

Inheritance of foliar resistance to ascochyta blight in lentil (*Lens culinaris*)

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Abstract Inheritance of foliar resistance to ascochyta blight in lentil (*Lens culinaris*) was studied using four resistant (ILL 5588, ILL 5684, 'Indianhead', and 'Laird') and two susceptible inbreds (W6 3192 and 'Titore') in a glasshouse. Isolate "Rakaia" of *Ascochyta lentis* was used in all the experiments. F₂, BC₁ (backcross to the resistant parent), and BC₂ (backcross to the susceptible parent) generations of the crosses between resistant and susceptible inbreds were used to detect the inheritance models. F₂ generations of the crosses between resistant and resistant inbreds and two 3-way crosses were used to test allelic relationships among resistance genes. Two dominant genes, one for resistance and one for moderate resistance, are present in ILL 5588. One dominant gene, which is allelic to the one for resistance in ILL 5588, confers the resistance in ILL 5684. One recessive gene is responsible for the resistance in cultivar 'Laird'. The resistance in 'Indianhead' is under control of two recessive genes with additive effects. Two complementary genes, one in W6 3192 and one in 'Titore', are responsible for the resistance observed in the F₂ generation of the cross between these two susceptible cultivars.

Keywords ascochyta blight; *Ascochyta lentis*; inheritance model; *Lens culinaris*; resistance

INTRODUCTION

Ascochyta blight, caused by *Ascochyta lentis*, is the major disease in many lentil (*Lens culinaris* Medik) production areas (Muehlbauer et al. 1995). The disease has considerable effect on both seed quality and yield (Morrall & Sheppard 1981; Gossen & Morrall 1983). Gossen & Morrall (1983) estimated that foliar infection has caused yield losses of up to 40%, but economic losses from infected seed have reached more than 70% in Canada. Considerable efforts have been devoted to the study of the dispersal of *Ascochyta* (Pedersen et al. 1993, 1994), the influence of environmental factors on disease severity (Pedersen & Morrall 1994), and chemical control (Beauchamp et al. 1986; Ahmed & Beniwal 1991). Agrichemicals such as Benomyl and Daconil (Ahmed & Beniwal 1991), Bravo and Crown (Morrall 1997) are very effective. However, effective, chemical control can often not be used by farmers because of economic reasons. This is particularly true in developing countries, which are the main producers of lentil. Breeding for improved host resistance is expected to be the most effective, efficient, and environmentally friendly method of control (Erskine et al. 1994; Ye et al. 2000a, 2002).

Resistance sources were identified in both cultivated and wild lentil species, and were summarised by Ye et al. (2000a, 2002). The genetics of ascochyta blight resistance in lentil has been studied using F₂ populations of different crosses, and was reviewed by Ye et al. (2000a, 2002). As a summary, the following inheritance models were proposed: (1) single dominant gene (Tay & Slinkard 1989; Ahmad et al. 1997; Vakulabharanam et al. 1997; Ford et al. 1999); (2) single recessive gene (Tay 1989; Chowdhury et al. 2001); (3) two duplicated recessive genes (Andrahennadi 1997); (4) one dominant and one recessive gene (Sakr 1994); (5) two complementary genes (Tay 1989; Ahmad et

al. 1997; Andrahennadi 1997); and (6) one partial dominant gene large effect and one dominant gene with less effect (Ye et al. 2000b). In most of the studies, the sample sizes used were small (<100), and only one segregating population (F_2) of each cross was used to infer the inheritance model. Therefore, these proposed models are inconclusive, and need to be confirmed. In addition, no study has tested the allelic relationships among resistance genes identified. The purpose of this study is to investigate the inheritance of foliar resistance to ascochyta blight in four resistant and two susceptible cultivars and to test the allelic relationships among the resistance genes detected.

