GENETICS OF LEAF RUST RESISTANCE OF SELECTED URUGUAYAN WHEAT CULTIVARS.

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GENETICS OF LEAF RUST RESISTANCE OF SELECTED URUGUAYAN WHEAT CULTIVARS

BY

SILVIA GERMAN

A Thesis/Practicum submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements for the degree of

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To my daughter, Romina

my sons Alejandro, Martín and Rafael

and my husband Hugo

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ABSTRACT.

Leaf rust (caused by *Puccinia recondita* f.sp. *tritici*) is one of the most important diseases of wheat (*Triticum aestivum*) in Uruguay and on a worldwide basis. The genetic basis for leaf rust resistance in Uruguayan cultivars is unknown. Incorporation of different resistance genes in the germplasm pool to ensure genetic diversity and longer lasting resistance is more difficult if the identity of the resistance genes present is not known. The objective of this research was to determine which leaf rust resistance genes are present in seven Uruguayan cultivars released by INIA La Estanzuela. A single plant selection of each cultivar was crossed with the susceptible cultivar Thatcher. F_1 plants were selfed to obtain F_2 plants and backcrossed to Thatcher to obtain BCF_1 plants. The number of seedling genes present in the cultivars was determined based on the number of resistant or segregating and susceptible BCF_2 and F_3 families. The cultivars and BCF_3 lines with single resistance genes were tested with a number of leaf rust isolates differing in virulence to postulate the seedling genes present. BCF_2 families were field tested to study adult plant resistance (APR). The presence of APR genes *Lr13* and *Lr34* was studied in intercrosses of the selected cultivars and the Thatcher lines with these genes. The presence of genetic markers for *Lr26* (absence of gamma gliadin 45), *Lr13* (hybrid necrosis allele *Ne2m*) and *Lr34* (leaf tip necrosis *Ltn*) in the cultivars was also assessed. Estanzuela Tarariras had *Lr3bg*

and APR genes *Lr13* and *Lr34*. Est. Benteveo had *Lr3*, *Lr14a*, *Lr26* and APR gene *Lr13*. Est. Pelón 90 had *Lr1*, *Lr17*, *Lr26* and possibly *Lr14a* and APR gene *Lr34*. INIA Boyero had *Lr26*, additional seedling resistance, APR genes *Lr13*, *Lr34* and possibly a previously unidentified APR gene. Est. Calandria had *Lr3bg*, *Lr16*, *Lr24* and possibly *Lr34*. Est. Federal had *Lr10*, an additional seedling resistance gene and *Lr34* or a different effective APR gene. Est. Halcón had *Lr10*, *Lr16* and additional seedling resistance, which could be conditioned by one or both *Lr14* alleles or previously unidentified seedling genes.

1. INTRODUCTION.

Spring wheat (*Triticum aestivum* L. em. Thell) is sown in Uruguay during the winter, from April to August, and harvested from mid November to the beginning of January. In the last ten years, an average of 190,000 hectares were planted to wheat annually, with an average yield of 1.85 tons/ha. The wheat growing area extends between 31 and 35° South, not over 100 m above sea level.

The humid climate and mild springs in Uruguay favor development of wheat diseases. Leaf rust (caused by *Puccinia recondita* Roberge ex Desmaz. f.sp. *tritici* Eriks.) is one of the most important wheat diseases in Uruguay (Perea and Díaz, 1981), and on a worldwide basis (Samborski, 1985; Roelfs et al., 1992).

Initial leaf rust infections are generally observed from mid August to mid September. In certain years infections in early May are observed in early planted crops, indicating the rust probably oversummers locally. The long growing season allows many infection cycles which makes leaf rust a very destructive disease (Germán and Kolmer, 1994) causing yield losses as high as 50 % (Germán et al., 1986).

Uruguay and the adjacent areas of Argentina, Brazil and Paraguay and the lowlands of Bolivia together comprise one epidemiological area of leaf rust (Saari and Prescot, 1985). Movement of rust inoculum is not restricted by natural barriers within this area, from which the same leaf rust races

have been found (Vallega, 1943; Medeiros and Barcellos, 1994).

Traditionally, the control of leaf rust worldwide and in Uruguay has been based on the selection of resistant cultivars. The resistance in Uruguayan cultivars was initially based on selections by Dr. A. Boerger from land cultivars. Americano 44d, released in 1918, has been identified as a source of durable resistance to leaf rust (Roelfs, 1988b). From 1918 to 1950 the germplasm originated mostly from Uruguay, Argentina and Brazil (Luizzi et al., 1983). In later years, rust resistant germplasm was also selected from the USDA International Spring Rust Nursery and from nurseries organized by the Rockefeller Foundation and later by CIMMYT (Luizzi et al., 1983).

Cultivars when initially released are highly resistant to leaf rust. However the resistance is often eroded due to selection of rust races virulent to resistance genes in the cultivars. The high level of resistance in released Uruguayan cultivars has been short lived (Germán, 1995) as has often occurred worldwide (Roelfs, 1988b). The high level of resistance to leaf rust in Uruguayan cultivars is probably due to the combination of seedling and APR. APR remaining after the pathogen population adapts to the seedling resistance is not enough to prevent yield losses, and cultivars are withdrawn from cultivation. Another reason for the rapid adaptation of leaf rust populations worldwide, is that single seedling resistance genes are often the only effective genes

in newly released cultivars (Roelfs, 1988b). The basis of the most durable resistance to leaf rust in common wheat has been combinations of APR genes *Lr13* and *Lr34*, and perhaps also *Lr12* and *Lr34* (Roelfs, 1988b). Combinations of effective resistance genes have provided the longest lasting resistance to leaf rust (Kolmer et al., 1991).

The leaf rust resistance in Uruguayan cultivars appears to have been derived from a number of different sources. However, the number and identity of the resistance genes are unknown. The genetic basis of the current resistance may be narrow, with the possible risk that resistance is conditioned by the same few genes in many cultivars. Incorporation of different resistance genes in a germplasm pool to ensure genetic diversity and longer lasting resistance is also more difficult if the identity of the resistance genes present is unknown.

The objective of this research was to determine which leaf rust resistance genes are present in selected cultivars released by the Uruguayan breeding program of the Instituto Nacional de Investigaciones Agropecuarias (INIA) at La Estanzuela.

2. LITERATURE REVIEW.

2.1. WHEAT LEAF RUST IN URUGUAY.

Spring wheat is fall or winter sown in Uruguay since mild winters allow a very long planting season. Two types of wheat were developed to cover the entire planting season: photoperiod sensitive late maturity wheats, recommended for planting from April to June, and photoperiod insensitive early maturity wheats, recommended for planting in June and July (Castro, 1995). Later sowing dates are common. Traditionally, late maturity wheats have been used in Uruguay for grazing and grain production (Tavella et al., 1995). The two wheat types head in October - mid November and are harvested from mid November to early January.

Average rainfall of 1000 to 1100 mm is evenly distributed throughout the year. The average temperature of the coldest month is slightly above 10 C. Wheat diseases are favored by warm temperature and rainfall during the spring. Prevalent diseases are fusarium head blight (caused by *Gibberella zeae* (Schw.) Petch.), septoria leaf blotch (caused by *Septoria tritici* Rob. ex Desm.), leaf rust (caused by *Puccinia recondita* Roberge ex Desmaz, f.sp. *tritici* Eriks. and Henn) and stem rust (*Puccinia graminis* Pers. f.sp. *tritici* Eriks. and Henn). In recent years, tan spot (caused by *Pyrenophora tritici-repentis* (Died.) Drechs.) has increased in importance (Díaz, 1995).

In Uruguay leaf rust occurs annually with varying

intensity among years. An average leaf rust severity of 10% (modified Cobb scale, Peterson et al., 1948) with an average incidence of 62% of farm fields was found over a 12 year survey (1968-1979) (Perea and Díaz, 1981). Yield losses vary with seasonal weather, cultivar resistance and growth stage at the onset of the epidemic. Losses of 10 to 15% have been measured in epidemics that started late in the growing season (Díaz and Germán, 1983) and losses as high as 50 % were estimated in the early infected (40 S in boot stage), highly susceptible cultivar La Paz INTA (Germán et al., 1986).

Severe epidemics of leaf rust have been recorded since the 1920's. The Argentine cultivar 38 MA was severely damaged by leaf rust in 1927 (Boerger, 1943). In 1944 the most common wheat cultivars were severely damaged by leaf and stem rust (Ribeiro, 1953). In 1985, a new leaf rust race virulent to *Lr9* became prevalent in the region and caused a severe epidemic on the Argentine cultivar La Paz INTA wich has *Lr9* (Germán et al., 1986). In 1994 the Uruguayan cultivar Estanzuela Federal (Est. Federal) had losses of 30% or more due to leaf rust (Díaz and Kohli, 1995). Leaf rust surveys started in 1989 (Germán and Kolmer, 1994) showed that the predominant races have changed very rapidly in Uruguay, which can affect leaf rust infection on wheat cultivars. Susceptibility to leaf and stem rust historically have been the most important causes of wheat cultivar replacement in Uruguay (Luizzi et al, 1983). On average, resistance in cultivars released after 1960 has been

effective for four to five years (Germán, 1995).

Leaf rust resistance in new wheat cultivars is one of the main objectives of the INIA wheat breeding program at La Estanzuela. Resistance has been selected under field conditions with naturally occurring epidemics of the leaf rust fungus (Germán, 1982).

2.2. WHEAT BREEDING IN URUGUAY.

Wheat breeding in Uruguay was started in 1912 by the German scientist Alberto Boerger. The first cultivars released in 1918 were derived from single plant selections of heterogeneous land races. Americano 26n, Americano 44d and Pelón 33c (Boerger, 1928) were grown extensively in Uruguay and also in Argentina, where these cultivars were known as Universal I, Universal II and Favorito (or Ideal 1), respectively. Boerger's first selections were the basis for the traditional wheats in both countries.

After 1918 the wheat cultivars released in Uruguay were derived from crosses between selections of land races, and later, mostly from adapted germplasm from the region (Uruguay, Argentina and Southern Brazil). Many cultivars from the Klein and Buck breeding program in Argentina, and some from Brazil, including Frontana, were also grown in Uruguay, and used as parents at La Estanzuela (Ribeiro, 1953). After the 1950's, wheat lines selected from the USDA International Spring Wheat Rust Nursery, the Rockefeller Foundation and CIMMYT germplasm

were used as sources of leaf and stem rust resistance in crosses with locally adapted wheats (Luizzi et al., 1983).

Based on the germplasm used in the breeding program and selection for leaf rust resistance under field conditions, it is very likely that APR has been selected throughout the century in the Uruguayan national program and may be present in current cultivars.

The presence of APR in Uruguayan cultivars has probably caused some misinterpretations regarding cultivar resistance and the importance of leaf rust in yield loss. As an example, Marcos Juarez INTA, an Argentine cultivar considered susceptible to leaf rust, was widely grown in Uruguay and Argentina over a period of several years, but did not have significant yield reductions (Germán and Abadie, 1986). Buck Ñandú, another Argentine cultivar considered highly susceptible to leaf rust, had maximum 10% yield reduction with a leaf rust severity of 80% in dough stage. This led to the erroneous concept that leaf rust usually started late in the growing season and was not a very important disease in terms of economic yield loss (Díaz and Germán, 1983).

In 1985, leaf rust severities on La Paz INTA of 40% in the boot stage, 70% at heading and 100% at watery stage caused yield losses of 50% in late planted crops (Germán et al, 1986). It became clear that other cultivars grown in previous years were not highly susceptible when compared with La Paz INTA. Cultivars such as Marcos Juarez INTA probably carry APR

while La Paz INTA probably has only seedling resistance. The loss of effective resistance in La Paz INTA demonstrated the yield loss potential of leaf rust and the importance of APR.

