Inheritance of Leaf Rust Resistance in Wheat Cultivars Morocco and Little Club

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ABSTRACT

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Wheat cultivars Morocco and Little Club were considered to lack resistance genes to the leaf rust pathogen, *Puccinia recondita* f. sp. *tritici*, until several hundred cultures avirulent to one or both were obtained in a worldwide survey conducted by the Cereal Rust Laboratory, St. Paul, Minnesota. These cultures were obtained from many countries and were most commonly isolated from durum wheat. Two of these cultures are 89BGR4136-3, avirulent to Morocco, and 87ETH4090-4, virulent to some durum cultivars but avirulent to all but a few bread wheat cultivars. Progeny of a cross of two bread wheat cultivars Morocco/Little Club generally reported as susceptible to wheat leaf rust were evaluated. Morocco possesses a recessive resistance gene (*Lr*Mo) to the former isolate, whereas Little Club has a dominant resistance gene (*Lr*LC) to the latter isolate.

Resistance to leaf rust was first reported in the wheat cultivar Malakof (to race 12) by Mains et al in 1926 (11). This gene was designated *Lr*1 by Ausemus et al in 1946 (2). Currently, over 35 loci are known for resistance to wheat leaf rust, and nearly all the genes are inherited as a dominant character. However, *Lr*13 and *Lr*14a are incompletely dominant (4,13) and *Lr*30 is recessive (5). Most of the genes for leaf rust resistance are detectable in the seedling stage of plant growth, but *Lr*12, 13, 22a, 22b, 34, and 35 are primarily effective after the boot formation stage (14,16). Most resistance genes act independently to produce resistance; two exceptions are *Lr*27 and *Lr*31, which act in a complementary manner (17). Linkages between leaf rust, stem rust, and stripe rust resistance genes are common, especially when resistance is transferred between species. For example, *Lr*19 is linked to *Sr*25, *Lr*20 to *Sr*15 (11), *Lr*26 to *Sr*31 and *Yr*9 (7), *Lr*24 to *Sr*24 (12), *Lr*34 to *Yr*18, and *Lr*37 to *Sr*38 and *Yr*17. Expression of leaf rust resistance is often modified by the host background, and inheritance may vary depending on host background, environmental conditions (9), and pathogen culture.

A recent worldwide survey of wheat rust virulence (8) conducted by the USDA Cereal Rust Laboratory, St. Paul, Minnesota, detected many previously unknown avirulences. The importance of leaf rust to wheat production makes it essential to determine the limits of the virulence and avirulence of the pathogen population. This study was undertaken to see if the resistance in wheat cultivars Morocco and Little Club was inherited as single genes to two cultures from rather diverse sources. Because of the extreme avirulence of the two cultures used, including avirulence to host cultivars previously thought to be universally susceptible, the possibility existed that resistance might not be of the gene-for-gene type.

MATERIALS AND METHODS

Plant material. Morocco (PI 431591) is an early maturing, medium-tall cultivar with soft white kernels and awned spikes. This spring cultivar has been used by CIMMYT (Centro Internacional de Mejoramiento de Maiz y Trigo) as a susceptible check to the three rusts (leaf, stem, and stripe) on a worldwide basis for over 20 yr. The origin of Morocco is obscure, but it is considered to be a North African cultivar. Little Club (CI 4066) was probably introduced into the United States from Chile, but its earlier history is not known. Its plants are of spring habit and midseason maturity and have awnless spikes and short, soft kernels. Little Club is distinguished from other white glumed club wheats in having longer, more slender pointed kernels. It has been used as a susceptible seedling host for leaf rust in North America and Europe for 70 yr.

Pathogen isolates. The two isolates of the wheat leaf rust pathogen, *Puccinia recondita* Roberge ex Desmaz. f. sp. *tritici* (Eriks. & E. Henn.) D.M. Henderson, selected to evaluate the Morocco/Little Club progeny were 89BGR4136-3 and 87ETH4090-4. Isolate 89BGR4136-3 was collected from bread wheat in Bulgaria and is designated as race TCSB (7,9) with a virulence/avirulence formula of p1,2a,2c,3a, 3ka,11,17,26/9,10,16,18,21,23,24,30 (8). Although virulent to many bread wheats, 89BGR4136-3 is avirulent to Morocco, the widely used susceptible host. Isolate 87ETH4090-4 was collected from durum wheat in Ethopia and is avirulent to nearly all bread wheat cultivars but virulent to many modern durum cultivars. No race designation could be obtained for 87ETH4090-4 because the background parent of the line used for differential hosts, Thatcher, was resistant, as were most other bread wheats. These cultures were obtained in the worldwide survey of wheat rust virulence (8).

Evaluation of F_2 seedlings. A total of 96 F_2 seeds of the cross Morocco/Little Club were sown in 7.5-cm pots containing vermiculite. Six pots, 16 seeds (four rows of four seeds each) per pot, were placed in a 15 × 23 cm tray and kept in a greenhouse at 16–24 C. Seedlings were inoculated with isolate 89BGR4136-3 7 days after planting, when the first leaf was fully expanded.

