate 1.2.1	1	2	3	4
1	Ribari	R	R	R	R	R
2	Cebada capa	R	R	R	R	R
3	Sudan	S	S	R	S	S
4	Peruvian	S*	S	S*	MR	MR
5	Quinn	S	MS	MS	MR	MR
6	Bolivia	S*	S*	S*	MR	MR
7	Armelle	S	S	R	MR	MR
8	Egypt 4	MS	MS	MR	MS	S
9	CI 1243	MS	MS	S	MR	S
10	Gold	S	S	S	S	S
11	Sundance	S	S	S	S	S
12	35	S	S	S	S	S
13	102	S	S	S	S	S
13	137	S	S	S	S	S
14	288	S	S	S	S	S
15	320	S	S	S	S	S
16	435	S	S	S	S	S
17	439	S	S	S	S	S
18	570	S	S	S	S	S
19	629	S	S	S	S	S
20	645	S	S	S	S	S
21	725	S	S	S	S	MR
22	880	S	S	S	S	S
23	913	S	S	S	S	S
24	915	S	S	S	S	S
25	1055	S	S	S	S	S
26	1242	S	S	S	S	S
27	1248	S	S	S	S	S
28	1341	S	S	S	S	S
29	1620	S	S	S	S	S
30	L94**	S	S	S	S	S
31	Vada**	S	S	S	S	S

* Reactions that show a 2 to 3 day delay of sporulation.

** These cultivars do not carry any identified or unidentified major resistance gene but represent a wide range in partial resistance.

Table 2. Reaction of differential barley cultivars to five isolates of *Puccinia hordei*. R= resistant, MR= moderately resistant, MS= moderately susceptible, S= susceptible.

		Isolate*				
Cultivar	Gene	1.2.1	1	2	3	4
Sudan	(Pa)[1]	S	S	R	S	S
Peruvian	(Pa2)[3]	S**	S	S**	MR	MR
Ribari	(Pa3)[4]	R	R	R	R	R
Gold	(Pa4)[1]	S	S	S	S	S
Quinn	(Pa2+5)[1]	S	MS	MS	MR	MR
Bolivia	(Pa2+6)[2]	S**	S**	S**	MR	MR
Cebada Capa	(Pa7)[5]	R	R	R	R	R
Egypt 4	(Pa8)[6]	MS	MS	MR	MS	S
CI 1243	(Pa9)[7]	MS	MS	S	MR	S
Armelle	(Pa+Pa2)[8]	S	S	R	MR	MR
Sundance	(Pax)[8]	S	S	S	S	S

* 1.2.1 is an isolate from the Netherlands and isolates 1 to 4 are Ethiopian isolates (1 = Asasa; 2 = Bekoji; 3 =Sheno; and 4 = Holetta).

** Reactions that show a 2-3 day delay of sporulation

[1] Roane and Starling (1967)
[2] Roane and Starling (1970)
[3] Starling (1956)
[4] Brückner (1971).
[5] Parlevliet (1976)
[6] Tan (1977)
[7] Clifford and Jones (1981).
[8] Parlevliet (1983)

Table 3. Reaction of 1750 barley lines from Ethiopia to isolate 1.2.1 of the barley leaf rust in seedling and flag leaf stages (see Chapter 7). R= resistant, MR= moderately resistant, S= susceptible.

Reaction class	Barley entries	
	Seedling	Flag leaf*
R	0	0
MR	2	22
S	1750	1205

* Not all lines were tested.

Discussion

Of the currently known resistance genes from cultivated barley only Pa3 and Pa7 were effective against all isolates studied. This is in agreement with the observations reported by others; Pa3 and especially Pa7 are effective to most races. Studies in different countries such as in USA (Roane and Starling,1967), England (Clifford, 1974), Germany (Rintelen, 1976), Israel (Anikster et al., 1976), and the Netherlands (Parlevliet, 1976) showed that Pa7 in Cebada Capa has been effective to all cultures of the barley leaf rust worldwide. However, there are a few reports which indicate that some cultures, isolated from the alternate host (*Ornithogalum* spp.) in Israel, were virulent on seedlings of these cultivars (Clifford & Udeogalanya, 1976; Golan et al., 1978). Parlevliet (1983) also reported one isolate, among 30 isolates he studied that was virulent to Pa7 and several others that were virulent to Pa3. Of the Ethiopian isolates, isolate 1 is more virulent than the others and much closer to 1.2.1 in its pattern of virulence. Isolates 3 and 4 seem very similar in their virulence spectra. They are moderately virulent to several differential cultivars. The virulence patterns of the Ethiopian isolates were not basically different from those reported from Europe.

Ethiopian barleys did not express any resistance reaction to any of the isolates, except line 725 which gave an intermediate IT to isolate 4. This suggests the absence or near-absence of major resistance genes in Ethiopian barleys against *Puccinia hordei*. This

result agrees with previous study on over 1700 Ethiopian barley landrace lines that did not show any major race-specific resistance genes after infecting them with barley leaf rust race 1.2.1 at both seedling and flag leaf stages (Table 3). Since the Ethiopian and the European races are not basically different from each other the testing of the 1700 landrace lines with a European isolate was therefore quite representative for what one can expect in Ethiopia.

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Chapter 9

Inheritance of Resistance to Leaf Rust in Ten Partially Resistant Ethiopian Barley Landrace Lines.

Summary

The inheritance of partial resistance to barley leaf rust, *Puccinia hordei,* in ten Ethiopian barley landrace lines was studied using 38 crosses among the partially resistant lines, between the lines and L94, a highly susceptible cultivar with no known resistance genes, and between the lines and Vada, a partially resistant cultivar with 5 to 6 minor genes.

The progenies at F1, F2, and F3 or F4 were assessed for the latent period (LP) in the young flag leaf stage, which is the major component of partial resistance. In the F1 most crosses showed an intermediate or recessive inheritance, except three crosses which showed dominance. In the F2 nearly all crosses showed clear segregation, the plant values ranging from those of the low to those of the high parent and beyond. In most crosses significant transgression was observed. This was confirmed in the F3 or F4 progenies.

The generation mean analysis for 19 crosses, where comparable parental, F1 and F2 data were available, showed that in four crosses (L94 x 645; 288 x Vada; 439 x 1242 and 915 x 1242) no epistasis was present, while in the others some epistasis appeared to occur.

Introduction

Partial resistance to barley leaf rust, *Puccinia hordei,* is a form of quantitative resistance, which is characterized by a reduced epidemic build-up in spite of a susceptible infection type (Parlevliet & Van Ommeren, 1975). It is caused by a reduced infection frequency, a longer latent period, a reduced rate of spore production per lesion and a shorter infectious period (Neervoort & Parlevliet, 1978). Partial resistance was thought to be race-non-specific and polygenic in nature (Van Der Plank, 1963; Robinson, 1976).