2.3. WHEAT LEAF RUST RESISTANCE.

The control of leaf rust has traditionally been based on the use of isolate specific genes. Forty six genes determining leaf rust resistance (*Lr* genes) at 40 different loci have been identified to date and given official designations which are found in the Catalogue of Gene Symbols for wheat (McIntosh, 1993). The characteristic low infection type (IT), chromosome location and linkage relationships are known for most genes and have been reviewed by several authors (Browder, 1980; Roelfs, 1988b; Knott, 1989; Long and Kolmer, 1989; Roelfs et al., 1992; McIntosh et al., 1995; Kolmer, 1996). Twenty five resistance genes were originally present in wheat (most in *Triticum aestivum*) and 21 have been introgressed from related species within the tribe *Triticeae*: *Triticum umbellulatum* (*Lr9*), *Agropyron elongatum* (*Lr19, Lr24, Lr29*), *Triticum tauschii* (*Lr21, Lr22a, Lr32, Lr39, Lr40, Lr41, Lr42, Lr43*), *Secale cereale* (*Lr25, Lr26, Lr45*), *Aegilops speltoides* (*Lr28, Lr35, Lr36, Lr37*), *Agropyron intermedium* (*Lr38*), *Triticum aestivum spelta* (*Lr44*).

Most of the identified leaf rust resistance genes are expressed from the first leaf stage (seedling resistance genes), but others are optimally expressed at a later stage of

plant development (APR): *Lr12, Lr13* (Dyck et al., 1966), *Lr22a, Lr22b, Lr34, Lr35*, Roelfs et al., 1992).

Specific virulence in *P. recondita* f.sp. *tritici* can be found to most leaf rust resistance genes used in wheat cultivars (McIntosh et al., 1995). Following the release of resistant cultivars, isolates with the corresponding virulences are selected in the leaf rust population. These isolates rapidly increase in frequency and render the resistance ineffective, as has occurred to wheats in the prairie region of Canada (Kolmer, 1989).

Genetic studies have indicated that the same leaf rust resistance genes were present in wheat collections that had very different origins (Shang et al., 1986; Claude et al., 1986). This indicates that the leaf rust resistance gene pool in common wheat may be nearly exhausted. Since the usable genetic base is narrow, and the pathogen has adapted to most deployed resistances, a continuing search for new resistance in wheat and related species is required (Kolmer, 1996).

2.4. EXPRESSION OF RESISTANCE GENES.

Resistance genes in wheat and avirulence genes in *Puccinia recondita* f.sp. *tritici* operate in what has been described a gene-for-gene basis (Samborski and Dyck, 1968). Genetic specificity in host - parasite systems was first demonstrated by Flor (1955) in the flax - flax rust system. Generally for each resistance gene in the host there is a

corresponding avirulence gene in the pathogen. Incompatible ITs occur on resistant genotypes when the rust isolates have the complementary allele conditioning avirulence. Compatible ITs result when the host is susceptible (lacks resistance genes) or when the pathogen genotype lacks avirulence genes.

For some corresponding resistance and avirulence genes, the interaction differs from the classical one-to-one relationship. There are three alleles at the *Lr2* locus, but avirulence in the pathogen to all three is conditioned by a single gene and a modifier (Samborski and Dyck, 1968; Dyck and Samborski, 1974). Three alleles were also described at the *Lr3* locus (Haggag and Dyck, 1973). The corresponding virulence genes in the pathogen were independently inherited. Virulence to *Lr3bg* is conditioned by two complementary genes in *P. recondita tritici* (Haggag et al., 1973).

2.4.1. Gene interaction.

When two or more genes for rust resistance occur in a wheat line, the gene conditioning the lowest IT is epistatic to other genes (Dyck and Kerber, 1985), and should determine the IT expressed by the line. However, there are reports of interaction between leaf rust resistance genes. Singh and McIntosh (1984a) found the two complementary genes *Lr27* and *Lr31* (Singh and McIntosh, 1984b) in the Australian cultivar Gatcher. Both genes must be present for the resistance to be expressed. Samborski and Dyck (1982), Sawhney et al. (1989),

Kolmer (1992) and Germán and Kolmer (1992) reported several gene combinations that expressed enhanced resistance compared to lines with the individual genes.

2.4.2. Effect of host and pathogen genotype.

Kolmer and Dyck (1994) tested several corresponding resistance gene - avirulence gene pairs and clearly demonstrated that IT expression and dominance relationships were modified for some gene pair combinations, depending whether heterozygous or homozygous host and/or pathogen genotypes were tested. The ITs of some resistance genes (*Lr2a, Lr2c, Lr3ka, Lr11* and *Lr30*) when homozygous were low or intermediate when tested with isolates of *P. r. tritici* that were homozygous or heterozygous, respectively. Resistance genes *Lr3* and *Lr17* were incompletely dominant when tested with homozygous avirulent leaf rust isolates, and recessive when tested with heterozygous isolates. Avirulence to *Lr3* and *Lr17* was almost completely dominant when tested with homozygous resistant host lines, and recessive when tested with heterozygous resistant host lines.

2.4.3. Host genetic background.

Genetic background can also affect response and dominance expression of resistance genes. The *Lr2* alleles were backcrossed to Thatcher, Prelude and Red Bobs (Dyck and Samborski, 1968). The alleles expressed the most resistance in

Thatcher. *Lr2b* in Prelude was partially dominant in crosses with Thatcher and completely dominant in crosses with Red Bobs; *Lr2c* in Prelude was recessive in crosses with Thatcher and dominant in crosses with Red Bobs (Dyck and Samborski, 1968). *Lr17* was backcrossed to Thatcher and Prelude (Dyck and Samborski, 1968a), and expressed more resistance in the Thatcher (IT 1, Stakman et al., 1962) background, where it was partially dominant. In the Prelude background, *Lr17* had IT 1+ and was recessive.

The cultivar Sinvalocho carries *Lr3*. Certain leaf rust isolates were avirulent to Sinvalocho/*2Thatcher but virulent to Sinvalocho/*6Prelude. A gene in Prelude inhibited the expression of *Lr3* to certain *Lr3* avirulent isolates (Haggag and Dyck, 1973).

2.4.4. Temperature sensitiveness.

The expression of some Lr genes is temperature sensitive. Dyck and Johnson (1983) and Statler and Christianson (1993) found Thatcher lines with *Lr18* were more resistant at lower temperatures, and became completely susceptible at 25-30°C. Thatcher lines with *Lr16*, *Lr17* and *Lr23* had lower ITs at higher temperatures. The temperature sensitivity of these genes was highly dependent on the leaf rust isolate used.

Adult plant resistance genes are also temperature sensitive. *Lr13* is expressed in the seedling stage at 25°C to a limited number of leaf rust isolates (Pretorius et al.,

1984). Under cool temperature *Lr34* can be detected in the seedling stage (Dyck and Samborski, 1982; Singh, 1992c) and expressed higher levels of resistance at the adult plant stage (Pretorius et al., 1994).

2.5. METHODS TO STUDY GENETICS OF RESISTANCE TO RUSTS.

2.5.1. Gene postulation.

Gene postulation has frequently been used to indicate which leaf rust seedling resistance genes are likely present in wheat cultivars (Rizvi and Buchenau, 1994; McVey and Long, 1993; Singh, 1993a; Singh and Rajaram, 1991; McVey, 1989; Statler, 1984; Rizvi and Statler, 1982; Browder, 1973; Loegering et al., 1971).

This method was first developed by Loegering et al. (1971) followed by Browder (1973) based on Person's (1959) analysis of Flor's gene-for-gene concept (Flor, 1955). Gene postulation is based on the comparison of ITs produced on lines with unknown resistance and lines with known resistance genes, using leaf rust isolates which differ in virulence. For wheat leaf rust it is highly advantageous that a complete set of near-isogenic lines (NIL) with single genes for resistance in a common Thatcher background is available (Anderson, 1961). These lines were developed by R.G. Anderson and P.L. Dyck (Kolmer, 1996) at Agriculture and Agri-Food Canada Winnipeg Research Center. Leaf rust isolates with the appropriate combinations of virulences must be available to successfully

use this technique (Roelfs et al., 1992, Kolmer, 1996).

Intercrosses of NILs with the resistance genes have usually supported gene identities generated from IT data (McVey, 1989; Dyck and Jedel, 1989; Rizvi and Buchenau, 1994). Gene postulation provides evidence but not complete proof of resistance gene identity in wheat cultivars (Roelfs et al., 1992).

The identity of APR genes is difficult to prove using gene postulation since adult plant genes generally are not optimally expressed in the seedling stage (Kolmer, 1996). Interaction between resistance genes, as shown for *Lr13* and *Lr34* when combined with effective seedling resistance genes (Kolmer, 1992; Germán and Kolmer, 1992; Samborski and Dyck, 1982) can complicate gene postulation. *Lr34* can express some seedling resistance at cooler temperatures and low light intensities (Dyck and Samborski, 1982; Singh, 1992c). Singh and Rajaram (1991) postulated the presence of *Lr34* in CIMMYT wheat cultivars based on the expression of variable intermediate ITs by certain isolates at 18-22°C, compared with high IT at higher temperatures of 24-27°C. Also, *Lr13* was postulated to be in certain wheat cultivars based on the expression of a mesothetic seedling IT by *Lr13* avirulent isolates in tests at 18-22°C (Singh and Rajaram, 1991).

Gene postulation is a convenient method to identify seedling resistance conferred by one or two genes, since results can be obtained within four weeks (Roelfs et al.,

1992) and a large number of lines can be analyzed (Kolmer, 1996). It is more difficult to infer results for genotypes with three or more resistance genes, and it is not possible to postulate the identity of *Lr* genes when none of the available leaf rust isolates are virulent to the wheat lines being studied.

2.5.2. Genetic analysis of host resistance.

Conventional genetic analysis have been used to estimate the number and identity of resistance genes segregating in crosses between two wheat lines. Genetic analysis is the only method that can be used to conclusively determine the number and identity of seedling and especially APR genes.

Genetic studies of leaf rust resistance have been conducted since 1926 (Mains et al., 1926). Wheat lines are crossed with a susceptible test line and F_1 plants selfed to obtain F_2 plants and/or backcrossed to the susceptible parent to obtain BCF_1 plants. F_2 and/or BCF_1 plants are progeny tested as F_3 and/or BCF_2 families with one or more leaf rust isolates as seedlings and as adult plants in field tests (Kolmer, 1996). Data from F_3 and BCF_2 families are more reliable than data from single F_2 and BCF_1 plants and the segregating material can be tested simultaneously with different leaf rust isolates (Roelfs et al., 1992; Kolmer, 1996).

Using BCF_2 families has the major advantage of requiring smaller number of families compared to using F_3 families

(Kolmer, 1996). More than 300 F_3 families would be needed when three or more resistance genes are segregating to properly use the chi-square statistic for evaluating the goodness of fit of observed to expected segregation ratios (Steel and Torrie, 1980). Only 40 BCF_2 families are required to use the chi-square test for a three gene segregation. Single resistance genes can also be isolated and characterized more easily in BCF_2 families if two or more genes are segregating since many F_3 families would have more than one gene. An additional advantage of the backcross method is that it provides a more uniform genetic background in the segregating populations, which is convenient for field testing when the parents have different maturity or vernalization requirements (Kolmer, 1996; Dyck, 1991).