MATERIALS AND METHODS

Plant materials

Two resistant cultivars ('Indianhead', 'Laird'), two resistant inbreds (ILL 5588 and ILL 5684), and one susceptible cultivar ('Titore') of *L. culinaris*, and one susceptible inbred (W6 3192) of *L. ervoides* were crossed in all possible combinations. The F_1 s were selfed to produce F_2 populations, and backcrossed to both resistant and susceptible parents to obtain BC_1 and BC_2 , respectively. Out of the six crosses between resistant and resistant parents only 'Indianhead' \times 'Laird', ILL 5588 \times 'Laird', and ILL 5684 \times ILL 5588 provide information about the allelic relationships between resistance genes. The other three crosses are omitted from analysis. Two 3-way crosses, 'Titore' \times (ILL 5684 \times W6 3192) and 'Titore' \times (ILL 5588 \times W6 3192), were also made for testing allelic relationship. The method described by Ahmad et al. (1995) was used to obtain F_1 seed of the crosses with W6 3192 as one parent. Single nodal culture described by Ye et al. (2000c) was then used to enlarge the F_1 populations so that large F_2 populations were obtained.

Inoculum preparation and evaluation of blight reaction

An isolate of *A. lentis* ("Rakaia") isolated from infected seed of 'Invincible' was obtained from the New Zealand Institute for Crop & Food Research Limited. Inoculum was prepared from a 15-day culture grown on V_8 -juice agar medium under near ultraviolet light at 18°C on a laboratory bench. Spores were washed from the culture plates using distilled water and filtered through muslin cloth. Two drops of Tween 20 were added per 100 ml as a

surfactant. The concentration of the spore suspension was measured using a haemocytometer and adjusted to 7.5×10^4 conidia/ml by dilution.

All parental cultivars/inbreds and progeny seed were sown in 10 cm diameter pots (5 plants/pot). For parental cultivars/inbreds 20 plants were used. For progenies the number of plants varied (see Tables 2 and 3) depending on the seed availability.

Seedlings with four to five expanded leaves growing in pots in the glasshouse were inoculated with the suspension (1 ml/seedling) using an atomiser. After inoculation, pots were kept in a controlled environment cabinet (18°C and high humidity) for 24 h and then moved to a greenhouse bench for disease development to occur. Negative controls were seedlings of susceptible cultivar 'Titore' sprayed with distilled water plus Tween 20 only.

Data collection and analysis

Disease scores were recorded 7, 15, and 21 days after inoculation according to a standard five-point scoring procedure on a 1–9 scale developed by the International Centre for Agricultural Research in the Dry Areas (Erskine & Bayaa 1991). Plants were scored in the following manner: 1 = no visible lesions; 3 = few scattered lesions after careful examination; 5 = lesions common and easily observed, no defoliation; 7 = lesions very common, defoliation moderate; 9 = extensive lesions on all plant parts with stem girdling. Based on the observed resistance levels of parental cultivars, individual plants were classified as resistant (R) with ratings 1 and 3 and susceptible (S) with ratings 5, 7, and 9. Alternatively, plants were categorised into three categories: resistant (R) with ratings 1 and 3, moderately resistant (MR) with rating 5, and susceptible (S) with ratings 7 and 9. χ^2 statistic was used to test the goodness of fit of the observed ratio to expected ratios.

RESULTS

Ascochyta blight reactions of parental cultivars

No symptoms were observed in plants used as negative controls, indicating that the disease development in the inoculated pots occurred due to spraying with the inoculum.

On Day 7, disease development was poor, only sporadically found on a few plants of susceptible cultivars/inbreds. There were only slight differences

in disease scores between the remaining two dates for all the resistant materials. However, many of the susceptible materials died before Day 21. Therefore, the results of Day 15 are used in all later analyses.

Table 1 shows the blight reactions of the parental lines/cultivars in the order of their observed level of resistance. All plants of ‘Indianhead’, ILL 5588, and ILL 5684 were consistently scored 1 or 3, suggesting that they are resistant. All plants of ‘Laird’ were scored 5, indicating that ‘Laird’ is moderately resistant. All plants of ‘Titore’ and W6 3192 were scored 7 or 9, suggesting that they are susceptible.