Partial resistance has been previously studied and described (Clifford, 1972; Parlevliet, 1975; Parlevliet and Ommeren, 1975; Parlevliet & Kuiper, 1977; Neervoort & Parlevliet,

1978). Barley cultivars vary greatly in the level of partial resistance they carry (Parlevliet & Van Ommeren, 1975; Parlevliet 1976a) and also the various components of partial resistance vary considerably (Parlevliet, 1975; Parlevliet & Kuiper 1977, Neervoort & Parlevliet, 1978). The cultivar effects on partial resistance in the field appeared very strongly correlated (r = 0.92 to 0.97) with the latent period (LP) in the young flag leaf stage (Parlevliet & Van Ommeren, 1975; Parlevliet et al., 1985). Parlevliet (1986) also showed that infection frequency and LP are pleiotropically controlled by the same genes. This, together with the fact that partial resistance in the field and LP are so strongly correlated, makes LP a very good estimator of partial resistance. Parlevliet (1977) also showed that LP can be measured with much greater accuracy than the other components of partial resistance and than partial resistance itself. Because of that Parlevliet (1976b) studied the inheritance of LP in two very susceptible cultivars, L94 and L92, and in two partially resistant cultivars, Minerva and Vada by analyzing the F1's, and their F2 and F3 progenies. The LP's on the young flag leaves of the four cultivars were 8.0, 8.6, 16.9 and 17.1 days respectively. L94 was assumed to carry no genes (alleles) for a longer LP. The long LP of Minerva and Vada, assuming no linkage, was thought to be effectuated by the cumulative action of several genes (alleles). He also showed that the genetic effects appeared largely of an additive nature, with some dominance for shorter LP. Epistasis or gene interaction was either absent or insignificant compared with the additive and dominance effects. Parlevliet (1978) continued with these studies using L94 and four cultivars with different levels of partial resistance again by analyzing their F1's, F2's, and F3's. These studies confirmed that the genes are acting predominantly additively with some dominance for short LP (for the - alleles). Vada was thought to carry 5 to 6 polygenes for a longer LP.

Studies on Ethiopian barley landraces indicated considerable differences in partial resistance to leaf rust (Parlevliet and Moseman, 1986; chapter 7). Nearly all landrace lines had a high IT (8-9 on the 0-9 scale).

To study the inheritance of the partial resistance in the Ethiopian barley landraces, ten landrace lines with varying levels of partial resistance were intercrossed and crossed with the highly susceptible cultivar L94 and the partially resistant cultivar Vada.

Materials and Methods

The ten barley landrace lines used in this study with their LP relative to that of L94 are shown in Table 1. Cultivar L94 was used in the crosses because it is assumed to carry no genes for increased LP to leaf rust while cultivar Vada carries 5 to 6 minor genes for increased LP (Parlevliet, 1978).

Table 1. Ten Ethiopian barley landrace lines used as parents with their infection type (IT) after inoculation with two leaf rust races, 1.2.1 and A and the latent period (LP), relative to L94 = 100 and Vada = 193 in the young flag leaf stage.

Landrace line		IT		LP	
		1.2.1	A	1992	1994
L94		S	S	100.0	100.0
35	(3252)[1]	S	S	131.0	125.1
435	(3432)	S	S	143.7	152.6
439	(3432)	S	S	144.0	155.7
629	(3288)	S	S	165.4	162.1
645	(3288)	S	S	-	127.1
288	(212938)	S	S	177.3	164.5
913	(212845)	S	S	-	160,2
915	(212845)	S	S	167.6	175.6
1242	(218850)	S	S	141.7	126.5
1248	(218850)	S	S	123.7	129.5

[1] Landrace from which the corresponding line was derived.

In 1991 the lines were crossed each to L94 and Vada and crossed to each other at WAU. Certain lines were unable to produce the required F1 seed especially when the lines were intercrossed with each other probably due to the high temperatures that occurred during the crossing. The Ethiopian landraces evolved in a cool climate and might be more sensitive to such high temperatures as far as the production of viable pollen or egg cells is concerned. So, only 28 F1's were successfully obtained, but the number of F1 seed was so small that nearly all of it was used to advance to the F2. So it

was necessary to make F1 crosses (38 in total) in 1993 again.

In 1992 of each of the parental landrace lines and L94 and Vada 10 to 15 plants were sown at weekly intervals to have them available at each inoculation series. Of the crosses available 60 or more F2 plants and up to 10 F1 plants were raised in 12 x 12 cm plastic pots in the greenhouse. Of all F2 plants assessed seed was harvested and F4's through the single seed descent procedure produced. Of some crosses only the F3 was produced.

In 1994 the same procedure was followed. The parental landrace lines and L94 and Vada were sown at weekly intervals in 12 x 12 cm plastic pots, 10 to 15 plants per week per parent. Of each F3 or F4 about 100 plants were grown. The plants were inoculated with leaf rust race 1.2.1 at the young flag leaf stage. Plants with a similar flag leaf stage were placed in an inoculation compartment to be inoculated. The spores (1.0 mg per plant) were then dusted over the leaves with the aid of a cyclone duster. To obtain a more even distribution the spores were diluted about 20 times with Lycopodium spores. After this inoculation the plants were incubated at 100% r.h overnight for at least 12 hr. The next morning the plants were transferred to a greenhouse compartment with day temperatures varying from 18-25°C and night temperatures from 15-18°C.

Due to the fact that the F2's, F3's and F4's segregated for heading date and the crosses differed in mean heading date the plants of a cross did not reach the inoculation stage (the young flag leaf stage) at the same time. So, every few days, those plants that were in the right stage, were collected across the various crosses, and placed in the inoculation compartment together with plants of the parents of the crosses in that series, L94 and Vada in the same young flag leaf stage. In order to obtain a good LP assessment the plants must be in similar stage as the LP decreases with increasing age of the plant and flag leaf (Parlevliet, 1975). Because the temperatures to which the inoculated plants were exposed between inoculation (= infection) and assessment, some 7 to 17 days later, varied and so affected the LP (Parlevliet, 1975), all observations measured in days from inoculation were transformed into relative values, relative to the LP values of L94 (set at 100) and of Vada (set at 193) in the same series. In this way the relative LP of the plants in the various series became comparable. This is confirmed by comparing the mean of the relative LP's of the parental Ethiopian landrace lines obtained in 1992 with those from 1994. The values were 149.3 and 149.0 respectively (Table 1).

The LP of each plant was evaluated by estimating the moment at which 50% of the

ultimate number of the urediosori became visible (Parlevliet, 1975; 1976b). At this moment nearly all successful infections are visible, either as young brown urediosori or as light specks, in the middle of which the urediosorus will develop. The evaluation was done in the middle part of the flag leaves of several tillers of each plant. As the LP is affected by the age of the leaf (Parlevliet, 1975) very young and old leaves were excluded from consideration.

Results

The relative LP of the 12 parents ranged from 100 (L94) to 193 (Vada) with those of the Ethiopian landrace lines ranging in between (Table 1). The mean relative LP of those parents during 1992 and 1994 were strongly correlated ($r = 0.92$) even when the Vada value of 193 was not considered.

Table 2 presents the F1 values relative to those of their parents and to the mid-parent value. The majority of the crosses showed an F1 value similar to the mid-parent value or smaller. Only in three crosses the F1 value was significantly larger than the mid-parent value. These three crosses were those between the lines 35, 629 and 915.

In some crosses the F1 was even considerably lower than the most susceptible (least resistant) parent (288 x 629; 439 x 629; 439 x Vada) or higher (629 x 915) than the least susceptible (most resistant) parent. The F1 values of line 439 x Vada and of lines 629 x 915 were significantly ($P < 0.01$ and 0.05 respectively) beyond the low and the high parent respectively, the other two F1 values were close to significantly lower than the low parent.

Table 3 gives the frequency distributions of the parents, F1, F2 and F3 or F4 values available. Of 28 crosses F2 or F2 and F3 or F4 data were available. In most crosses segregation was observed in the F2 and later generations as the variance was larger than the variance of the parents and the variance of the F1. Of the 28 crosses nine crosses were with L94, 12 among the landrace lines and seven between landrace lines and Vada. Two of the nine crosses with L94 showed evidence of transgression. Of the 12 crosses among the landrace lines nine had transgressive segregation. Among the crosses with Vada only one cross (with line 1242) did not give clear indications of transgressive segregation. It was decided to speak of transgressive segregation when in the F2, F3, or

F4 individuals were observed, that were at least two relative LP classes beyond the range of either parent.