The backcross method to study inheritance of resistance was used by Anderson (1961), Dyck (1977, 1989; Dyck and Samborski, 1982; Shang et al., 1986) at the Agriculture Canada Research Centre in Winnipeg. In BCF_2 families that segregate for single resistance genes, plants with the lowest infection type can be selected and progeny tested to obtain lines that are homozygous for resistance (Kolmer, 1996). Homozygous BCF_3 lines can be tested with a collection of *P. recondita tritici* isolates to determine if the resistance is due to a previously identified gene or an uncharacterized gene. The definitive proof of gene identity is to cross the cultivar or derived line with a line with the postulated resistance gene. Lack of

susceptible F_2 plants or $_3F$ families when tested with an avirulent leaf rust isolate confirms the identity of the resistant gene present in the cultivar.

2.5.3. Genetic markers.

Genetic markers can also be used to assist in identification of resistance genes in wheat cultivars. Morphological traits, storage proteins, enzymes and other disease resistance genes have been mapped and used as markers for rust resistance genes (McIntosh, 1993). Howes et al. (1989) developed an ELISA immunoassay to detect the absence of a specific protein coded by the substituted wheat chromosome section in wheats with the 1BL/1RS translocation, which carries *Lr26* (Singh et al., 1990).

A considerable effort is currently being dedicated to identify molecular markers for disease resistance genes. Schachermayr et al. (1994) found three random amplified polymorphic DNA (RAPD) markers and two restriction fragment length polymorphism (RFLP) markers for *Lr9*. McMillin et al. (1993) found endopeptidase *Ep-D1d* was closely linked with *Lr19*. RFLP markers have also been found for gene *Lr37* (Bonhomme et al., 1995), and RAPD markers for *Lr25* and *Lr29* (Procunier et al., 1995). Molecular markers thus far have been identified only for leaf rust resistance genes that were originally derived from *Triticum taushii*, *Agropyron* and *Secale* spp. Markers have not yet been identified for resistance genes

originally derived from hexaploid common wheat.

Genetic markers are also available for APR genes. Leaf tip necrosis (*Ltn*) of flag leaves is associated with *Lr34* (Singh, 1992a; Dyck, 1979). Singh (1993) used *Ltn* as a marker for *Lr34*. Resistance gene *Lr13* is linked to hybrid necrosis gene *Ne2m* (Hawthorn, 1981). Wheat lines with *Ne2m*, crossed with a line which carries the complementary gene *Ne1s*, produce F_1 progeny that display necrosis before heading. Extensive lists of genotypes carrying *Ne2m*, including some South American wheats, have been published (Hermsen, 1963; Zeven, 1965, 1967, 1968, 1969). Singh and Gupta (1991), Singh and Rajaram (1991), Singh (1993) and Souza (1994) used *Ne2m* as a marker for the presence of *Lr13*.

2.6. LEAF RUST RESISTANCE GENES IN SOUTH AMERICAN WHEATS.

Detailed genetic studies have been conducted on selected Argentine and Brazilian wheat cultivars which have been used in different breeding programs as sources of leaf rust resistance. Some of these cultivars derive their resistance from Americano 44d and Alfredo Chaves 6.21, which were selected from local landraces in Uruguay and Brazil, respectively (Roelfs, 1988b).

Perez et al. (1991) tested the resistance of a number of Argentine wheats. The Uruguayan cultivars Americano 25c, Americano 26n, Americano 44d, Pelón 33c, and Polyssu and Alfredo Chavez from Brazil were in the pedigrees of all

cultivars which were more resistant than the Thatcher lines with *Lr13* (Tc*Lr13*) and *Lr34* (Tc*Lr34*). The Argentine cultivar Buck Manantial, an Americano 25c derivative, has been resistant since release in 1964. Buck (1986) determined that seedling resistance in Buck Manantial was due to three genes. Dyck (1989) identified in this cultivar seedling resistance genes *Lr3* or an allele, *Lr16* and *Lr17*, APR gene *Lr13* and an unidentified gene which could be *Lr34*. Rafaela MAG, a parent of Buck Manantial, has *Lr14b* and *Lr17* (Dyck and Kerber, 1977). María Escobar has *Lr14b* (Dyck and Samborski, 1970) and *Lr17* (Dyck and Samborski, 1968a). *Lr17* was identified in Klein Lucero (Dyck and Samborski, 1968a), *Lr3* in Sinvalocho MA and *Lr3ka* in Klein Aniversario (Haggag and Dyck, 1973).

Antonelli (1994) reported two previously unidentified seedling resistance genes in Barletta 7D, a landrace selection from Argentina, and Americano 44d. These genes were temporally designated *Lr7D* and *Lr44d*. *Lr7D* express IT 0; to 1 to certain leaf rust isolates and IT 2 to 2^{+} to other isolates. *Lr44d* expresses IT 2 to 2^{++} to all avirulent isolates. Both genes are present in Klein Sin Rival. *Lr44d* is present in Klein Vencedor and *Lr7D* is present in Klein Progreso, Klein Lucero, Klein 75, and Klein Aniversario.

The early Brazilian cultivars Frondosa, Fronteira and Surpresa, selected by Beckman, probably have *Lr13* derived from Afredo Chavez 6.21 (Roelfs, 1988b). Frontana, selected from the cross Fronteira/Mentana, has *Lr13* (Dyck et al., 1966),

Lr34 and *LrT3* (Dyck and Samborski, 1982). Singh and Rajaram (1992) also found *Lr13* and *Lr34* in Frontana and claimed evidence for additional APR genes. *Lr1* was found in Centenario (Dyck and Samborski, 1968b) and *Lr3bg* was identified in Bagé (Haggag and Dyck, 1973).

BH 1146, another Brazilian cultivar, has partial resistance to leaf rust (Jacobs and Broers, 1989). Partial resistance has been described as a reduced rate of disease development on cultivars that have a susceptible IT (Parlevliet, 1985). One of the main components of partial resistance to leaf rust is a longer latent period. Longer latent period in BH 1146 was conditioned by two or three partially recessive genes. BH 1146 also carries a semidominant gene for hypersensitive resistance (Jacobs and Broers, 1989), which could be *Lr13* (Broers and Jacobs, 1989). Since BH 1146 was selected from the cross Ponta Grossa 1//Fronteira/Mentana (Kohli, 1986) it is possible that one of the genes affecting latent period is *Lr34*, since this gene has been shown to increase latent period (Drijepondt et al., 1991)

More recently released cultivars in South America have been derived from germplasm obtained from CIMMYT and other breeding programs. *Lr24* is present in Cargill Trigal 800 (Antonelli, 1995), which has been widely used in crosses in Argentina and Uruguay. Seedling genes *Lr1, Lr3, Lr3bg, Lr10, Lr14a, Lr16, Lr17, Lr19, Lr23, Lr26, Lr27* and *Lr31* were postulated to be in CIMMYT germplasm (Singh and Rajaram, 1991,

Singh, 1993). *Lr26* is probably the most widely distributed of these genes since it is present in many high yielding CIMMYT lines that have been used directly as cultivars or in crosses in the Southern Cone of South America (Kohli, 1986). Also genes *Lr13, Lr34* and other APR genes are in CIMMYT germplasm (Singh and Rajaram, 1992; Singh and Huerta-Espino, 1995).

2.7. LEAF RUST RESISTANCE GENES FOUND IN SELECTED URUGUAYAN WHEAT CULTIVARS.

2.7.1. Seedling resistance genes.

Mains et al. (1926) studied the inheritance of leaf rust resistance in several wheat cultivars. Ausemus et al. (1946) assigned the gene symbol *Lr1* to the gene found by Mains et al. in Malakoff. *Lr1* expressed IT ; in response to avirulent isolates and was dominant, although a few plants were slightly less resistant with IT 1. In later work, Dyck and Samborski (1968b) confirmed Malakoff had *Lr1*. Soliman et al., (1963) located *Lr1* on chromosome 1B.

Lr3 was first identified in Mediterranean and Democrat, and was located on chromosome 6B (Soliman et al., 1963). Haggag and Dyck (1973) examined the inheritance of resistance of four wheat cultivars with three different alleles at the *Lr3* locus. Gene *Lr3* was present in Democrat and Sinvalocho, and expressed intermediate dominance to races 1 and 9 and appeared to be recessive to race 11. The gene giving IT 0; in Bagé was partially dominant and was designated as *Lr3bg*. The

gene in Klein Aniversario was named *Lr3ka*.

Anderson (1961) designated *LrE* a gene which expressed an IT 2 in the wheats Exchange and Selkirk. Both cultivars also carried gene *LrL*, as did Lee and four other cultivars studied. *LrL* had an IT ;1⁻, and was dominant in BCF_2 families from Exchange, Selkirk, Mayo 52 and Mayo 54. *LrL* was recessive in progenies from Lee, Gabo and Timstein, and dominant in a second test with the same leaf rust isolate. These results were attributed to differential IT of the heterozygotes under different temperature and light conditions. Dyck and Samborski (1968a) designated genes *LrL* and *LrE* as *Lr10* and *Lr16*, respectively.

Two alleles at the *Lr14* locus were found by Dyck and Samborski (1970). A dominant gene in Selkirk, determining an IT X was designated *Lr14a*. A gene present in María Escobar and Bowie, also conditioning an IT X to different leaf rust races, was not completely dominant and was designated *Lr14b*. These genes are not true alleles, since a single recombinant with both genes, was recovered from a population of 644 plants.

Lr17 was first found in Klein Lucero and María Escobar (Dyck and Samborski, 1968a) and backcrossed to Thatcher. Lines homozygous for *Lr17* had IT 1 and heterozygous plants within segregating lines had IT 1^+ to 2, indicating the gene was partially dominant.

Leaf rust resistance in Agent was derived from *Agropyron elongatum* (Smith et al., 1968). The dominant resistance gene

(Gough and Merkle, 1971) is also present in Agent derivatives Blueboy II and Fox (Browder, 1973) and was designated *Lr24* by McIntosh et al. (1976).

The 1BL/1RS translocation, introgressed into wheat from Petkus rye (Mettin et al., 1973; Zeller, 1973) carries a leaf rust resistance gene designated *Lr26* (McIntosh, 1988). Singh et al., (1990) described the exact gene location and linkage relationship of *Lr26* and other rust disease resistance genes located on the rye segment (stem rust resistance gene *Sr31*, stripe rust resistance gene *Yr9*). The 1BL/1RS translocation is present in Kavkaz and Avrora (Mettin et al., 1973; Zeller, 1973), which were used as parents in the CIMMYT breeding program.

2.7.2. Adult plant resistance genes.

The combination of *Lr13* and *Lr34* has been identified as one of the most durable sources of leaf rust resistance (Roelfs, 1988b). Durable resistance has been defined as resistance that has been adequate for a number of years over a range of environments (Johnson, 1981). *Lr13* and *Lr34* are present in Frontana, which has been widely used as a source of resistance in wheat breeding programs in North America (Ezzahiri and Roelfs, 1989; Kolmer et al., 1991) and CIMMYT (Rajaram et al., 1988).

Lr12 and *Lr13* were the first adult plant leaf rust resistance genes to be isolated and characterized. Dyck et al.

(1966) designated a gene conferring APR in Frontana as *Lr13*. This gene is located on chromosome 2B, and linked to *Ne2m*, (Hawthorn, 1981).