Table 1 Disease reaction of lentil (*Lens culinaris*) parental lines to isolate “Rakaia” of *Ascochyta lentis*.

Cultivar/lines	Disease categories				
	1	3	5	7	9
Indianhead	10	10	0	0	0
ILL 5588	5	15	0	0	0
ILL 5684	0	20	0	0	0
Laird	0	0	20	0	0
W6 3192	0	0	0	12	8
Titore	0	0	0	16	4

Segregation of resistance to ascochyta blight

The inheritance patterns for the crosses to both susceptible parents (‘Titore’ and W6 3192) were entirely consistent. Further discussion will concentrate on the ‘Titore’ crosses.

In the F₂ progenies of ‘Indianhead’ × ‘Titore’, seven plants were resistant, 40 were moderately resistant, and 55 were susceptible (Table 2). When the 20 moderate resistant plants were regarded as susceptible, the results indicated a good fit to the expected 1 R:15 S ratio on the assumption that two duplicated recessive genes confer resistance. The segregation ratios in the backcrosses also fitted this model well (Table 2). These two recessive genes were designated as Abr1 and Abr2, respectively. However, the high number of plants with moderate resistance suggested one of the two genes could confer moderate resistance. Under the assumption that two recessive genes confer moderate resistance, and the accumulated effect of these two genes give resistant phenotypes, the expected segregation ratios in F₂, and BC₁ are 1 R:6 MR:9 S, and 1 R:2 MR:1 S. The observed segregation ratios supported this model (Table 2).

In the F₂ population of the cross ‘Titore’ × ILL 5588, the observed numbers of resistant, moderate resistant, and susceptible plants were 73, 20, and 7 (Table 2). When the 20 moderate resistant plants were regarded as susceptible, the result fitted the

Table 2 Observed segregation patterns of reactions to *Ascochyta lentis*, and χ^2 test for the goodness of fit to various inheritance models. (G = generation; R = resistant; MR = moderately resistant; and S = susceptible.)

Cross (inheritance model)	G	R	MR	S	Expected ratio	P
Titore × Indianhead (two additive recessive genes)	F ₁	90				
	F ₂	7	40	55	1:6:9	0.887
	BC ₁	16	30	13	1:2:1	0.851
	BC ₂	—	—	59	—	—
Titore × ILL 5588 (one dominant R, one dominant MR)	F ₁	100				
	F ₂	73	20	7	12:3:1	0.893
	BC ₁	28	17	15	2:1:1	0.819
	BC ₂	55	—	—	—	—
Titore × ILL 5684 (one dominant R)	F ₁	95				
	F ₂	98		30	3:1	0.683
	BC ₁	35		30	1:1	0.535
	BC ₂	60	—	—	—	—
Titore × Laird (one recessive MR)	F ₁		87			
	F ₂	—	25	70	1:3	0.767
	BC ₁	—	28	42	1:1	0.146
	BC ₂	—	—	60	—	—
Titore × W6 3192 (two complementary genes)	F ₁	20				
	F ₂	39	—	29	9:7	0.855

expected 3 R:1 S segregation ratio under the assumption that one dominant gene confers resistance very well. The backcross data supports this model well.

Using the same argument as for 'Indianhead' × 'Titore' the moderate resistance may be conferred by another gene. The observed segregation ratio of the F₂ gave a good fit to a 12 R:3 MR:1 S ratio expected under a model of one dominant gene for resistance and one dominant gene for moderate resistance (Table 2). The expected segregation ratio under this two-gene model is 2 R:1 MR:1 S in the BC₁ progeny, which were strongly supported by the observed segregation (Table 2). Therefore, apart from the gene for resistance, there was another gene conferring moderate resistance. The gene for resistance was designated AbR3 and that for moderate resistance was designated as AbR4.