Table 4 shows the data of 19 crosses of which Parental, F1, and F2 data had been obtained. On these data the generation mean analysis can be carried out. In case of absence of epistasis the total of $4\bar{F}_2 - 2\bar{F}_1 - \bar{P}_1 - \bar{P}_2$ should not differ significantly from zero. Of the 19 crosses this was the case with 4 crosses. The other 15 crosses showed values, that albeit not large, deviated significantly from zero.

Discussion

Most crosses showed intermediate to recessive inheritance for partial resistance just as Parlevliet (1976, 1978) observed. The deviation in the crosses between the lines 35, 629, and 915 are not easy to explain. From the data one might conclude that especially line 35 carries dominant alleles for a longer LP. If so the genes carried by line 35 should be different from those of other lines such as those of the lines 435 and 1248 where F2 data are available. In the cross with 1248 transgressive segregation was observed, as expected if the genes differ, but not so in the cross with 435. The data therefore are not unambiguous. That the F1 was in some cases beyond the extreme parent is quite possible if the inheritance is of a recessive or dominant nature. It means that the two parents have alleles for resistance at different loci, and that this occurs is corroborated by the high frequency of transgressive segregation in various crosses between parents with partial resistance.

The high frequency of transgressive segregation in crosses between landrace lines (nine out of 12) means that these lines were at least partly carrying resistance alleles at different loci, and these loci were apparently for a good deal different from those in Vada as especially with Vada transgressive segregation was observed. The transgressive segregation, although little, in the crosses with L94 was not expected as it was assumed that L94 did not carry any partial resistance. This may not be true; L94 might harbour a minor gene for a longer LP. From recent research at the Plant Breeding Department of WAU similar indications came forward (Parlevliet, personal communication).

The data in table 4 suggest some epistasis. This epistasis may have different causes. Parlevliet (1976, 1978) already suggested some reasons for such apparent epistasis. One of the reasons he described was that the genes might not have the same expression.

Which means that, if only a few are present their effect might be relatively small, if more are present their effect could be larger. In other words, gene effects become larger the more there are. This is in fact a form of epistasis, but not the usual one. The second reason he described was related to earliness effects. In the F2 especially differences in earliness may have distorted the results somewhat, although it was tried to neutralize that by inoculating plants in the same young flag leaf stage. The reality is of course that some differences in earliness do remain and especially in genotypes with a longer latent period this may cause variation in the LP. The LP is affected by the age of the flag leaf and so by differences in earliness if inoculated at the same time, and even differences in leaf age within the same plant can play a role and depending on the genotype these differences may be smaller or larger. All these effects can cause a deviation in the F2 assessment.

This latter effect is not an epistasis effect but just an effect that could unjustly lead to the conclusion that there are epistasis effects.

The observation, that all landraces carry at least some partial resistance genes and that even a small sample of landrace lines harbour minor genes that are at least partly different from one another, while they also differ to a fair extent from those in the European cultivar Vada, shows that the landraces of barley in Ethopia together must form a very rich source of partial resistance. It is there everywhere, but fairly strongly diluted and so not very obvious.

This rich source is very promising for the breeding for durable resistance. And there is no reason to believe that the pathosystem barley-barley leaf rust is an exceptional case. On the contrary it is quite probably that such forms of quantitative resistance are abundantly present in landraces of various crops. Unfortunately when screening germ plasm collections the attention is almost solely for complete or high level resistance, often of a non-durable nature, and hardly ever for quantitative resistance.

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Table 2. Mean relative latent period (LP) of parents, F1 and mid parent (MP) values in the flag leaves stage inoculated with barley leaf rust, *Puccinia hordei*, relative to L94 = 100 and Vada = 193. Data from 1994 trials.

Cross	F_1	P_1	P_2	MP	Inheritance of longer LP*
L94 x 35	113.3	100.0	125.1	112.6	I
L94 x 288	121.6	100.0	164.5	132.3	R
L94 x 629	118.0	100.0	162.1	131.6	R
L94 x 645	110.3	100.0	127.1	113.6	I
L94 x 913	101.0	100.0	160.2	130.1	R
L94 x 1242	111.9	100.0	126.5	113.3	I
L94 x 1248	110.1	100.0	129.5	114.8	I
35 x 288	147.0	125.1	164.5	144.8	I
35 x 439	143.6	125.1	155.7	140.4	I
35 x 629	159.2	125.1	162.1	143.6	D
35 x 915	163.3	125.1	175.6	150.7	D
35 x 1242	124.2	125.1	126.5	125.8	I
35 x 1248	132.6	125.1	129.5	127.3	I
35 x Vada	141.9	125.1	193.0	159.1	R
288 x 439	160.1	164.5	155.7	160.1	I
288 x 629	153.3	164.5	162.1	163.3	R
288 x 915	166.7	164.5	175.6	170.1	I
288 x 1242	144.4	164.5	126.5	145.5	I
288 x 1248	138.8	164.5	129.5	144.5	I
288 x Vada	164.4	164.5	193.0	178.8	R
439 x 629	144.9	155.7	162.1	158.9	R
439 x 915	160.2	155.7	175.6	165.7	R
439 x 1242	130.3	155.7	126.5	141.1	R
439 x 1248	128.9	155.7	129.5	142.6	R
439 x Vada	140.6	155.7	193.0	174.4	R
629 x 915	187.7	162.1	175.6	168.9	D
629 x 1242	135.2	162.1	126.5	144.3	R
629 x 1248	133.9	162.1	129.5	145.8	R
629 x Vada	154.7	162.1	193.0	177.6	R
645 x 915	136.8	127.1	175.6	151.4	R
645 x 1242	120.6	127.1	126.5	126.8	R
645 x 1248	121.2	127.1	129.5	128.3	R
645 x Vada	142.1	127.1	193.0	160.1	R
915 x 1242	143.1	175.6	126.5	151.1	R
915 x 1248	148.0	175.6	129.5	152.6	I
1242 x 1248	123.7	126.5	129.5	128.0	I
1242 x Vada	152.4	126.5	193.0	159.8	I
1248 x Vada	143.5	129.5	193.0	161.3	R

* I = intermediate, R = recessive, D = dominant inheritance

Table 3. Frequency distribution of F1 and F2 plants, F3 and F4 lines in 17 LP classes of 38 crosses of 8 barley landrace lines and two cultivars (L94 and Vada).

Cross	LP class (beyond L94 = 100%)																	Mean LP	S_x^2	S_x^3
Low	<0	0	5	11	21	31	41	51	61	71	81	91	101	121	141	161	181			
High			10	20	30	40	50	60	70	80	90	100	120	140	160	180	200			
L94																		100.0	0.0	0.0
645				1	10	4												127.1	5.7	1.5
35				3	10	1												127.3	3.9	1.1
1242				1	21	6												127.9	4.5	0.9
1248				2	16	4	6	1										128.3	9.1	1.7
439						4	1	2	1	2		1						151.5	19.1	5.7
435						11	4	1	1	4	3							152.4	19.6	4.0
913							8	8	6	5								160.2	10.9	2.1
629							4	5	9	3								163.0	9.0	2.0
288							3	3	3	3	2							167.8	12.8	3.5
915								2	4	8	3	1	1					174.1	12.1	2.8
Vada																		193.0	0.0	0.0
L94 x 35, MP[1]																		113.8		
F1			2	5														113.3	2.2	0.8
F2	3		7	28	20	15	8	2		2			1					125.3	16.9	1.8
F4	3	2	13	14	37	19	7											123.3	12.3	1.3
L94 x 288, MP																		133.9		
F1				1	5													121.6	7.4	3.5
F2	1			21	15	31	13	9	3									132.8	13.7	1.4
F4	2	2	10	9	14	9	11	4	1									126.1	11.1	1.4
L94 x 439, MP																		127.8		
F2	7	5	13	29	27	14	7	1	3	3								122.9	17.7	1.7
F4	1	4	20	27	24	15	3											118.9	11.6	1.2