Lr13 is present in many North American cultivars: Manitou (Dyck et al., 1966), Chris, Redcoat, Atlas 66 (Roelfs, 1988b), Era (Ezzahiri and Roelfs, 1989), Columbus, Neepawa, Katepwa (Samborski and Dyck, 1982), Kenyon (Dyck, 1989), Pasqua (Dyck, 1993a), Roblin (Dyck, 1993b), Genesis and Biggar (Kolmer, 1994). *Lr13* is in several Klein and La Previsión cultivars from Argentina (Roelfs, 1988b), Buck Manantial (Dyck, 1989) and old Brazilian cultivars from the Beckman breeding program (Roelfs, 1988b). *Lr13* is present in several cultivars from Australia (McIntosh, 1992), in many CIMMYT (Rajaram et al., 1988; Singh and Rajaram, 1991; Singh, 1993) and Indian (Singh and Gupta, 1991) wheats. With certain isolates, *Lr13* can be detected in the seedling stage at warm temperature (25.5°C, Pretorius et al., 1984). Dyck et al. (1966) observed that *Lr13* expressed some resistance in the third leaf stage, but the first leaf was susceptible. In the adult plant stage, *Lr13* in Manitou conferred an intermediate IT and was recessive to race 5. *Lr13* in Frontana conditioned a higher level of resistance compared to Manitou (IT 0; to 0;1) and was partially dominant to race 5, which suggested the presence of modifying genes. Kolmer (unpublished data) tested over 80 leaf rust isolates for IT to adult plants of the Thatcher line with *Lr13*. The individual isolates produced IT ;, ;2, 22^{+} and $3^{+}4$ on the *Lr13*

Thatcher lines.

Thatcher lines with combinations of *Lr13* and effective seedling resistance genes expressed enhanced resistance compared to lines with either gene singly, in seedling and field tests (Kolmer, 1992). *Lr13* and *Lr16* interact to condition a lower than expected infection type in Columbus (Samborski and Dyck, 1982).

Leaf rust resistance gene *Lr34* was initially described as a modifier of the APR genes *Lr13* in Frontana and *Lr12* in Exchange (Dyck et al. 1966). *Lr34* was first backcrossed to Thatcher from PI58548 (Dyck, 1977). This gene was described as partially dominant, giving IT 2^{+} without chlorosis in the seedling stage, and interacted with *Lr33* for enhanced resistance (Dyck, 1977). *Lr34* was designated as *LrT2* in Terenzio, Frontana and a group of cultivars of diverse origin (Dyck and Samborski, 1982). *Lr34* was given final designation when mapped to chromosome 7D (Dyck, 1987). Dyck et al. (1994) showed that *Lr34* in the Thatcher line RL6058 is located on chromosome 7DS, and also found evidence that *Lr34* in RL6077 may have been translocated onto another chromosome.

Gene *Lr34* is distributed among wheats worldwide (Dyck and Samborski, 1982; Shang et al., 1986; Dyck, 1994a, 1994b). It is present in the North American wheats Glenlea (Dyck et al., 1985), Sturdy (Dyck, 1991), Pasqua (Dyck, 1993a), Roblin (Dyck, 1993b), Laura (Kolmer, 1994), Era (Ezzahiri and Roelfs, 1989), in CIMMYT germplasm (Dyck, 1987; Singh and Rajaram,

1991; Singh, 1993; Singh and Rajaram, 1992) and in South American germplasm. *Lr34* is most likely in the old Uruguayan cultivar Americano 44d and the Argentine derivatives La Previsión 3, 25, 28 and 32 (Roelfs, 1988b). Even though *Lr34* has been present in wheat cultivars grown extensively for many years, leaf rust isolates with virulence to Lr34 have not been found (J.A. Kolmer, unpublished data), and thus has provided durable resistance (Roelfs, 1988b).

Besides leaf rust resistance, *Lr34* pleiotropically conditions resistance or is closely linked to adult plant stripe rust resistance gene *Yr18* (Singh, 1992b; McIntosh, 1992), and to gene *Bdv1* for tolerance to barley yellow dwarf virus (BYDV) (Singh, 1993b). *Lr34* also enhances stem rust resistance when present in a Thatcher background (Dyck, 1989; Dyck, 1991).

Dyck (1979, 1991) indicated a possible linkage between *Lr34* and a characteristic leaf "tip die back". Close genetic linkage or pleiotropism of *Lr34* with leaf tip necrosis (designated *Ltn*) was demonstrated by Singh (1992a), providing an easily scorable marker for *Lr34*.

Lr34 is best expressed in the adult plant stage (Dyck and Samborski, 1982). *Lr34* resistance is associated with longer latent period, decreased number and size of uredinia, starting at the fourth leaf stage (Drijepondt et al., 1991).

In the field, *Lr34* is expressed as variable pustule size and low severity of infection (Dyck, 1987). The resistance

conditioned by *Lr34* is similar to slow rusting or partial resistance in wheat and other cereals. Dyck (1977) stated that the phenotype of reduced pustule size expressed by *Lr34* may be one of the factors considered a slow rusting characteristic. This type of resistance was also described for Tc*Lr34* by Perez and Roelfs (1987). Drijepondt and Pretorius (1989) reported that *Lr34* affected infection frequency, latent period and pustule size, similar to partial resistance. Rubiales and Niks (1995) found *Lr34* increased latent period and decreased infection frequency, due to reduced rates of haustorium formation in early stages of infection, not associated to cell death. The durability of the resistance conferred by *Lr34* may also be regarded as another characteristic associated with slow rusting or partial resistance.

Lr34 can be detected in the seedling stage under cool temperature (Singh, 1992c) and low light conditions (Dyck and Samborski, 1982). Under these conditions, a reduced pustule size in the seedling stage is accompanied by little or no chlorosis (Dyck, 1977; Dyck and Samborski, 1982; Drijepondt and Pretorius, 1989).

Lr34 has been selected in many breeding programs since it enhances the expression of other resistance genes (Dyck et al., 1966; Dyck and Samborski, 1982; Drijepondt et al. 1991). Germán and Kolmer (1992) demonstrated that *Lr34* interacts with other genes for enhanced resistance when the additional gene conditions some degree of resistance. This may also contribute

to the durability of leaf rust resistance in cultivars with *Lr34* (Sawhney et al., 1989; Germán and Kolmer, 1992; Kolmer, 1992).

Other uncharacterized adult plant leaf rust resistance genes are probably present in wheat. Dyck (1989) found that APR in Buck Manantial was due to *Lr13* and another resistance gene, which could be *Lr34* or an unidentified gene. Adult plant resistance in BCF_2 lines derived from accessions V488, V624 and V860, of the A.E. Watkins wheat collection was different from *Lr13* and *Lr34* (Dyck, 1994a). Kolmer (1994) determined the APR in Biggar was due to *Lr13* and a second gene which had a different expression than known APR genes. The Brazilian cultivar Toropí has only APR, which is due to two recessive genes different from previously identified genes (Barcellos, 1994).

Singh and Rajaram (1992) claimed that three additive genes, different from previously identified genes, conditioned APR in Frontana, Parula, Trap and Mango. Singh and Huerta-Espino (1995) found a minimum of two slow rusting genes in Ciano 79 and Papago 86. This APR was different from the genes in Frontana. Knott and Yadav (1993) studied the resistance of 12 wheat lines, whose field effective resistance was due to APR. Both *Lr13* and *Lr34* were probably present in some of the lines, but additional genes may have been involved.

3. MATERIALS AND METHODS.

3.1. PLANT MATERIALS.

Maturity class, year of release, pedigree and origin of the studied Uruguayan wheat cultivars are listed in Table 1.

Table 1. Uruguayan wheat cultivars studied and their progenitors.

Cultivars	Year of Release	Pedigree	Origin
Early maturity			
Est.[a] Tarariras	1974	Bagé/4/Thatcher/3/ Frontana//Kenya 58/Newthatch	INIA LE[b]
Est. Benteveo	1989	Avrora//Kalyansona/Blue Bird /3/Woodpecker (Bobwhite'S')	CIMMYT[c]
Est. Pelón 90	1990	Kavkaz/Torim	CIMMYT
INIA Boyero	1994	MN72-131/Bobwhite'S'	INIA LE
Late maturity			
Est. Calandria	1986	Prelude/L10//Est.Tarariras	INIA LE
Est. Federal	1987	Est.Hornero/CNT 8	INIA LE
Est. Halcón	1991	Buck 6/MR 74507	INIA LE

[a] Estanzuela
[b] INIA La Estanzuela Wheat Breeding Program
[c] Centro Internacional de Mejoramiento de Maiz y Trigo (Maize and Wheat International Breeding Center).

Detailed diagrams of the ancestors and possible sources of leaf rust resistance genes are presented in Appendices 1-5.

Est. Benteveo is a different Bobwhite sib line than the Bobwhite selection in the pedigree of INIA Boyero.

Early maturity cultivars are photoperiod insensitive and

head in approximately 90 days when planted in July. Recommended sowing date for these wheats is mid May - mid August. Late maturity cultivars are photoperiod sensitive and head in approximately 115 days when planted in July. Recommended sowing dates for these wheats is April - mid July (Tavella et al., 1995; Castro, 1995).

The cultivars Estanzuela Tarariras, INIA Boyero, Est. Federal, Est. Calandria and Est. Halcón were selected from crosses made at La Estanzuela. Est. Benteveo, and Est. Pelón 90 were selected from CIMMYT germplasm.

Based on genetic studies on lines in the pedigrees of the selected cultivars, resistance genes listed in Table 2 may be present (Anderson, 1961; Dyck et al., 1966; Dyck and Samborski, 1968; Dyck and Haggag, 1973; McIntosh, 1973; Mettin et al., 1973; Zeller, 1973; McIntosh and Dyck, 1975; Dyck, 1979; Reedy and Rao, 1980; Dyck and Samborski, 1982; Roelfs, 1988b; Singh and Rajaram, 1991; Singh, 1993a; Antonelli, 1994; Dyck, 1994; McIntosh et al., 1995).

Table 2: Possible *Lr* genes based on lines in the pedigrees of selected Uruguayan wheat cultivars.

Cultivars	*Lr* genes
Est.[a] Tarariras	*Lr3bg,13,14a,18,22b,34,T3*
Est. Benteveo	*Lr1,3,13,14a,17,22b,26,34,T3,7D,44d*
Est. Pelón 90	*Lr1,13,17,26,34,7D,44d*
INIA Boyero	*Lr13,17,22b,26,34,T3,7D,44d*
Est. Calandria	*Lr3bg,13,14a,18,22b,34,T3*
Est. Federal	*Lr10,13,14a,18,22b,23,34,T3,44d*

[a] Estanzuela

The pedigrees of the parents of Est. Halcón are not known.

Near isogenic lines in a Thatcher (Tc) background, with single *Lr* genes were used as controls for comparison, and as parents in genetic analyses (Table 3).

Table 3. Gene designation, tester line (RL #) and cross, characteristic infection type (IT) and chromosome location of leaf rust resistance genes (McIntosh et al. 1995).