In the F₂ generation of the cross 'Titore' × ILL 5684, 98 individuals were resistant, and 30 were susceptible, and none were moderately resistant (Table 2). This fitted to the 3 R:1 S ratio very well, suggesting a single dominant gene controls resistance. In the progeny of backcross with the resistant parent all plants were resistant, whereas the segregation ratio in the progeny of backcross with the susceptible parent was very close to 1 R:1 S (Table 2). These ratios suggest one dominant resistance gene confer resistance observed in ILL 5684. The gene was designated AbR5 though it could be allelic to AbR3.

In the F₂ progenies of 'Titore' × 'Laird', 25 plants were moderately resistant and 70 were susceptible (Table 2). This could be fitted to the 1 MR:3 S ratio. The backcross with the resistant parent showed a 1 MR:1 S, whereas the backcross with the susceptible

Table 3 Observed segregation patterns of *Ascochyta lentis* reactions of lentil (*Lens culinaris*) crosses made to test allelic relationships, and χ^2 test for the goodness of fit. (G = generation; R = resistant; MR = moderately resistant; and S = susceptible.)

Cross	G	R	MR	S	Expected ratio	P
Titore × (ILL 5684 × W6 3192)	F ₁	87	–	23	All resistant*	–
Titore × (ILL 5588 × W6 3192)	F ₁	57	9	12	All resistant†	–
Indianhead × Laird	F ₁	–	–	95		
	F ₂	7	68	50	1:1:2‡	0.000
ILL 5588 × ILL 5684	F ₁	97	–	–		
	F ₂	100			All resistant§	–

* Assuming that AbR5 is allelic to AbR7 or AbR8.

† Assuming that AbR3 is allelic to AbR7 or AbR8.

‡ Assuming that AbR6 is allelic to AbR1 or AbR2.

§ Assuming that AbR5 is allelic to AbR3.

Table 4 Genotypes of the five lentil (*Lens culinaris*) cultivars and one inbred of *L. ervoides* for the seven genes confer resistance to *Ascochyta lentis* after the allelism has been tested. (Only one allele is given for each gene; allele in bold confers resistance.)

Cultivars/ inbreds	Loci						
	1	2	3	4	5	6	7
Indianhead	Abr1	Abr2	Abr3	Abr4	AbR5	Abr6	Abr7
ILL 5588	AbR1	AbR2	AbR3	AbR4	AbR5	AbR6	Abr7
ILL 5684	AbR1	AbR2	AbR3	Abr4	AbR5	AbR6	Abr7
Laird	AbR1	AbR2	Abr3	Abr4	Abr5	Abr6	Abr7
Titore	AbR1	AbR2	Abr3	Abr4	AbR5	AbR6	Abr7
W6 3192	AbR1	AbR2	Abr3	Abr4	AbR5	Abr6	AbR7

parent showed that all plants were susceptible (Table 2). These segregation patterns suggested one recessive gene confers moderate resistance in 'Laird', and it is designated as *Abr6* though it could be *Abr1* or *Abr2*.

The F_1 plants of 'Titore' \times W6 3192 were resistant despite that neither parent was resistant. For the F_2 progenies, 39 plants were resistant and 29 were susceptible, which was close to the 9:7 ratio expected under a model of two dominant complementary genes are responsible for the resistance. The gene in 'Titore' is designated as *AbR7* and that in W6 3192 as *AbR8*.

Six resistance genes in the four resistant cultivars/inbreds and two resistance genes in the two susceptible cultivars/inbreds were postulated with the assumption that they are different. However, it is possible that *Abr6* is allelic to *Abr1* or *Abr2*, whereas *AbR5* may be allelic to *AbR3*.