Table 3. Continued

Cross	LP class (beyond L94 = 100%)																	Mean LP	S_x^2	S_x^3
Low High	<0	0	5 10	11 20	21 30	31 40	41 50	51 60	61 70	71 80	81 90	91 100	101 120	121 140	141 160	161 180	181 200			
L94 x 629, MP																		131.1		
F1				6	2													118.0	4.1	1.5
F2	1	1		12	25	21	19	8	7	1								135.6	15.4	1.6
F4	2	11	21	39	17	18	8	3				1						129.8	17.4	1.6
L94 x 645, MP																		113.6		
F1			6	4														110.3	2.0	0.6
F2	5	5	13	12	10	5	1											113.4	12.4	1.7
F4	3	9	31	21	7													109.6	7.7	0.9
L94 x 913, MP																		130.1		
F1	3	7																101.1	1.6	0.5
F2	1	1	4	6	8	9	4	3	1									131.0	21.1	3.3
F4	3	5	9	17	22	12	8	2	4	1	2							125.5	17.9	1.9
L94 x 915, MP																		137.8		
F2			1	8	17	16	23	12	5	6	3	1						142.9	18.9	1.9
F4	1	1	1	8	15	6	4	3										127.5	13.9	2.2
L94 x 1242, MP																		113.3		
F1			1	9														111.9	1.6	0.5
F2	3	1	4	24	6	4	2											118.6	11.0	1.5
L94 x 1248, MP																		114.8		
F1			5	4														110.1	2.9	0.9
F2	3	1	11	24	9	2	5	4				1						120.9	17.6	2.3
F4	2	4	13	5	5		1											110.4	11.2	2.0

Table 3. Continued.

Cross	LP class (beyond L94 = 100%)																	Mean LP	S_x^2	S_x^3
Low High	<0	0	5 10	11 20	21 30	31 40	41 50	51 60	61 70	71 80	81 90	91 100	101 120	121 140	141 160	161 180	181 200			
35 x 288, MP																		144.8		
F1						1	6	3										147.0	4.7	1.5
35 x 435, MP																		132.3		
F2			4	23	31	2	2	1	1									122.6	9.7	1.2
F3				2	84	17	7											127.2	6.2	0.6
35 x 439, MP																		140.4		
F1					2		6	1	1									143.6	10.8	3.4
35 x 629, MP																		143.6		
F1							1	5	3	1								159.2	9.1	2.9
35 x 915, MP																		150.7		
F1							2	3	1	2	2							163.3	15.2	4.8
35 x 1242, MP																		125.8		
F1					6	3												129.0	4.3	1.4
F2			1	5	16	13	4	7	1	1								134.0	15.1	2.2
F3				7	42	29	5	1	2	2								131.5	11.1	1.2
35 x 1248, MP																		127.3		
F1					3	2												132.6	4.7	2.1
35 x Vada, MP																		159.1		
F1						4	5	1										141.9	7.4	2.3

Table 3. Continued

Cross	LP class (beyond L94 = 100%)																	Mean LP	S_x^2	S_x^3
Low High	<0	0	5 10	11 20	21 30	31 40	41 50	51 60	61 70	71 80	81 90	91 100	101 120	121 140	141 160	161 180	181 200			
288 x 435, MP																		158.6		
F2				1	7	8	7	1	3	2			1					142.8	20.1	3.7
F3					7	29	34	15	5	1								143.9	10.4	1.1
288 x 439, MP																		160.1		
F1						2	2	6										149.2	8.7	2.8
288 x 629, MP																		163.3		
F1							4	4		1								153.3	7.6	2.5
288 x 915, MP																		170.1		
F1							1	4	1	1	1	1						166.7	15.5	5.2
288 x 1242, MP																		145.5		
F1						3	4	1	1									144.4	9.2	3.2
F2			1	3	5	9	7	7	7	7	5	1						151.9	22.7	3.2
F3					25	18	14	14	11	6	2							144.5	17.9	1.9
288 x 1248, MP																		147.0		
F1				3	1	3	1											138.8	11.5	4.1
F2		1		5	5	6	12	4	7	3	6	2	1					150.8	24.8	3.4
F3					3	13	25	15	7	5	3		1					150.4	15.0	1.8
288 x Vada, MP																		178.8		
F1								2	3									164.4	10.8	4.4
F2					1	8	7	18	19	20	11	7	2	1	1			168.1	20.3	2.1
F4				1	1	5	5	20	27	22	22	19	21	9	1	2	1	181.1	30.6	2.5

Table 3. Continued.

Cross	LP class (beyond L94 = 100%)																	Mean LP	S_x^2	S_x^3
Low High	<0	0	5 10	11 20	21 30	31 40	41 50	51 60	61 70	71 80	81 90	91 100	101 120	121 140	141 160	161 180	181 200			
435 x 1242, MP																		139.6		
F2			2	3	5	9	2	2	3		1							135.4	20.0	3.9
F3				1	4	8	4		2									144.8	14.0	3.2
435 x 1248, MP																		141.1		
F2		1		5	10	4	6	11	10	1	3	1						146.1	21.5	3.0
F4			1	12	23	21	9	2	2	2		1						133.8	15.5	1.8
435 x Vada, MP																		172.8		
F2				1		1	5	1	18	5	10	2	5	1				173.7	21.1	3.0
F4						2	7	11	13	4	10	6	4	3	1	1	1	178.6	31.2	4.0
439 x 629, MP																		158.9		
F1						3	4	2	1									144.9	10.8	3.4
439 x 915, MP																		165.7		
F1							1	3	2	2								160.2	10.0	3.5
439 x 1242, MP																		141.1		
F1				1	4	4	1											130.3	5.6	1.8
F2	1	1	4	9	5	9	6	9	1									134.3	23.4	3.4
F4		1	1	11	18	11	8	4										131.3	13.5	1.8
439 x 1248, MP																		140.1		
F1					7	2	1											128.9	5.4	1.7
439 x Vada, MP																		174.4		
F1					1	5	1	3										140.6	9.7	3.1

Table 3. Continued.

Cross	LP class (beyond L94 =100%)																Mean LP	S_x^2	S_x^3
Low High	<0	0	5 10	11 20	21 30	31 40	41 50	51 60	61 70	71 80	81 90	91 100	101 120	121 140	141 160	161 180	181 200			
629 x 915, MP																		168.9		
F1										3	3	3	1					187.7	11.4	3.6
629 x 1242, MP																		144.3		
F1					5	2	2	1										135.2	10.3	3.3
629 x 1248, MP																		145.8		
F1					5	3	1	1										133.9	9.5	3.0
F2				4	6	5	15	4	6	6	5							149.7	20.8	2.9
F4			1	5	20	24	24	18	3	3								142.1	17.6	1.8
629 x Vada, MP																		177.6		
F1							1	4	1									154.5	5.4	2.2
F2				1	5	12	14	16	17	9	8	5	4	1				160.2	22.5	2.4
F4						1	2	6	6	13	13	6	18	10	6	3		197.2	30.3	3.3
645 x 915, MP																		151.4		
F1						8	2											136.8	4.5	1.4
645 x 1242, MP																		126.8		
F1				4	6													120.6	3.1	1.0
645 x 1248, MP																		128.3		
F1				3	5													121.2	1.6	0.6
645 x Vada, MP																		160.1		
F1						2	8											142.1	3.4	1.1

Table 3. Continued.