NIL	RL #	Cross	Characteristic resistant IT	Chromosome location
Tc*Lr1*	6003	Tc*6/Centenario	0;	5DL
Tc*Lr2a*	6016	Tc*6/Webster	;	2DS
Tc*Lr2b*	6019	Tc*6/Carina	01c	2DS
Tc*Lr2c*	6047	Tc*6/Brevit	;1	2DS
Tc*Lr3*	6002	Tc*6/Democrat	;c	6BL
Tc*Lr3bg*	6042	Bagé/*8Tc	;c,23[a]	6BL
Tc*Lr3ka*	6007	Tc*6/K.Aniversario	12	6BL
Tc*Lr9*	6010	Transfer/*6Tc[b]	0;	6BL
Tc*Lr10*	6004	Tc*6/Exchange	;,2c[a]	1AS
Tc*Lr11*	6053	Tc*6//E-1/Hussar	2;	2A
Tc*Lr13*	4031	Tc*6/Frontana	APR	2BS
Tc*Lr14a*	6013	Selkirk/*6Tc	X	7BL
Tc*Lr14b*	6006	Tc*6/Maria Escobar	X	7BL
Tc*Lr15*	6052	Tc*6/W1483	;c	2DS
Tc*Lr16*	6005	Tc*6/Exchange	;1n	2BS
Tc*Lr17*	6008	K.Lucero/*6Tc	;12	2AS
Tc*Lr18*	6009	Tc*7/Africa 43	;1,2[a]	5BL
Tc*Lr19*	6040	Tc*7/Translocation 4[c]	0	7DL
Tc*Lr20*		Thew	0;	7AL
Tc*Lr21*	6043	Tc*6/RL5406[d]	;2-	1DL
Tc*Lr23*	6012	Lee 310/*6Tc	;2-	2BS
Tc*Lr24*	6064	Tc*6/3/Agent// *2Prelude/*8Marquis[c]	;	3DL
Tc*Lr26*	6078	Tc*6/St-1-25[e]	;	1BL
Tc*Lr30*	6049	Tc*6/Terenzio	2	4BL
Tc*Lr33*	6057	Tc*6/PI58548	1[+]	1BL
Tc*Lr34*	6058	Tc*6/PI58548	APR	7D
Tc*LrB*	6051	Tc*6/Carina	2c	

[a] two different IT when tested with different avirulent leaf rust isolates.
[b] *Aegilops umbellulata*
[c] *Agropyron elongatum*
[d] *Aegilops squarrosa*
[e] *Secale cereale*

3.1.1. Plant growing conditions.

Seedlings were grown on beds or flats, filled with a mixture of equal parts of soil, sand and substrate (Plantmax, Eucatex, Brazil), which contained expanded vermiculite and organic matter. Plants were fertilized weekly with NPK (foliar fertilizer ISUSA NPK + micronutrients, 12-8-5) applied as a soil drench. Light levels were supplemented for 6 to 8 hours daily (high pressure sodium SON lamps, 400 W, Philips, Belgium) during the fall and winter months (April - September).

Plants for adult plant tests were grown in 10 cm diameter plastic pots, filled with the same mixture of soil, sand and substrate used for seedling tests. Fertilization was as described for seedlings.

Field plots at La Estanzuela were planted in the first week of August. No artificial inoculation was done in the field. Spreader rows with the leaf rust susceptible Thatcher and Little Club wheats were planted at right angles to the plots to favor increase and spread of the endemic leaf rust population. Nitrogen and phosphate fertilizers were applied according to soil tests. Weeds were controlled with herbicide (Chlorsulfuron, 15 g/ha) and manually.

3.2. Puccinia recondita ISOLATES.

Puccinia recondita isolates of the collection maintained at the Agriculture and Agri-Food Canada Winnipeg Research

Centre, were used for tests conducted in Canada. Isolates from Brazil, provided by Dr A. Barcellos, and from Uruguay were used for tests conducted in Uruguay. Inoculum was increased on seedlings of Little Club treated with maleic hydrazide, and stored as vacuum dried urediniospores in sealed glass vials.

The avirulence/virulence formulae of the leaf rust isolates used during the study are given in Table 4 (data reported in the Results section) and Appendix 6 (data reported in the Appendix).

Table 4. Selected *Puccinia recondita* isolates, their Ptr code, origin and avirulence/virulence formulae.

Isolate	Ptr code[a]	Origin	Avirulence/Virulence formula.
Race 1	BBB	Canada	1,2a,2c,3,3bg,3ka,9,10,11,16,17,18,23,24,26,30,B / 14a,14b,20
Race 9	SBD	Canada	3,3ka,9,11,16,18,24,26,30,B / 1,2a,2c,10,14a,17
Race 15	CHB	Canada	1,2a,2c,3ka,9,11,17,18,24,30,B /3,3bg,10,14a,14b,16,20,23,26
B25	LCG	Brazil	2a,2c,3,3ka,3bg,9,16,17,20,24,30,B / 1,11,10,14a,14b,23,26,18
B26	MBR	Brazil	2a,2c,9,14b,16,17,18,24,26,B / 1,3,3ka,3bg,10,11,14a,20,23,30
B27	LBB	Brazil	2a,2c,3,3ka,3bg,9,11,16,17,18,24,30,B / 1,10,14a,14b,20,23,26
B29	TDT	Brazil	9,10,14b,16,18,20,23,26,B / 1,2a,2c,3,3ka,3bg,11,14a,17,24,30
B31	CBT	Brazil	1,2a,2c,9,10,14a,16,20,23,24,26,B / 3,3ka,3bg,11,14a,17,18,30
B33	TGG	Brazil	3ka,9,10,11,14a,14b,16,18,23,24,26,30,B / 1,2a,2c,3,3bg,17,20
B34	MCG	Brazil	2a,2c,3ka,9,14b,16,17,18,20,24,30,B / 1,3,3bg,10,11,14a,23,26
B37	SLG	Brazil	3,3ka,3bg,10,16,17,18,20,24,26,30,B / 1,2a,2c,9,11,14a,14b,23
B38	TBD	Brazil	9,3ka,11,16,23,24,26,30,B / 1,2a,2c,3,3bg,10,14a,14b,17,18,20
B39	CGT	Brazil	1,2a,2c,9,10,18,20,24,26,B / 3,3ka,3bg,11,14a,14b,16,17,23,30
19-3	MCR	Uruguay	2a,2c,9,16,17,18,20,24 / 1,3,3ka,3bg,10,11,14a,14b,23,26,30,B
41-2	MFR	Uruguay	2a,2c,9,10,16,17,18,20,B / 1,3,3ka,3bg,11,14a,14b,23,24,26,30

[a] Long and Kolmer (1989).

3.2.1. Inoculation procedure.

Seedling plants were inoculated when the first leaf was fully expanded, usually eight to 10 days after planting. Seedlings were inoculated with either a mixture of

urediniospores and talc in approximately a 1:10 proportion (weight to weight) dusted with a blower, or a suspension of urediniospores in nonphytotoxic light industrial mineral oil in approximately 1:60 proportion (weight to volume) that was atomized with microinoculators. Inoculated seedlings were placed in humid chambers overnight for a minimum of 14 hours. Plants grown in greenhouse beds were covered with black plastic and continually misted overnight with a humidifier. Plants grown on flats or pots were moved to a humidified room for incubation, then moved to greenhouse benches the following morning.

Adult plants were inoculated at heading to watery stage (10.5 - 10.5.4 growth stages, Feeks, 1941) with a suspension of urediniospores in nonphytotoxic oil, in a 1:60 proportion (weight to volume). Plants were then placed in a humidified room overnight (minimum 14 hours) and returned to greenhouse benches after incubation.

Seedling and adult plants were maintained generally at greenhouse temperatures between 15°C - 25°C, and occasionally higher temperatures of 20° - 30°C during warm sunny periods.

3.2.2. Leaf rust recording.

Infection types for seedling tests were assessed 11 - 13 days after inoculation, according to the scale used by Stakman et al. (1962) (Appendix 7). Infection types 0 - 2 were considered resistant and IT 3 - 4 susceptible. Mesothetic IT

X, Y and Z were described by Roelfs (1988a) as variable sized uredinia distributed at random, decreasing in size with distance from the leaf tip, and decreasing in size with distance from the leaf base, respectively. A range of IT was indicated by listing the most frequent IT first followed by the least frequent IT (Roelfs, 1988a). Infection types for adult plants were assessed as described for seedlings, 11 - 13 days after inoculation. The percentage of infection was determined according to the modified Cobb scale (Peterson et al., 1948).

Leaf rust severity (%) in field plots was determined on flag leaves using the modified Cobb scale (Peterson et al., 1948), and response was determined according to Stakman et al. (1962) (Appendix 7). Leaf rust severity and response readings were taken when the susceptible check Thatcher had readings of 70% severity with a susceptible response (S) to 90 S. Readings were taken 1-2 weeks later for families which had later maturity than Thatcher. In BCF_2 or F_3 families which segregated for leaf rust resistance, the range of leaf rust severities and responses were recorded.

3.3. SEEDLING RESISTANCE.

3.3.1. Seedling resistance test.

Greenhouse seedling tests were conducted in Canada (Agriculture and Agri-Food Canada, Winnipeg Research Centre) from February to May in 1991 and in Uruguay (INIA La

Estanzuela) from April to November in 1994 and 1995.

For genetic analysis, one plant of each cultivar was crossed and backcrossed to the susceptible cultivar Thatcher. The resistant cultivars were used as the pollen parents and Thatcher as the female parent. Plants from each cultivar used in crosses were field progeny tested (100 plant progeny per plant) to confirm identity and homozygosity.

F_1, backcross F_1 (BCF_1) and F_2 plants were grown in the field at La Estanzuela from 1991 - 1993, to advance generations. All available BCF_1 seed and 500 F_2 seeds per cross were hand planted. Seeds were spaced 0.20 m apart in both directions. Several fungicide treatments (propiconazole, 150 cc/ha) during the growing season were applied to prevent rust development in order to ensure good quality seed from resistant and susceptible plants. BCF_1 and F_2 plants were harvested and threshed individually to obtain BCF_2 and F_3 families.

Approximately 20 seeds per BCF_2 and/or F_3 family were planted in clumps and tested as seedlings in greenhouse beds with leaf rust isolate race 1, which is avirulent to most seedling resistance genes (Table 4). The number of seedling resistance genes (n) in the cultivars was estimated from the ratio of segregating to homozygous susceptible BCF_2 families (2^n-1:1), and the ratio of homozygous resistant and segregating lines to homozygous susceptible F_3 lines (4^n-1:1). Chi square values for goodness of fit of actual to expected

ratios were calculated. When the expected number of plants in one class was lower than 5, the Yates correction factor (Yates, 1934) was used. The number of plants with very low IT (0; - 1), intermediate IT (1^+ - 2^+), and high IT (3 - 4) within each BCF_2 or F_3 family was also recorded.

To determine the identity of the resistance genes in the cultivars, approximately 5(n) BCF_2 families which segregated for a single seedling resistance gene were selected. Twenty seeds from each selected BCF_2 family were planted in the field in 1994 to increase seed; plants were treated with several fungicide applications of propiconazole. The BCF_3 lines were harvested and threshed individually. BCF_3 lines with single seedling resistance genes were tested with leaf rust isolates from Canada, Brazil and Uruguay for gene postulation.

3.3.2. Monoclonal antibody test for the presence of 1BL/1RS translocation and Lr26.

Howes et al. (1989) reported that wheats with the translocation 1BL/1RS lack gamma gliadin 45. Monoclonal antibody P24B which binds specifically to this storage protein provides a basis for discriminating wheat genotypes that carry the translocation and *Lr26* (Singh et al.,1990).

The protocol used for the ELISA test was described by Howes et al. (1989). Two experiments were done, using individual kernels of the Uruguayan cultivars per ELISA reaction. The first test, done in Agriculture and Agri-Food

Canada Winnipeg Research Center under the supervision of N. Howes, consisted of 10 ELISA reactions per cultivar. The second test, done in División de Protección Agrícola, Ministerio de Agricultura y Pesca, Uruguay, under the supervision of Dr A. Peralta, consisted of eight ELISA reactions per cultivar. Genotypes with known positive (without *Lr26*) and negative reaction (with *Lr26*) were included as checks.

3.4. ADULT PLANT RESISTANCE.

3.4.1. BCF_2 family field test.

BCF_2 families were separated into three categories for the field test, based on seedling IT to race 1: a) families which were homozygous susceptible, b) families segregating to race 1 for single seedling resistance genes, selected for testing with different isolates and c) other families segregating for race 1. Twenty seeds from each BCF_2 family that was homozygous susceptible to race 1 (a) were planted in 1994 in two rows 1.5 m long, spaced 0.20 m apart with 0.40 m between plots. Thatcher, and the Thatcher lines with *Lr13* (Tc*Lr13*) and Tc*Lr34* were included as checks between families from different crosses. Selected BCF_2 families which segregated for single seedling resistance genes (b) were field tested in 1995, in plots as the seedling susceptible BCF_2 families. Thatcher was used as the susceptible check between families from different crosses. The remaining BCF_2 families

(c) were field tested in 1994 as 1.5 m rows 0.40 m apart, with more than 50 plants. Thatcher was included as the susceptible check between families from different crosses.