Allelic relationships

Because a dominant gene complementary to the dominant gene in W6 3192 presents in 'Titore', the susceptible cultivar, the presence or absence of this gene in other resistant cultivars need to be confirmed before the nature of genes in these cultivars can be determined. 'Indianhead' does not contain *AbR7* and *AbR8* because the crosses of 'Indianhead' with both W6 3192 and 'Titore' have the same segregation pattern in the F_2 generation. The same argument holds true for 'Laird'.

If the *AbR5* gene is allelic to *AbR7* (*AbR8*), both *AbR7* and *AbR8* must be in presence in ILL 5684 (because it is a resistant cultivar), and all the progenies of cross 'Titore' \times (ILL 5684 \times W6 3192) should be resistant. This clearly is not supported by the observation, thus, *AbR5* is not allelic to *AbR7* (Table 3). Under the condition that *AbR5* is independent, if ILL 5684 contained *AbR7* or *AbR8* one of the crosses to 'Titore' or W6 3192 would give the ratio of 57 R:7 S, rather than the 3 R:1 S produced. Therefore, ILL 5684 does not contain *AbR7* and *AbR8*. Consequently, *AbR5* is an independent locus of *AbR7* and *AbR8*, and ILL 5684 does not contain either of these two genes. Based on the same arguments, *AbR3* is independent of *AbR7* and *AbR8*, and ILL 5588 does not contain these two genes. Therefore, the genes conferring high resistance in ILL 5588 and ILL 5684 do not require a complementary gene to express resistance, and the dominant gene for moderate resistance in ILL 5588 does not show complementary effect to the gene in 'Titore'.

In the F_2 progenies of ILL 5588 \times ILL 5684, no plants were moderately resistant or susceptible. Therefore, the dominant gene in ILL 5684 (*AbR5*) is allelic to the dominant gene conferring resistance in ILL 5588 (*AbR3*) (Table 3). The observed segregation ratio in the F_2 population of the cross of 'Laird' \times 'Indianhead' was 7 R:68 MR:50 S ratio (Table 3), which was highly significantly different from the expected segregation 1 R:1 MR:2 S ratio under the assumption that the gene in 'Laird' was allelic to one of the two genes in 'Indianhead' ($P < 0.001$). Therefore, the recessive gene in 'Laird' (*Abr6*) was independent of the recessive genes in 'Indianhead' (*Abr1* and *Abr2*). The observed segregation could fit the 4 R:33 MR:27 S ratio expected under the assumption that recessive gene in 'Laird' is independent of the two recessive genes in 'Indianhead'.

Based on the above results, the genotypes of the six cultivars (lines) with regards for the seven resistance loci were given in Table 4.

DISCUSSION

The segregation ratios observed in this study suggested that ILL 5588 had two dominant genes, one for resistance and one for moderate resistance. Ford et al. (1999) proposed a single dominant gene model for the foliar resistance in ILL 5588. However, their data would support our model if they had regarded plants scored as 5 as moderately resistant. It is likely that the gene identified by Ford et al. (1999) was the one for resistance (data not shown). This highlights an important issue of scoring methods used to infer inheritance models for disease resistance using segregation analysis. Using different thresholds may lead to different inheritance models. A simple way to set thresholds is to use the resistance levels of the parents as a reference. All plants that are within the level of resistance shown by resistant parent should be regarded as resistant and vice versa. The plants with scores that do not fall in the resistance ranges of either parent need to be classified carefully. 'Laird', a cultivar showed score 5 in this study, has been used as cultivar with moderate resistance for long time in Canada (Morrall 1997). Therefore, we grouped plants with score 5 as moderately resistant. We are not aware of reported studies of the inheritance of foliar resistance to ascochyta blight of the other three resistant cultivars.

Two models could interpret the inheritance of resistance in 'Indianhead'. Two recessive genes with

additive effect are responsible for resistance when plants scored as 5 are separated from susceptible and resistant classes and regarded as moderately resistant. Two independent recessive genes are suitable when they were regarded as susceptible. Chowdhury et al. (2001) proposed a single receive gene model using a small F_2 population (60) of 'Indianhead' \times 'Eston'. Because the correspondence between foliar rating and the percentage of seed infection used for grouping plants into resistant and susceptible categories was unknown, these results may, or may not, be consistent with the model of two duplicated recessive genes proposed for seed resistance in this cultivar (Andrahennadi 1997).