Cross	LP class (beyond L94 = 100%)																	Mean LP	S_x^2	S_x^3
Low	<0	0	5	11	21	31	41	51	61	71	81	91	101	121	141	161	181			
High			10	20	30	40	50	60	70	80	90	100	120	140	160	180	200			
913 x Vada, MP																		176.6		
F2					2	1	2	5	6	7	9	3	1					169.6	20.2	3.4
F4							3	1	7	5	8	8	24	11	7	8	1	210.4	33.3	3.6
915 x 1242, MP																		151.1		
F1					1	3	3	1	1									143.1	10.8	3.6
F2			5	3	7	5		8	4	5	2		1					149.8	24.4	4.0
F4		2	2	3	17	22	18	10	12	10	5	1		1				147.1	22.7	2.2
915 x 1248, MP																		152.6		
F1							7	3										148.0	6.0	1.9
F2				3	4	6	7	9	7	8	7		2	1	1			159.5	23.5	3.2
F4			1	11	29	18	20	11	7	6	2		1	2				141.5	20.1	1.9
915 x Vada, MP																		184.3		
F2				2	9	13	22	23	13	12	12	3	1					157.0	21.5	2.1
F4					11	8	10	8	12	11	6	11	5		1			164.6	27.6	3.0
1242 x 1248, MP																		128.0		
F1				3	5	2												123.7	8.7	2.8
F2			1	5	6	6	14	8	8	2	2							145.2	19.2	2.7
F4			4	43	45	28												123.8	6.6	0.6
1242 x Vada, MP																		159.8		
F1						3	4	1	1									152.4	23.5	7.4
F2			3	3	11	18	19	9	2	1		1	1					140.8	18.2	2.2
F4			2	2	20	39	13	4	3		2	1	1					164.6	27.6	2.9

Table 3. Continued.

Cross	LP class (beyond L94 = 100%)																	Mean LP	S_x[2]	$S_{\bar{x}}$[3]
Low	<0	0	5	11	21	31	41	51	61	71	81	91	101	121	141	161	181			
High			10	20	30	40	50	60	70	80	90	100	120	140	160	180	200			
1248 x Vada, MP																		161.3		
F1					3	1	3	2		1								143.5	14.3	4.5
F2				2	3	4	7	10	5	8	5	5	5	5	1			165.5	25.8	3.5
F4				4	4	5	11	11	9	22	6	3	7	2	2			168.0	28.3	3.1

[1]MP = mid-parent value.
[2]S_x = standard deviation of that population.
[3]$S_{\bar{x}}$ = standard deviation of the mean of that population.

Table 4. Mean relative latent period (LP) of parents, F1 and F2 in the flag leaves of barley inoculated with barley leaf rust, *Puccinia hordei;* relative to L94 = 100 and Vada = 193. Data from 1992 and 1994 combined.

Cross	$\bar{F}2$	$\bar{F}1$	$\bar{P}1$	$\bar{P}2$	MP	$4\bar{F}_2 - 2\bar{F}_1 - \bar{P}_1 - \bar{P}_2$
L94 x 35	125.3 ± 1.8	113.3 ± 0.8	100.0 ± 0.0	127.3 ± 1.7	113.7	47.3 ± 4.1***
L94 x 288	132.8 ± 1.4	121.6 ± 3.5	100.0 ± 0.0	167.8 ± 3.2	133.9	20.2 ± 6.5**
L94 x 629	135.6 ± 1.6	118.0 ± 1.5	100.0 ± 0.0	163.0 ± 2.9	131.5	43.4 ± 5.4***
L94 x 645	113.7 ± 1.7	110.3 ± 0.6	100.0 ± 0.0	127.1 ± 1.5	113.6	7.1 ± 3.8 ns
L94 x 913	131.0 ± 3.3	101.1 ± 0.5	100.0 ± 0.0	160.2 ± 2.2	130.1	61.6 ± 7.0***
L94 x 1242	118.6 ± 1.5	111.9 ± 0.5	100.0 ± 0.0	127.9 ± 0.9	114.0	22.7 ± 3.2***
L94 x 1248	120.9 ± 2.3	110.9 ± 0.9	100.0 ± 0.0	128.3 ± 1.6	114.2	33.5 ± 5.0***
35 x 1242	134.0 ± 2.2	129.0 ± 1.4	127.3 ± 1.7	127.9 ± 0.9	127.6	22.8 ± 5.2***
288 x 1242	151.9 ± 3.2	144.4 ± 3.1	167.8 ± 3.2	127.9 ± 0.9	147.9	23.1 ± 8.4**
288 x 1248	150.8 ± 3.4	138.8 ± 4.1	167.8 ± 3.2	128.3 ± 1.6	148.1	29.5 ± 9.6**
288 x Vada	168.1 ± 2.1	164.4 ± 4.4	167.8 ± 3.2	193.0 ± 0.0	180.4	-17.2 ± 8.2 ns
439 x 1242	134.3 ± 3.5	130.3 ± 1.8	151.5 ± 2.9	127.9 ± 0.9	139.7	- 2.8 ± 8.0 ns
629 x 1248	149.8 ± 2.9	133.9 ± 3.0	163.0 ± 2.9	128.3 ± 1.6	145.7	40.1 ± 7.9***
629 x Vada	160.2 ± 2.3	154.5 ± 2.2	163.0 ± 2.9	193.0 ± 0.0	178.0	-25.0 ± 6.3***
1248 x Vada	165.5 ± 3.3	143.5 ± 4.5	128.3 ± 1.6	193.0 ± 0.0	160.7	53.7 ± 9.3***
1248 x 1242	145.2 ± 2.7	123.7 ± 2.8	128.3 ± 1.6	127.9 ± 0.9	128.1	77.2 ± 6.9***
1242 x Vada	140.8 ± 2.2	152.4 ± 7.4	127.9 ± 0.9	193.0 ± 0.0	160.5	-62.5 ± 11.4***
1242 x 915	149.8 ± 4.0	143.1 ± 3.6	127.9 ± 0.9	174.1 ± 2.8	151.8	11.0 ± 9.9 ns
1248 x 915	159.5 ± 3.2	148.0 ± 1.9	128.3 ± 1.6	174.1 ± 2.8	149.2	39.6 ± 7.6***
Mean						22.4

** = significantly different from zero at $p < 0.01$;
*** = significantly different from zero at $p < 0.001$.

Chapter 10

General Discussion

Landraces of self-fertilizing crops always appeared genetically variable. To investigate the degree of genetic variation both between and within landraces and to understand what type of resistance is present an inventory of 18 Ethiopian barley landraces was made for six characteristics among which resistance to the pathogens leaf rust, caused by *Puccinia hordei*, and representing a biotrophic, air borne fungus, and leaf scald, caused by *Rhynchosporium secalis*, representing a hemi-biotrophic, splash borne fungus.

Variation for agronomic traits

In total six characteristics were evaluated. For all six the variation between and within the landraces was large. The resistance to the two pathogens is discussed separately below.

Amazing was the large variation within the landraces. This large variation was not limited to a few landraces. It was a general pattern. As an example the range in earliness within many landraces was larger than the range between the landraces, which was already quite considerable with 35 days. With plant length a similar situation appeared to exist.