The number of genes which conditioned effective field resistance in the BCF_2 families was determined separately in families that were segregating and susceptible for seedling resistance. The actual ratios of segregating to susceptible BCF_2 families were fit to expected ratios using the chi square test. Yates correction factor was used when the expected number of families was lower than 5 (Yates, 1934).

3.4.2. Intercrosses with TcLr13 and TcLr34.

The selected Uruguayan cultivars were directly crossed with Tc*Lr13* and Tc*Lr34* to determine if these genes are present in these cultivars. The same plants of the cultivars used for crosses with Thatcher or a plant directly derived from the original plant were used for the crosses with Tc*Lr13* and Tc*Lr34*. The F_1 seed was harvested and selfed to obtain F_2 families.

From 1992 - 1994, 700 seeds from each F_2 population were hand planted 0.20 m apart in the field during one growing season at La Estanzuela. Segregation for susceptible adult plants was recorded. Susceptible F_2 plants or plants with high leaf rust severity were marked and progeny tested as adult plants in field tests the following year. The F_2-derived F_3 seeds were planted in rows 1.5 m long 0.40 m apart, with

Thatcher, Tc*Lr13* and Tc*Lr34* as checks every 20 rows.

3.4.3. Greenhouse progeny test of selected field resistant, seedling susceptible BCF_2 plants.

Field resistant plants in BCF_2 families that were seedling susceptible and had different leaf rust severity and resistance response were marked and individually harvested. Sixteen BCF_3 plants from each selected BCF_2 plant were grown in four pots (four plants per pot). Each plant was trimmed leaving two tillers. Plants in two pots were tested at the adult plant stage with race 1 which is avirulent to *Lr13*, and plants in other two pots with leaf rust isolate B27 which is virulent to *Lr13*. Adult plants of Thatcher, Tc*Lr13* and Tc*Lr34* were also inoculated with race 1 and isolate B27 as checks. The same BCF_3 lines were also tested for APR in field tests in 1995. Approximately 60-80 seeds from each line were planted in 1.5 m rows 0.4 m apart.

3.4. Test for hybrid necrosis (Ne2m), a genetic marker for Lr13.

The selected Uruguayan cultivars were crossed with Spica, an Australian cultivar which carries *Ne1s* (McIntosh, 1988). Plants of the Uruguayan cultivars used for these crosses were derived directly from the plants used for initial crosses with Thatcher. Tc*Lr13* also was crossed to Spica. In 1995, the seven Uruguayan cultivars, Tc*Lr13*, Spica, and F_1 seed from at least

two crossed heads were field planted in single rows of 3 to 10 single plants. Plots were sprayed with propiconazole to prevent leaf rust development. Hybrid necrosis was evaluated at stem elongation by comparing the appearance of the F_1 plants from the different crosses with F_1 of Spica/Tc*Lr13*.

3.4.5. Leaf tip necrosis (Ltn), a genetic marker for Lr34.

The cultivars in the hybrid necrosis test were also evaluated for the expression of leaf tip necrosis (*Ltn*) which is genetically associated with *Lr34* (Singh, 1992). Adult plants with *Ltn* show leaf necrosis beginning from the tip extending downward along the sides of the leaves.

4. RESULTS.

4.1. SELECTED URUGUAYAN CULTIVARS.

4.1.1. Field leaf rust severity and response of selected Uruguayan cultivars.

The selected cultivars expressed moderate to high levels of resistance to wheat leaf rust in Uruguay from 1993-1995 (Table 5).

Table 5. Leaf rust severity and response of seven Uruguayan wheat cultivars and the susceptible cultivar Thatcher in field tests at La Estanzuela, Uruguay, from 1993-1995.

Wheat cultivar	1993	1994	1995
Early maturity			
Est.[a] Tarariras	2 M[b]	5 M	20 M-60 MSS
Est. Benteveo	30 MRMS	T-20 M	10-30 M
Est. Pelón 90	10 R	T R	T R
INIA Boyero	T R	T R	T R
Late maturity			
Est. Calandria	T R	T R	T R
Est. Federal	10 M	5 M	2 M
Est. Halcón	40 MRMS	20-60 MS	10 R-60 MRMS
Thatcher	90 S	80 S	80 S

[a]: Estanzuela
[b]: modified Cobb scale (Peterson et al., 1962).

Leaf rust severities and responses presented in Table 5 were recorded in plots of two 1 m rows. The susceptible cultivar Thatcher (Tc) had very high leaf rust severity levels, between 80-90S, in all three years, indicating that suitable conditions for leaf rust infection were present. Est. Pelón 90, INIA Boyero, and Est. Calandria were highly resistant in all years, with trace levels of small uredinia

surrounded by necrosis (T R ratings). Est. Federal had a mixed response (isolated moderate-large uredinia) with a severity between 2-10%. Est. Tarariras had mixed responses of 2 M - 5 M in 1993 and 1994, and higher levels between 20 M-60 MSS in 1995. Est. Benteveo and Est. Halcón had moderate-high severity levels between T - 20 M and 20 - 60 MS.

4.1.2. Seedling infection types and gene postulation.

All seven cultivars expressed seedling leaf rust resistance, either to all, or to particular leaf rust isolates (Table 6, Appendices 8-10).

Table 6. Seedling infection type of Uruguayan wheat cultivars and Thatcher lines with single resistance genes tested with different leaf rust isolates.

Wheat line	BBB Race1	CGT B39	SLG B37	TBD B38	LCG B25	TDT B29	MBR B26	LBB B27	CBT B31	TGD B33	MCG B34	MCR 19-3	MFR 41-2	SBD R9	CHB R15
Est.Tarariras	0;[a]	2-2=;	0;	23	-[b]	23	3+2;X	0;	2=3=;c	3-3+	33-	1-2-;	23-	;	;3
Est.Benteveo	0;	;	0;	0;	;	0;	0;	0;	;	0;	2-2cn	3-	32	;	;1-
Est.Pelón 90	0;	0;	0;	0;	1	0;	0;	;1=	0;	0;	;	;	;1=	;	0;
INIA Boyero	0;	;	0;	0;	3+4	0;1=	0;	--	0;	0;	;12	1-2-;n	1=;	;	;3
Est.Calandria	0;	;	0;	0;	0;	1;nc	;	0;	;	;	0;	;	22+cn	;	;
Est.Federal	0;	;	0;	2+3	1-n;Z-	0;	32;n	X-c	;	;	;1=	3-	;	;	2+3
Est.Halcón	;1=	;	0;	1n	1-1n	0;	2-c	2-c	;	0;	1-n	11+cn	;	;	2+3
Thatcher	4	33+	33+	3+4	3+4	4	3+4	3+	3	3+	3+	33+	3+	4	4
Lr1	0;	0;	3+	3+	33+	4	33+	3+	0;	33+	3+	33+	3+	3	0;
Lr2a	0;	0;	33+	3+	0;	4	0;	1;	0;	3	0;	0;	0;	3	0;
Lr2c	;1=	;	33+	3+	;	4	0;	23;	;	3	;	0;	;	3	;
Lr3	;1-	33+	;	3+	;1=	4	33+	;	33+	3	3+	33+	3+	;	4
Lr9	0;	0;	3	0;	0;	;	0;	0;	0;	;	0;	0;	0;	;	0
Lr16	1-n	3-3+	1-n	1n	1n	1-n	11+n	1+2cn	1-1n	3	1-2-cn	11+nc	12-nc	;	3+
Lr24	0;	0;	0;	0;	0;	4	0;	0;	0;	0;	;	0;	3	;	;
Lr26	;1-	;	;1=	0;	3+4	1=;	;	2+	1-;	1=;	3	33+	3+	;	2+
Lr3ka	1=;	33+	2=;	22-	1-1c	4	33+	1-;	33+	1-;	2	3	3	;	;1+
Lr11	2-2	33+	33+	2	4	4	33+	2	33+	2+2	3	33+	3	;1=	;1
Lr17	1-;	33+	;1=	3+	12=n	4	1-2=;	;1=	33+	33+	1-;n	2-	1-1n	3	;
Lr30	2-	33+	1-	2-	12=	4	3+	2	33+	1-2-;c	2-	33+	33+	;	;1-
Lr10	;1=	;1=	1-;	3+	3+	0;	3+	3+	1-;	1-2-;c	33+	33+	1-;c	3	3+
Lr18	2-1	2	2	3+	3+	12=;	2+	2	3	11+n	2+3n	2+3	22+	;	22-
Lr23	1+2	33+	3+	22+	3	0;	3	3	2-2	;1=	3=3	3	3	--	--
Lr14a	33+	33+	3+	3+	4	4	3+	33+	33+	X	33+	3	33+	3+	4
Lr14b	3	3	33+	3	4	0;	23	3	2-c	3+2;X+	2+	3-	33+	--	--
Lr20	3+	;	;	3+	;	0;	33+	3;n	;	33+	;	;	;	--	--
Lr33	2	2	3-3c	2+3+c	--	--	2+3	3	3-	3	2+3	2+3	2+	--	--
Lr13	33+nZ	Z	33+	3+4	4	4	2+3+n	3+	3-3+n	3+3	33+	33+n	3	--	--
Lr34	3-3+c	3=3c	2=3;	32-c	3=3	2-3c	23	2-3	2-3	32-	2=3-;	2-3	2=3-	--	--
LrB	--	2	1+n	2cn	1+	2	2	23	1+2	11+n	1+	3	2c	1c	2c
Lr3bg	;	32;Y	;1=	3+	0;	4	33+	;	3	3+	33+	32;X+	33+	--	--

[a]: Stakman et al., 1962; Roelfs, 1988a.
[b]: Data not available

Results in Table 6 are from tests in Uruguay, except for isolates race 9 and 15, which were tested in Canada. Results from other seedling tests are listed in Appendices 8, 9 and 10.

It was not possible to postulate which seedling *Lr* genes may be present in Est. Pelón 90, and Est. Calandria based on the seedling tests since these cultivars had low infection type (IT) to all leaf rust isolates (Table 6).

Est. Tarariras had very low IT (0; to ;) to *Lr3* and *Lr3bg* avirulent isolates race 1, B37, and B27; intermediate IT ($2^{-}2^{=}$; and $1^{-}2^{-}$;) to isolates B39 and 19-3, which had Y and X^{+} IT to Tc*Lr3bg* and high IT to Tc*Lr3*; and IT from $2^{=}3^{=}$;c to 3^{+} to *Lr3* and *Lr3bg* virulent isolates. Est. Tarariras probably has *Lr3* or *Lr3bg*. The intermediate IT expressed to isolates virulent to *Lr3* and *Lr3bg* indicated that APR genes may also be present in Est. Tarariras.

Est. Benteveo had very low IT (0; to ;1^{-}) to isolates avirulent to *Lr3* or *Lr26*. Intermediate (2^{-}2cn) to high (3^{-}) IT to *Lr3* and *Lr26* virulent isolates B34, 19-3 and 41-2, indicated that this cultivar may have both *Lr3* and *Lr26*. The intermediate IT to *Lr3* and *Lr26* virulent isolates indicated that APR genes may also be present in Est. Benteveo.

INIA Boyero had very low IT (0; to ;) to *Lr26* avirulent isolates, and had intermediate IT (;12 to $1^{-}2^{-}$;n) to *Lr26* virulent isolates B34 and 19-3. Gene *Lr26* is probably in INIA Boyero. The low IT to isolate 41-2 ($1^{=}$;) and intermediate IT

to isolates B34 and 19-3 indicated that this cultivar may have additional seedling resistance and/or APR genes.