The inoculum was increased and stored at −45 C in size-00 gelatin capsules, which (with lids removed) were kept overnight in 80% RH. The next day,

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Table 1. Infection type produced on parental wheat cultivars and F_1 when inoculated in the seedling stage with selected leaf rust cultures

Isolate[a] Race[b]	Infection type[c] Morocco	Little Club	F_1
89BGR4136-3 TCSB	0	4	4
87ETH4090-4 ...	4	1C	12C

[a]Year of isolation, source country, collection number, and isolate; 89BGR4136-3 collected originally from bread wheat in Bulgaria, 87ETH4090-4 collected originally from durum wheat in Ethiopia.

[b]After Long and Kolmer (10), with fourth set consisting of *Lr*10, 18, 21, and 23. No race designation could be obtained for 87ETH4090-4 because the background parent, Thatcher, was resistant.

[c]0 = Immunity, 1C = minute uredinia surrounded by severe chlorosis, 12C = somewhat larger uredinia than 1C with chlorosis, and 4 = fully compatible.

the capsules were half-filled with Soltrol 130 (a light mineral oil used as a carrier) (15), the lids were replaced, and the capsules were shaken gently to make an oil suspension of the urediniospores. This suspension was atomized onto the leaves of seedlings in an inoculation booth (3). Seedlings were left on a bench for 30 min after inoculation to allow the oil to evaporate. Plants were then placed into a dew chamber and kept in darkness for 20 hr at 18–24 C. Water-soluble fertilizer (2.5 gm of 23-19-17 N-P-K) was added to each tray when plants emerged, when they were removed from the dew chamber, and after removal of leaves from the first test. Infection types, determined by lesion characteristics, were recorded 13–15 days after inoculation.

After data were collected on the inoculation with isolate 89BGR4136-3, F_2 leaves were removed from the plants. Ten days later, the regrowth was inoculated with isolate 87ETH4090-4.

RESULTS AND DISCUSSION

Isolate 89BGR4136-3 gave infection type 4 (fully compatible) on Little Club and infection type 0 (immune) on Morocco (Table 1). Of 95 viable F_2 seedlings, 22 were resistant and 73 were susceptible, like the parent and the F_1 plants; the χ^2 value for one gene ratio (3:1) was 0.125 (P = 0.70–0.90) (Table 2). Thus, Morocco is postulated to have a recessive gene for resistance to this isolate. None of the previously described 44 leaf rust resistance alleles have been reported to be present in Morocco, and Morocco has not previously been reported to be resistant to wheat leaf rust.

Table 2. Number of resistant and susceptible F_2 progeny in a cross of wheat cultivars Morocco/Little Club when inoculated with two selected leaf rust cultures in the seedling stage

Isolate	No. of F_2 plants[a] R	S	Total	χ^2
89BGR4136-3	22	73	95	0.125
87ETH4090-4	68	22	90	0.015

[a]R = resistant, S = susceptible; χ^2 for 1:3 or 3:1 ratios.

Hence, resistance to this isolate must be controlled by an allele different from those previously described. The allele has been temporarily designated *Lr*Mo (1).

Isolate 87ETH4090-4 gave infection type 1C (minute uredinia surrounded by chlorosis) on Little Club and infection type 4 (fully compatible) on Morocco (Table 1). Five of the 95 F_2 seedlings died. Of the remaining 90 seedlings, 68 were resistant and 22 were susceptible (Table 2). Analysis for a single hypothesis (1:3 ratio) gave a χ^2 value of 0.015 (P = 0.90–0.95) (Table 2). Little Club was also thought to lack genes for leaf rust resistance, and thus resistance found in this study has not been described before. The allele has been temporarily designated *Lr*LC.

The finding of two new resistance genes with only two (selected) cultures raises the question of how many more alleles for race-specific resistance exist. Culture 89BGR4136-4 is virulent to many of the differential hosts of the NA set (10), attacking *Lr*1, 2a, 2c, 3, 3ka, 11, 17, and 26, but is avirulent to Morocco, a widely used susceptible host in wheat leaf rust studies. Culture 87ETH4090-4, collected from durum wheat, is virulent to many durum cultivars but avirulent to most bread wheat cultivars (8), yet resistance to this culture in Little Club was due to a single gene. This culture produces a range of infection types on other bread wheats (8), leading us to believe that additional resistance genes could be detected with this culture.

The trend has been to consider durum wheat (AB genomes) more resistant to leaf rust than the bread wheats (ABD genomes). This is due in part to suppressors of resistance on the AB by the D genome of some bread wheat cultivars (6). However, the virulence of 87ETH4090-4 to durum wheat and the avirulence to nearly all bread wheat indicate that other genetic differences exist between these crops. The genes identified obviously have little use in breeding resistant wheats, but their presence could be of value in studying populations of *P. recondita* if they could eliminate a portion of the individuals. This would be most important in studying leaf rust populations from durum or other non-bread wheat hosts. These genes could also be important in studying progeny of crosses between pathogen cultures.

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