The variation between landraces for thousand grain weight was also large. This was partly due to the fact, that both two-rowed and six-rowed barley genotypes occurred. Within each landrace either the one or the other type predominated. Two-rowed barleys occur more frequently in the lower altitudes than in the higher ones (personal observation). This could indicate that two-rowed barleys are better adapted to the warmer, drier environments with less scald (see also the sub-chapter about ecological adaptation below).

Another cause of the variation in grain weight was the variation for scald severity. Highly susceptible landraces or genotypes undoubtedly had a much lower thousand grain weight than resistant ones due to the damaging effect of the disease. This is corroborated by the fairly high and significant rank correlation coefficient between the mean disease severity and mean thousand grain weight of the landraces of -0.73. However there was variation not affected by the disease as landrace 3441 shows. It is almost completely

resistant. Nevertheless the thousand grain weights within that landrace varied from below 35 g to beyond 55 g. The between landrace variation can be seen when landraces with the same disease severity are compared. Within these groups considerable differences still existed.

The various characteristics varied in association with one another. This is discussed below in the sub-chapter about ecological adaptation.

Variation of resistance to *Rhynchosporium secalis*

The disease development in 1993 was slightly less than the one that occurred in 1991, but it did not change the variation pattern observed in 1991. The variation for disease severity was very large between as well as within landraces. The between variation led the landraces to be classified as ranging from extremely resistant to extremely susceptible (see chapter 5). The passport data about landraces provided by the Plant Genetics Resources Centre of Ethiopia (PGRC/E) showed that extreme resistance was found especially in collections from high altitude areas, where the conditions for the disease are far more conducive (cooler and more humid), while highly susceptible landraces were collections from lower altitude areas. Here too it was found that the association of resistance with altitude was positive and highly significant (see chapter 5). The resistance showed an inverse relationship with earliness; i.e early landraces were the most susceptible, while the late maturing ones were the most resistant. A similar inverse association with leafiness appeared to exist, i.e landraces with low degrees of leafiness had a high disease severity and vice versa (see also "ecological adaptation" below). Even, after the effects of earliness, plant height, and leafiness were removed through regression analysis, the remaining variation, the variation for real resistance, was still very high. This result agrees with previous reports stating that Ethiopian landraces are very good sources of resistance to many diseases of barley (Vavilov, 1951; Takahashi, 1955; Harlan, 1969 and 1976; Qualset, 1975; Mulugeta, 1985). But again the within landraces variation was remarkable, an observation not yet so clearly reported.

Variation of resistance to *Puccinia hordei*

From the studies in the seedling and the adult plant stage it is clear that neither known, identified nor non-identified, effective, race-specific major resistance genes are present at a measurable frequency in the barley landraces of Ethiopia. This made it relatively easy to make an inventory of the quantitative (partial) resistance, which is known from the European situation to be durable (Parlevliet, 1993). All landraces had at least some partial resistance (see chapter 7). The variation between landraces was fairly large. The variation within landraces was even larger and genotypes (the landrace lines) with a level of susceptibility as high as that of the extremely susceptible L94 occurred at very low frequencies. This too runs parallel with the situation in Europe, where cultivars as susceptible as L94 are rare. Most cultivars carry some partial resistance, but the genes carried in all those cultivars seem to be more or less the same, only the number varies (Parlevliet, 1978).

The genetic analysis indicated, that the genes for partial resistance in the landraces were to a fair extent different from those in the cultivar Vada, which is representing the European germ plasm. The genes carried by the lines were to some extent also different from one another. This together with the fact that the majority of the barley genotypes in Ethiopia carry some partial resistance makes this region into a vast reservoir of genes for durable resistance to barley leaf rust.

World wide large collections of various crops have been made and they are screened for their resistances to a wide array of pathogens. But this screening is almost solely directed at major resistance genes, which are often of a non-durable nature. The quantitative resistance, abundantly present in most hosts to many pathogens (Parlevliet, 1993; Koch and Parlevliet, 1991; Roumen, 1994) and again confirmed here is usually overlooked. With it a large source of potential durable resistance is disregarded.

Durable resistance in landraces

Landraces of self-fertilizers are assumed to be heterogeneous to a certain extent and the resistance to endemic pathogens it carries must be of a durable type. This durability of the resistance could be due to the multiline principle or due to genetically durable

resistance.

In order to prevent the build-up of more complex races that could effectively neutralize most to all of the race-specific resistance genes in a multiline or cultivar mixture stabilizing selection is required. In case of many components in the mixture the degree of stabilizing selection needed can be quite low (see chapter 2). The presence of race-specificity in the barley landraces indicated that the multiline principle is operating in these landraces to *Rhynchosporium secalis* and forming therefore at least part of the durable protection against this pathogen.

With barley leaf rust the situation is quite different. Here there is no indication of the operation of the multiline principle. The durable protection to this pathogen appears to be based solely on the genetically durable partial resistance.

The different strategies in protecting the barley against the two pathogens are most likely caused by the different dispersal mechanisms, splash borne (slow rate of dispersal) versus air borne (fast rate of dispersal), and by the difference in severity, scald being on average much more severe than leaf rust, requiring possibly two systems for durable protection, the multiline strategy on top of partial resistance.

Ecological adaptation of landraces

It is generally assumed that landraces are adapted to the ecological conditions in the region where they are grown. But clear evidence of that is scarce. In this study some indications of such an adaptation have been obtained.

Between the various characteristics associations appeared to exist. These associations meant, that the lower the altitude the higher the frequency of earlier, less leafy, somewhat shorter and more scald susceptible genotypes in the landrace. This might be related to the environmental restrictions of which rainfall is probably the most important one. With increased altitude the temperatures decrease, the amount of rainfall increases, while also the growing season might on average become slightly longer as the rains may start slightly earlier and go on slightly longer the higher the altitude. Due to this combination of higher temperatures and less rainfall the water stress on the crop will increase rapidly the lower the altitude requiring earlier, less leafy and shorter genotypes. This of course goes at the expense of yield potential and it means that barley as a crop will be replaced

by better yielding crops when going down in altitude. At the higher altitudes more resistance to scald is required because of the more conducive conditions for this disease. The observed associations of characteristics do indeed suggest that the landraces were adapted to the ecological conditions to which they were exposed.

About the cause of this large variation in the Ethiopian barley landraces various ideas have been brought forward. Earlier some workers indicated that incidental outcrossing and natural selection (Harlan, 1968), mutation (Schiemann, 1951) and disruptive selection (Mulugeta, 1985b) could be driving factors in creating within landrace variation. It should also be realised that farmers consciously or unconciously may mix up the seed of different landraces incidentally and this seen over a large area and over large time spans together with the driving factors mentioned above undoubtedly would result in a large variation in these landraces.

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Summary

It is known, that landraces of self-fertilizing crops can harbour a lot of variation. Ethiopia is a centre of diversity for barley. This crop has been grown in this area for a few thousands of years. The present area of 900,000 ha is still planted largely with landraces. Due to the topographic situation there is a large ecological diversity in the region. One may therefore expect a considerable variation between the landraces and earlier research confirmed this. About the variation within the landraces less is known. It also is interesting to investigate apart from the variation for resistance also the type of resistance present in the landraces, because the resistance in landraces against endemic pathogens has to be durable to be effective over time.

The aim of this research was to investigate the variation between and within barley landraces for several traits, including resistance to two pathogens. The pathogens were leaf rust, *Puccinia hordei*, and leaf scald, *Rhynchosporium secalis*. Resistance to both pathogens is of two types; race-specific, non-durable, major genic resistance and polygenic partial resistance of a more durable nature. The leaf rust is an air borne biotroph, leaf scald a splash borne hemi-biotroph. Leaf rust occurs at the lower altitudes of the barley growing area, while leaf scald is especially severe at the higher altitudes.