Est. Federal expressed very low IT (0; to ;) to *Lr10* avirulent isolates race 1, B39, B37, B29, B31, B33 and 41-2. Gene *Lr10* is most likely in Est. Federal. Additional seedling resistance was indicated by the IT 1n;(Z^-), X^-c, ;1^- and ; to *Lr10* virulent isolates B25, B27, B34 and race 9, respectively.

Est. Halcón had low to intermediate IT to all isolates except to R15. This cultivar had very low IT (0; to ;1^-) to *Lr10* avirulent isolates and IT 1^-n to 2 c to *Lr10* virulent isolates B38, B25, B26, B27, B34, 19-3 and race 9. Resistance gene *Lr16* has a characteristic IT of 1n to 1^+n to avirulent isolates. Race 15, was the only isolate with an intermediate to high IT (2^+3) on Est. Halcón. This isolate is virulent to *Lr10* and *Lr16*. Est. Halcón most likely has both *Lr10* and *Lr16*.

4.1.3. Monoclonal antibody test for the presence of 1BL/1RS translocation and Lr26.

Monoclonal antibody P24B binds strongly to gamma gliadin 45, which is missing in hexaploid wheats that carry the 1BL/1RS translocation. The absence of the protein can be used as a marker for resistance gene *Lr26* which is located on the 1B/1RS translocation.

Table 7. Binding of monoclonal antibody P24B to proteins from single wheat kernels from seven Uruguayan wheat cultivars.

	ELISA absorbance					
	Experiment 1			Experiment 2		
Wheat cultivar	Avg[a]	N[b]	Range	Avg	N	Range
Est.[c] Tarariras	--[d]	--	--	1.13	5	0.99-1.30
Est. Benteveo	0.07	10	0.06-0.09	0.01	8	0.00-0.03
Est. Pelón 90	0.06	10	0.06-0.07	0.01	7	0.00-0.06
INIA Boyero	0.07	10	0.06-0.09	0.01	8	0.00-0.06
Est. Calandria	0.53	9	0.37-0.64	1.22	4	1.10-1.30
Est. Federal	--	--	--	1.13	3	0.96-1.30
Est. Halcón	0.58	10	0.39-0.92	1.02	5	0.84-1.20
Check -	0.07	7	0.06-0.07	0.02	7	0.00-0.10
Check +	0.55	7	0.54-0.58	1.22	4	1.10-1.30

[a] Average.
[b] Number of kernels with readable results.
[c] Estanzuela
[d] Data not available.

According to the ELISA results, gamma gliadin 45 is present in Est. Tarariras, Est. Calandria, Est. Federal, and Est. Halcón. These cultivars lack the 1BL/1RS translocation and therefore should not have *Lr26*. The CIMMYT derived wheats Est. Benteveo, Est. Pelón 90, and INIA Boyero developed by INIA lack gamma gliadin 45, indicating that these cultivars have the translocation and most likely have *Lr26*.

4.2. GENETICS OF SEEDLING RESISTANCE.

4.2.1. Segregation of seedling resistance in BCF_2 and F_3 families.

Seedling resistance to race 1 was tested in BCF_2 and F_3 families from all seven cultivars crossed with the susceptible cultivar Thatcher (Table 8). A larger number of Thatcher/ INIA Boyero BCF_2 families were available, so F_3 families were not used for this cross. The number of seedling genes which conditioned resistance to race 1 was estimated based on the ratio of families that were homozygous susceptible (expressing only high IT) to families that were segregating for resistance (segregating for low IT). Race 1 has low IT to all seedling resistance genes except *Lr14a*, *Lr14b*, and *Lr20* (Table 4). The BCF_2 families derived from Tc/Est. Pelón 90, and Tc/Est. Calandria, were also tested with isolate 19-3, since this race was prevalent in Uruguay in 1994 when most BCF_2 families were also tested for APR in field tests.

Table 8. Segregation for seedling infection type to *P.recondita tritici* race 1 and isolate 19-3 in BCF_2 and F_3 families from crosses between seven Uruguayan wheat cultivars and the susceptible cultivar Thatcher.

Wheat cultivar	Isolate[b]	Genera tion	Nofamil.[a] R[c]/Seg[d]	S[e]	Exp. ratio	N[f]	X^2	P
Est.Tarariras	race 1	BCF_2	31	25	1:1	1	0.64	.50-.30
	race 1	F_3	93	26	3:1	1	0.63	.50-.30
Est.Benteveo	race 1	BCF_2	66	17	3:1	2	0.90	.50-.30
	race 1	F_3	139	7	15:1	2	0.53	.50-.30
Est.Pelón 90	race 1	BCF_2	41	3	7:1	3	1.30	.30-.20
					15:1	4	0.02	.90-.70
	race 1	F_3	143	1	63:1	3	0.25	.70-.50
					255:1	4	0.01	.95-.90
	19-3	BCF_2	24	20	1:1	1	0.36	.70-.50
INIA Boyero	race 1	BCF_2	50	70	1:1	1	3.33	.10-.05
Est.Calandria	race 1	BCF_2	59	5	7:1	3	1.29	.30-.20
					15:1	4	0.07	.90-.70
	race 1	F_3	112	3	63:1	3	0.28	.70-.50
					255:1	4	9.40	<0.01
	19-3	BCF_2	40	17	3:1	2	0.71	.50-.30
Est.Federal	race 1	BCF_2	30	31	1:1	1	0.02	.90-.70
	race 1	F_3	130	31	3:1	1	2.83	.10-.05
Est.Halcón	race 1	BCF_2	43	14	3:1	2	0.01	.95-.90
	race 1	F_3	160	11	15:1	2	0.01	.95-.90

[a] Number of families
[b] *Puccinia recondita* isolate
[c] Homozygous resistant (F_3 families)
[d] Segregating (BCF_2 and F_3 families)
[e] Homozygous susceptible
[f] Number of seedling resistance genes

The number of BCF_2 families was generally low (40 to 60) and were not large enough to discriminate between segregating ratios for three or four genes.

Est. Tarariras. When tested with race 1, the segregation of the BCF_2 and F_3 families fit an expected single gene (1:1

and 3:1, respectively) ratio. Lines with this seedling resistance had IT 0; to ;, which was partially dominant since presumed heterozygous seedlings had a ;1⁻ to 1 or ;2 IT.

Est. Benteveo. Resistance to race 1 segregated for two-gene ratios of 3:1 and 15:1 in BCF_2 and $_3F$ families respectively. One of the genes in Est. Benteveo expressed IT 0;1 to ;1⁻ and was dominant. The other gene was partially dominant, and expressed an IT 0; to ;1⁼ in plants assumed to be homozygous, and IT 12; to 2; in plants assumed to be heterozygous.

Est. Pelón 90. When tested with race 1, segregation of BCF_2 and F_3 families fit a three and a four expected gene ratios. One gene had an IT 0; and was dominant. A second gene was partially dominant, with IT 0; to ;1⁼ in plants assumed to be homozygous, and IT 2 in plants assumed to be heterozygous. A third gene expressed IT ;1⁼ to ;1⁻ and was dominant. When tested with isolate 19-3, the BCF_2 families segregated for a single resistance gene. This gene had an IT ;1⁼ and was partially dominant; plants assumed to be heterozygous had IT 22⁻. This gene was also segregating to race 1 since all susceptible families to race 1 were also susceptible to isolate 19-3. It is probably the same gene that expressed partial dominance to race 1.

INIA Boyero. Segregation of BCF_2 families fit a single gene ratio when tested with race 1. This gene had an IT ;1⁼ to 1⁻ and was dominant. In three BCF_2 families, classified as

homozygous susceptible, some plants had an IT Z, with an IT ;1n towards the leaf tip and large uredinia (IT $3^{+}4$) at the base of the leaf.

Est. Calandria. Segregation of BCF_2 families fit both three and four expected gene ratios when tested with race 1. Segregation of F_3 families fit only a three gene ratio. At least three seedling resistance genes are present in Est. Calandria. In the BCF_2 families one dominant gene had an IT 1n, and a second dominant gene had an IT 0;. The third gene was partially dominant, plants assumed to be homozygous had IT 0; and plants assumed to be heterozygous had IT $;1^{-}$ to 2^{-}. In tests with isolate 19-3 segregation of the BCF_2 families fit a two gene ratio. One gene had an IT 1 and was recessive, and the second gene had an IT 0; to ; and was dominant. These genes also conferred resistance to race 1 since BCF^{2} families susceptible to race 1 were also susceptible to isolate 19-3. Six BCF_2 families with IT Y (IT 3 uredinia at the leaf tip with flecks and uredinia surrounded by necrosis at the base of the leaf) were considered susceptible, since these were difficult to distinguish from the susceptible check Thatcher. If the families with IT Y are considered resistant, the ratio of 46 segregating : 11 susceptible families fits a 7:1 ratio, indicating three genes for resistance to isolate 19-3 are present in E. Calandria.

Est. Federal. Segregation of BCF_2 and F_3 families fit a single gene ratio when tested with race 1. The gene was

incompletely dominant and expressed an IT ;$1^{=}$ to 1^{-}; in plants assumed to be homozygous and IT 1^{+} to 2 in heterozygous plants.

Est. Halcón. Segregation among BCF_2 and F_3 families fit a two gene ratio when tested with race 1. One of the genes was dominant and had IT 1^{-}n to 1n. The second gene was incompletely dominant, plants assumed to be homozygous had IT ; to 1^{-};, and plants assumed to be heterozygous had IT 2 to 2^{+}.

4.2.2. Seedling resistance of selected BCF_3 lines.

BCF_3 lines from selected BCF_2 families which segregated for single seedling resistance genes were tested with seven different leaf rust isolates. Since the lines were segregating, only IT from resistant seedlings are listed in Table 9. Infection types are presented from two BCF_3 lines from each cross, for each *Lr* gene that was identified. The BCF_3 lines were tested with isolate B37 twice. The IT of the isolates on Thatcher lines nearly isogenic for single resistance genes are listed in Table 10.

Table 9. Seedling infection types of selected BCF_3 and F_4 lines from crosses of seven Uruguayan wheat cultivars with the cultivar Thatcher, tested with seven isolates of *P.recondita tritici*.