The segregation pattern of the two susceptible parents W6 3192 and 'Titore' confirmed the model of two dominant complementary genes proposed by Ahmad et al. (1997). However, their generalisation of this model was not supported, since these two genes were not present in all other cultivars tested.

Most previous studies of the inheritance of lentil ascochyta blight had used seed infection rate to develop the inheritance model. The lack of an established relationship between seed resistance and foliar resistance makes it difficult to compare our results with the reported findings. Though all the four resistant cultivars used in present study were resistant when seed infection rate was used to measure the resistance, the inheritance models established for foliar resistance in our study were different from those proposed for seed resistance. For instance, Tay (1989) suggested that two dominant complementary genes for resistance and one recessive gene for moderate resistance were responsible for seed resistance in ILL 5588. Two dominant complementary genes were proposed for seed resistance in ILL 5684 (Tay 1989), compared with one dominant gene for foliar resistance in our study. Similarly, two recessive genes with additive effect were responsible for foliar resistance in 'Indianhead' in this study, whereas two duplicated recessive genes were proposed for seed resistance (Andrahennadi 1997). The model for foliar resistance (one recessive gene) was the same as that proposed for seed resistance (Andrahennadi 1997) in 'Laird'.

The dominant gene for resistance in ILL 5684 was found to be allelic to the dominant gene conferring resistance in ILL 5588.

It should be pointed out that the inoculum used in this study was isolated from infected seed collected in New Zealand without going through the single spore culture step. Therefore, the inoculum

could be a mixture of several isolates. Though the distinctive disease reactions of parental inbred lines and cultivars suggested that the inoculum was suitable for quantifying the different disease reactions for our purpose, the possible genetic variations of pathogenicity among different isolates may contribute to the differences between our results and those of other authors. In fact, most of other authors also used inoculum of multiple isolates. The different pathogenicities of different isolates of *A. lentis* have been reported in the literature. For instance, Ahmed & Morrall (1996) grouped 84 isolates of *A. lentis* from western Canada, and isolates from 13 other countries into weak, intermediate, and high virulence forms based on their virulence on 10 lentil lines and cultivars (differentials). Nasir & Bretag (1997) identified six pathotypes based on the different reaction of six cultivars to 39 isolates from Australia. Most of the isolates were virulent to some of the cultivars. There were three isolates that infected all the cultivars, and five isolates that were avirulent to all the cultivars. More detailed studies using different pathotypes are needed to understand the host-pathogen relationships in lentil ascochyta blight so that more efficient breeding programs can be developed.

CONCLUSIONS

Seven genes that confer (moderate) resistance to foilar infection by *A. lentis* were identified in this study. These and other genes identified by other studies provide the basis to design an ascochyta blight resistance breeding program. The simplest strategy, which is used in many lentil breeding programs, is to use the dominant resistance gene contained ILL 5588, since it is easy to transfer a dominant gene. ILL 5684 can be used in the same way as ILL 5588, since it also contains this resistance gene. The receive genes identified in this study confer only moderate resistance. The fact that four pathotypes of *A. lentis* were identified (Nasir & Bretag 1997) necessitates genes confer resistance to different pathotypes to be combined into one cultivar to provide durable resistance. Whether these genes reported in this paper also confer resistance to other pathotypes is not clear, since only one isolate was used in this study. However, it is unlikely that the resistance conferred by these genes can all be overcome by other pathotypes, as other studies using different isolates showed that all the four resistance lines we used were resistant. Therefore, breeding for

resistance based on gene pyramiding can start with these genes. Ye et al. (2002) discussed the current and future strategies for breeding for ascochyta blight in more detail.

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