Variation between and within landraces

Of each of 18 landraces 100 single plant derived progenies were produced. The 1800 lines were field tested in 1991 and 1993 at Holetta Research Centre, Ethiopia. Earliness in days to heading, plant length in cm, leafiness, 1000-grain weight and leaf scald disease severity (DS) were measured. For each of the traits a large variation between and within the landraces was observed. Especially the variation within the landraces was unexpectedly large for all traits. DS of leaf scald was associated with earliness and leafiness. Adaptation of the landraces to the ecological situation became visible by associating the variation between landraces with the altitude they came from. The frequency of resistant genotypes in the landraces increased with the altitude from where the landraces came. With increased altitude the landraces headed later. With increased altitude the precipitation increases and so the leaf scald severity. The increased rainfall also allows later, and

so higher yielding landraces.

Resistance to *Rhynchosporium secalis*

Since the disease severity for leaf scald was correlated with earliness and leafiness a multiple regression analysis was carried out to remove the effects of earliness and leafiness from the variation for DS. After this correction the variation between and within the landraces was still large. The resistance between the landraces ranged from highly resistant to extremely susceptible. The same range of variation was observed within several landraces.

Within several landraces lines were found that were completely resistant in the one year and highly susceptible in the other, indicating the presence of race-specific resistance of the major genic type. In literature a range of such genes has been described. This means that the durability of the resistance in the barley landraces to this pathogen is at least partially based on the multiline principle. Non-durable, race-specific major genes can become quite durable in a multiline or variety mixture, provided that stabilizing selection (SS), sensu Van Der Plank (The fitness of a race decreases with an increased number of virulence factors), occurs to prevent the development of more complex races. In commercial multilines or variety mixtures the SS has to be fairly high because the number of components is rather small. The large within variation of the barley landraces allows for a larger number of components and so for a much smaller SS to keep the development of more complex races at bay. Also the spread of such more complex races to other fields, in case they would arise, is much smaller in this pathogen than in an air borne pathogen such as leaf rust.

Since these major genes cover up the partial resistance if present nothing definitive can be said about the presence of this type of resistance.

Resistance to *Puccinia hordei*

Over 1700 landrace lines were tested in the seedling stage with two races, race 1-2-1, virulent on 6, and race A, virulent on 2 or 3 of the 9 described race-specific resistance genes. Nearly all lines had a susceptible infection type (IT) for both races. This indicates

the near-absence of effective non-durable, race-specific major genes. Four Ethiopian isolates, that appeared to be four races, and race 1-2-1 were tested on the differential cultivar series, that together contains the 9 described resistance genes, and on 19 landrace lines from 14 landraces. The four Ethiopian races had virulence/avirulence patterns very similar to those known from Europe. Of the 19 x 5 landrace line x race combinations only one had an intermediate IT, all others were susceptible. This confirmed the near-absence of effective, race-specific major genes in the barley landraces.

Over 1200 landrace lines were inoculated with race 1-2-1 to evaluate the partial resistance present by measuring the latent period (LP) in the young flag leaf stage. Because the LP is very strongly correlated with partial resistance LP in the young flag leaf is a good estimator of partial resistance. Again nearly all lines had a susceptible IT. All landraces had at least some partial resistance. The variation between the landraces was fairly large. The variation within the landraces was even larger.

The resistance of the landraces to leaf rust is almost exclusively of the partial type, a genetically durable form of resistance. The multiline principle does not play a role of any significance in this pathosystem.

Inheritance of the partial resistance to leaf rust in the landraces

An extremely susceptible cultivar, L94, a partially resistant cultivar, Vada, and ten landrace lines from various landraces, representing a range of partial resistance, were intercrossed in 38 combinations. The LP was measured in adult plants of the F1 (38 crosses), F2 and F3 or F4 (28 crosses). The F1-values of most crosses suggested intermediate or recessive inheritance of the partial resistance. The generation mean analysis indicated the presence of some epistasis. The F2's showed a continuous variation with significant transgression in most crosses, and especially in the crosses with Vada. This was confirmed in the F3 or F4. It indicates that a few to several minor genes control the partial resistance of the eight landrace lines. These minor genes seem to be different for a fair extent from those in the European cultivar Vada. Also the minor genes in the landrace lines are for some part different from one another.

Conclusions

The Ethiopian barley landraces vary greatly. Also within the landraces a large variation appeared to exist, more than expected. This is important for the breeding of barley and not only for Ethiopia. The large within landrace variation means, that when collecting and maintaining landraces large samples should be collected and used for the maintenance.

The durability of the resistance to leaf scald is at least partially based on the multiline principle. Against leaf rust the resistance is of the genetically durable type. This quantitative type of resistance occurs in all landraces at low to moderate levels forming a very rich source of durable resistance.

Which type of resistance gives durable protection in the barley landraces depends on the pathosystem.

Samenvatting

Het is bekend, dat landrassen van zelfbevruchtende gewassen een flinke variatie kunnen herbergen. Ethiopië is een genencentrum voor o.a. gerst. Dit zelfbevruchtende gewas wordt hier al enkele duizenden jaren op grote schaal verbouwd. De huidige 900.000 ha worden nog steeds voor een groot deel beplant met landrassen. Door de topografische situatie is de ecologische verscheidenheid binnen het gebied, waar gerst geteeld wordt, groot. Er mag dan ook een grote variatie tussen de landrassen verwacht worden. Eerder onderzoek heeft dit ook aangetoond. Over de variatie binnen de landrassen is echter veel minder bekend. Daarnaast is het interessant te onderzoeken hoeveel variatie er voor resistentie tegen pathogenen aanwezig is en wat voor type resistentie het betreft. Resistentie in landrassen tegen van nature aanwezige pathogenen moet immers wel duurzaam zijn.

Het doel van dit onderzoek was dan ook om de variatie tussen en binnen een aantal gerstlandrassen te evalueren en om de resistentie tegen twee pathogenen te inventariseren. De pathogenen waren dwergroest, *Puccinia hordei*, en bladvlekkenziekte, veroorzaakt door *Rhynchosporium secalis*. Resistentie tegen beide pathogenen is van twee typen; monogene, fysiospecifieke resistentie, die niet duurzaam is en polygene, partiële resistentie, die in het geval van dwergroest zeker duurzaam is. De dwergroest is een "air borne" biotroof, terwijl *R. secalis* "soil borne" is en het waardweefsel hemi-biotroof exploiteert. Dwergroest komt vooral voor in de laagste teeltzones van gerst, terwijl de bladvlekkenziekte snel toeneemt met de hoogte waarop de gerst geteeld wordt.

Variatie tussen en binnen landrassen

Van ieder van 18 landrassen werden 100 individuele plantnakomelingschappen geproduceerd. Deze 1800 lijnen werden in 1991 en 1993 te velde geëvalueerd op het Holetta onderzoekcentrum in Ethiopië. De vroegheid (dagen van opkomst tot in aar komen), plantlengte (cm van basis tot langste aar), bladrijkdom, duizend-korrelgewicht en resistentie tegen bladvlekkenziekte werden waargenomen. Er was grote variatie voor alle eigenschappen, zowel tussen als binnen de landrasen. Vooral de variatie binnen de landrassen was onverwacht groot voor alle vijf de eigenschappen. Aantasting door de bladvlekkenziekte was geassocieerd met vroegheid en bladrijkdom. Aanpassing van de

landrassen aan de ecologische situatie werd zichtbaar door de variatie tussen de landrassen te associëren met de hoogte waarop het landras werd verzameld. De frequentie van resistente genotypen in de landrassen nam toe met de hoogte waar de landrassen vandaan kwamen. Met de hoogte nam de gemiddelde vroegheid van de landrassen af. Bij grotere hoogte neemt de neerslag toe en daarmee de ernst van de bladvlekkenziekte. Tevens kunnen latere en daardoor beter opbrengende rassen geteeld worden.

Resistentie tegen *Rhynchosporium secalis*

Omdat de mate van aantasting door de bladvlekkenziekte gecorreleerd bleek met vroegheid en bladrijkdom werd er via een meervoudige correlatie- en regressie-analyse gecorrigeerd voor deze associaties. Na het wegnemen van de effecten, veroorzaakt door deze eigenschappen, bleek de variatie binnen en tussen de landrassen nog steeds groot te zijn voor resistentie tegen dit pathogeen. De resistentie tussen landrassen variëerde van compleet (geen zichtbare aantasting) tot extreem vatbaar (alle plantweefsel genecrotiseerd). De resistentie tussen de landrassen variëerde van zeer hoog (de meeste genotypen niet of nauwelijks aangetast) tot zeer laag (alle genotypen voor 100% aangetast). Deze spreiding in variatie kwam ook binnen diverse landrassen voor.

Binnen diverse landrassen werden lijnen gevonden, die in het ene jaar zeer vatbaar waren en in het andere jaar zeer resistent. Dit duidt op fysio-specifieke resistentie, veroorzaakt door de fysiospecifieke hoofdgenen, waarvan er een flink aantal in de literatuur beschreven zijn. Dit betekent, dat de duurzame resistentie in de gerstlandrassen in ieder geval ten dele door het multilijnprincipe wordt verkregen. Niet duurzame fysiospecifieke resistentiegenen kunnen duurzaam effectief worden in een multilijn of rassenmengsel, mits er stabilizerende selectie (SS) optreedt, d.w.z. wanneer de fitheid van een fysio afneemt bij toename van het aantal virulenties. Om effectief te zijn moet de SS vrij hoog zijn bij weinig componenten, zoals in commerciële multilijnen of rassenmengsels. In de landrassen, hier bestudeerd, lijkt het aantal componenten hoog te zijn. Hierdoor kan al met een kleine SS duurzaamheid verkregen worden. Tevens is de snelheid waarmee nieuwe, complexere fysio's zich naar andere velden verspreiden, relatief laag door het "splash borne" verspreidingskarakter van het pathogeen.

Over de mate van voorkomen en over het effect op de duurzaamheid van de partiële

resistentie in dit pathosysteem is niets te zeggen, daar deze resistentie overdekt werd door de hoofdgenen-resistentie.

Resistentie tegen *Puccinia hordei*

Meer dan 1700 landraslijnen werden in het zaailingstadium getoetst met twee fysio's van dwergroest. Fysio 1-2-1 is virulent op zes, fysio A virulent op 2 of 3 van de negen beschreven fysiospecifieke resistentiegenen (er zijn er beduidend meer). Bijna alle lijnen vertoonden tegen beide fysio's een vatbaar infectietype (IT). Dit duidt er op, dat er vrijwel geen effectieve, fysio-specifieke resistentiegenen in de landrassen aanwezig waren. Vier isolaten uit Ethiopië, die evenzovele fysio's bleken te zijn, en fysio 1-2-1 werden getoetst op de differentiële rassenreeks, die gezamenlijk de negen bekende resistentiegenen bevatten, en op 19 landraslijnen, afkomstig uit 14 landrassen. De vier Ethiopische fysio's hadden virulentiepatronen, die zeer veel leken op de patronen bekend van Europese fysio's. Van de 19 x 5 landraslijn x fysio combinaties had er één een wat lager IT, de overigen hadden een vatbaar IT. Dit bevestigt de hierboven genoemde conclusie, dat de frequentie van effectieve, fysio-specifieke resistentiegenen, als ze al voorkomen, zeer laag is.

Ruim 1200 landraslijnen werden in het jong-volwassen plantstadium getoetst om de mate van partiële resistentie te evalueren. De latentie periode (LP) in het jonge vlagbladstadium is zeer hoog gecorreleerd met partiële resistentie en is daarom een goede maat voor deze resistentie. Ook nu weer hadden bijna alle lijnen een vatbaar IT. Alle landrassen hadden ten minste enige partiële resistentie. De variatie tussen de landrassen was vrij groot, binnen de landrassen was de variatie zo mogelijk nog groter.
De resistentie in de landrassen tegen dwergroest bestaat vrijwel uitsluitend uit partiële resistentie, een genetisch duurzame vorm van resistentie. Het multilijnprincipe speelt hier geen rol.

Overerving van de partiële resistentie tegen dwergroest in de landrassen

Een uiterst vatbaar ras (L94), een partiëel resistent ras (Vada) en 8 landraslijnen uit diverse landrassen en met verschillende niveau's van partiële resistentie werden in 38

combinaties met elkaar gekruist. De F1 van de meeste kruisingen duidde op intermediaire of recessieve overerving van partiële resistentie, gemeten als LP in het jonge vlagblad. De "Generation mean analysis" gaf aan, dat er ook sprake was van enige tussen-locus-interactie ("epistasis"). De F2's lieten een continu variatie, zien die bij de meeste kruisingen tot significant buiten de ouderwaarden liep. Dit werd in de F3 of F4 bevestigd. Vooral in de kruisingen met Vada trad transgressie vaak op. Dit duidt erop, dat er enkele tot verscheidene polygenen betrokken zijn bij de partiële resistentie van de acht landraslijnen. Deze polygenen lijken in belangrijke mate te verschillen van die in Vada, een Europees ras. Ook onderling zijn deze polygenen niet alle dezelfde.

Conclusies

De gerstlandrassen in Ethiopië blijken niet alleen onderling, maar ook intern een grote variatie te herbergen, groter dan vermoed werd. Dit is voor de veredeling van gerst belangrijk en niet alleen voor Ethiopië. De grote binnen-landrasvariatie betekent, dat er bij verzamelingen ook veel materiaal per landras verzameld dient te worden.

De duurzaamheid van de resistentie tegen de bladvlekkenziekte berust ten minste deels op het multilijnprincipe. Tegen dwergroest berust het op genetisch duurzame resistentie. Deze kwantitatieve resistentievorm komt in alle landrassen voor op een laag tot matig niveau en vormt daarmee een rijke bron van duurzame resistentie.

Welk systeem duurzame bescherming geeft is dus afhankelijk van het pathosysteem.

CURRICULUM VITAE

Fekadu Alemayehu Shiferaw was born on 16 November, 1952 in Gojam, Ethiopia. He took B.Sc. in plant sciences in 1977 from the Alemaya College of Agriculture, Addis Ababa University, Ethiopia. Between 1978 and 1980 he worked as a research officer in the Institute of Agricultural Research (IAR), Ethiopia. In 1982 he obtained a masters of science degree in plant breeding again from Alemaya College of Agriculture, Addis Ababa University, Ethiopia. In the period between February and October of 1983 he participated in the wheat breeding course at CIMMYT, Mexico. From October 1983 he served as a national barley improvement program team leader of IAR based at Holetta until he was awarded a fellowship in 1989 to undertake a Ph.D. study. During this period of leadership several improved cultivars of barley were identified from the program and released to farmers in various localities of Ethiopia.

Since January 1990, he worked intermittingly at the Department of Plant Breeding of the Wageningen Agricultural University, under the supervision of Professor J.E. Parlevliet. It was here, that several greenhouse trials involving the barley leaf rust were carried out. The trials involving the leaf scald of barley and other traits were conducted in the field conditions at Holetta, Ethiopia.