Wheat line	Lr gene	BBB Race1	MCR 19-3	CGT B39	SLG B37	TBD B38	LCG B25	TDT B29
Est.[a]Tarariras		0;[b]	2-3-;	2-2=;	0;	23	--[c]	23
BCF_3 15651-3	3bg	0;1	23;	2-;	0;1=	3+	;	4
BCF_3 15655-5	3bg	0;	2-3;	22+;	0;	3+	;	23
Est.Benteveo		0;	3	;	0;	0;	;	0;
BCF_3 15705-10	3	;1-	3+4	33+	;1=	3+	;1=	23+c
BCF_3 15706-1	3	;1=1	3+4	33+	;1=	3+	;1	4
BCF_3 15712-3	26	;1=	3+4	;	;1=1-	;	3+	1-;
BCF_3 15704-4	26	;1-	3+4	;	;1=	0;	3+	0;
Est.Pelón 90		0;	;1=	0;	0;	0;	1	0;
BCF_3 15715-5	1	0;	3+4	0;	3	3+	3-3	--
BCF_3 15719-8	1	0;	3+4	0; ;	3	3+	3+	4
BCF_3 15720-5	17	--	;1-	2-3-	;1=	23n	;	2-3-;Y
BCF_3 15727-3	17	;	1-1;	33+	2-c	3cn	;1c	4
BCF_3 15715-2	26	0;	3+4	0;	1=;	;	--	--
BCF_3 15723-2	26	0;1=	3-3+	;	;1=	;	3-3+	1-1
INIA Boyero		0;	2;3+	;	0;	0;	3+	0;1=
BCF_3 12627-1	26	0;	3+4	;	0;1=	0;	23	0;1=
BCF_3 12629-6	26	0;1=	3+4	;	;1=	0;	3-3+	0;1=1-
Est.Calandria		0;	;1-	;	0;	0;	0	1;nc
BCF_3 15658-6	3bg	;	23;	3	0;	3+	;	4
BCF_3 15659-4	3bg	0;1=	2-3+;	23	;1=	3+	;	4
BCF_3 15658-8	16	1n	1n	33+	1-n	1n	1n	1-;
BCF_3 15666-1	16	1-1+	1n	33+	1	1n	1-1n	1-n
BCF_3 15657-4	24	0;1-	;1=	;1=	0;	;1=	;	4
BCF_3 15659-1	24	0;1=	;1=	0;1=	0;	;	;	4
Est.Federal		0;	3+4	;	0;	2+3	;1-nZ	0;
BCF_3 12617-1	10	0;	3+4	;	;1=	3+	3+	0;
BCF_3 12620-9	10	0;1=	3+4	;1=	;1-2=	3+	3+	;
BCF_3 12617-7	10+	0;	3+4	;1=	;1=1-	3+	Z	;1=
BCF_3 12619-3	10+	0;	3+4	;1=	;1-	3+	Z	;
Est.Halcón		;1=	1+	;	0;	1n	1-1n	0;
BCF_3 12621-10	16	1-1+n	1n	33+	11+	1n	1-n	1=1-;
BCF_3 12621-11	16	1-1n	11+n	33+	1n	1n	1-1+Zn	;1=
BCF_3 12625-3	10	0;	3+4	0;	;1=	3+	3+	0;
BCF_3 12625-8	10	0;1=	3+4	;1=1-	--	3+	3+	;
BCF_3 12621-6	10+	;1=	3+4	;1=	;1=	3+	Z	1=;
BCF_3 12621-7	10+	0;1=	3+4	;1=	0;1=	3+	Z+	;1=

[a]: Estanzuela
[b]: Stakman et al., 1962; Roelfs, 1988a.
[c]: data not available.

Table 10. Seedling infection types of Thatcher and Thatcher backcross lines with single resistance genes tested with seven isolates of *Puccinia recondita tritici*.

Wheat line	BBB Race 1	MCR 19-3	CGT B39	SLG B37	TBD B38	LCG B25	TDT B29
Tc	3+4[a]	3+4	33+	3	3+	3+	4
Lr1	0;	3+	0;	3+	3+	33+	4
Lr2a	0;	0;	0;	33+	3+	0;	4
Lr2c	;1=	;1=	;	33+	3+	;	4
Lr3	;1-	3+	33+	;1=	3+	;1=	4
Lr9	0;	0;	0;	3	0;	0;	0;
Lr16	1-n	1n	3-3+	1-n	1n	1n	1-n
Lr24	0;	0;	0;	0;	0;	0;	4
Lr26	;1-	33+	;	;1=	0;	3+4	1=;
Lr3ka	1=;	3+	33+	2=;	22-	1-1c	4
Lr11	2-2	3+	33+	33+	2	4	4
Lr17	1-;	1-;	33+	;1=1-	3+	12=n	4
Lr30	2-	33+	33+	1-	2-	12=	4
Lr10	;1=	3+	;1=1-	1-;	3+	3+	0;
Lr18	2-1	22+	2	2	3+	3+	12=;
Lr21	1-;	21;	2-1;	2=1;	2-1	;12-	21;
Lr23	1+2	33+	33+	3+	22+	3	0;
Lr14a	33+	3+	33+	3+	3+	4	4
Lr14b	3	4	3	33+	3	4	0;
Lr20	3+	;	;	;	3+	;	0;
Lr33	2	2+3	2	3-3c	2+3+c	--[b]	--
Lr13	33+n(Z)	33+(Z+)	Z	33+	3+4	4	4
Lr34	3-3+c	2+3+	3=3c	2=3;	32-c	3=3	2-3c
Lr19	0	0;	0;	0;	0;	0;	0;
LrB	--	3+	2	1+n	2cn	1+	2
Lr3bg	;	32;	32;(Y)	;1=	3+	0;	4

[a]: Stakman et al., 1962; Roelfs, 1988a.
[b]: data not available.

Est. Tarariras. Seven BCF_3 lines were tested for seedling resistance. All lines expressed IT 0; to ; to race 1 and isolates B25 and B37, which are avirulent to *Lr3* and *Lr3bg*. These lines probably carry *Lr3* or *Lr3bg*. Further tests to differentiate between *Lr3* and *Lr3bg* confirmed that Est. Tarariras probably has *Lr3bg* (J.A. Kolmer, unpublished data).

Est. Benteveo. Eight BCF_3 lines were tested. Five lines expressed IT ; to ;1⁻ to *Lr26* avirulent isolates B39, B37, B38, B29 and race 1. These lines should have *Lr26*. Three lines

expressed IT ; to ;1 to isolates B37, B25 and race 1, which were avirulent to *Lr3*. These lines probably have *Lr3*.

Est. Pelón 90. Only ten of 41 BCF_2 families segregated for a single gene, since there was segregation for at least three genes in BCF_2 families derived from this cultivar. Seven F_4 lines derived from F_3 families which segregated for single genes were also tested for seedling leaf rust resistance. Two lines had IT 0; to *Lr1* avirulent race 1 and isolate B39 respectively. These lines should have *Lr1*. Two lines expressed IT 2^-3^- to 33^+, IT 23 to 3 and IT 2^-3^-; to 4 to *Lr17* virulent isolates B39, B38 and B29, respectively. These lines should have *Lr17*. Three lines had IT 0; to ;1 to *Lr26* avirulent isolates race 1, B39, B37, B38, and B29. These lines should have *Lr26*. Two lines (data not shown) had IT 33^+ to *Lr16* virulent isolate B39, and were resistant to all other isolates. One of these lines was further tested and had IT 33^+ to Lr16 avirulent and *Lr17* virulent isolate TBD, indicating that this line probably has *Lr17* J.A. Kolmer, unpublished data). The other line with IT similar to Tc*Lr16* may have been a mixture or resulted from an outcross. Other lines apparently segregating for single resistance genes did not have clear results.

INIA Boyero. Eight BCF_3 lines were tested. Four lines had IT 0; to 1^-; to all *Lr26* avirulent isolates (race 1, B39, B37, B38 and B29) and IT 23 to 3^+4 to *Lr26* virulent isolates 19-3 and B25, respectively. These lines probably have *Lr26*.

Est. Calandria. Seventeen BCF_3 lines with single gene segregation were tested. Five lines expressed IT 0; to ;1⁻ to *Lr3bg* avirulent isolates, B25 and race 1. These lines had IT 23; to 3 to isolates 19-3 and B39, which had IT 32; on *Lr3bg*. These lines probably have *Lr3bg*. Five lines expressed IT 3⁺4 to *Lr16* virulent isolate B39, and low IT to all other isolates. These lines may have *Lr16*. Seven lines had IT 3⁺4 to the only *Lr24* virulent isolate B29, and low IT to all other isolates. These lines should have *Lr24*.

Est. Federal. Five BCF_3 lines were tested. Two lines had high IT to *Lr10* virulent isolates 19-3, B38, and B25, and had low IT to all other isolates, which were avirulent to *Lr10*. These lines should have *Lr10*. Three other lines also expressed resistance to *Lr10* virulent isolates B25 (IT Z, Table 9) and B34 (IT 0;1, Table 11), indicating these lines carry *Lr10* and additional seedling resistance.

Table 11. Seedling IT of selected BCF_3 lines from Est. Federal to different *Puccinia recondita tritici* isolates.

	Leaf rust isolates					
Wheat line	MBR B26	CBT B31	TGG B33	MCG B34	MFR 41-2	PBL
Est.[a]Federal	X[b]	;	0;1=	0;	;	3
BCF_3 12617-7	X+	; ;1=	;1-	0;1-	; ;1-	3
BCF_3 12619-3	3n	;1- 2	;1- 2-	0;12	1- 2	3
Lr10	3	1-;	;	3	1-	3
Lr13	2n	2n	3	2+3-n	22-n	23-n
Lr34	3-3	2-3	3-3	23-	32	32

[a] Estanzuela
[b] Stakman et al., 1962; Roelfs, 1988a.

Est. Halcón. Nine BCF_3 lines were tested. Four lines had IT 3^+4 to *Lr16* virulent isolate B39, and had low IT to the other isolates. These lines should have *Lr16*. Two lines expressed IT 3^+4 to *Lr10* virulent isolates 19-3, B38, and B25 and low IT to *Lr10* avirulent isolates race 1, B39, B37, and B29. These lines probably have *Lr10*. Two lines expressed resistance to the *Lr10* avirulent isolates and had IT Z to *Lr10* virulent isolate B25. These lines should have *Lr10* and probably an additional resistance gene.

4.2.3. Seedling tests of BCF_2 families for Lr14a and Lr14b.

The isolate of race 1 used in the seedling tests is virulent to resistance genes *Lr14a*, *Lr14b*, and *Lr20*. These would not be detected by race 1 in the segregating BCF_2 families or in the BCF_3 line tests. Cultivars Est. Tarariras, Est. Benteveo, INIA Boyero, Est. Federal and Est. Halcón had intermediate or high ITs to isolate 19-3, which expressed IT ; to *Lr20*. Est. Pelón 90 had IT 1 to isolate B25, which expressed IT ; to *Lr20*. Est. Calandria had IT 22^+ to isolate 41-2, which expressed IT ; to *Lr20*. Therefore these cultivars do not have *Lr20*. To determine if *Lr14a* and *Lr14b* are present in these cultivars, selected BCF_2 families which were susceptible to race 1 were tested with isolates avirulent to *Lr14a* and *Lr14b* (Table 12).

Table 12. Seedling infection types of BCF_2 families derived from Uruguayan wheat cultivars, tested with *Puccinia recondita tritici* isolates, B29 and B33 for presence of genes *Lr14a* and *Lr14b*.

Wheat cultivar	BCF_2 family	Isolate B29	Isolate B33	Probable Gene
Est.[a]Benteveo	15705-4	3[b]	X+	*Lr14a*
	15707-5	3	X+	*Lr14a*
Est.Pelón 90	15725-1	23	X-	*Lr14a*
Est.Federal	12615-6	2-c;	2-2;c	*Lr14b*
	12617-10	2=1;c	2-2c	*Lr14b*
	12616-5	2=1;c	3	?
	12619-7	2=1;c	3	?
Est.Halcón	12622-6	2=c	X-	*Lr14b*
	12624-7	1-;n	X-	*Lr14b*
	12624-1	3	X	*Lr14a*
	12624-8	3	X	*Lr14a*
Lr14a		3	X-	
Lr14b		;	;1-2(X)	

[a] Estanzuela
[b] Stakman et al, 1962; Roelfs, 1988a.

Isolates B29 (which expresses an IT ; to *Lr14b)*, and B33 (which expresses IT X to both *Lr14a* and *Lr14b)* were used in the test. All seven BCF_2 families derived from Est. Tarariras, nine BCF_2 families derived from INIA Boyero, and four BCF_2 families derived from Est. Calandria expressed IT 3^+4 to both B29 and B33, indicating these lines do not have *Lr14a* and *Lr14b*.

Ten BCF_2 families from Est. Benteveo were tested; five families had IT 3^+4 to both B29 and B33 (data not shown), indicating these families do not have *Lr14a* and *Lr14b*. Five

families had IT X^+ to B33 and IT 3^+4 to B29 (Table 12). These families derived from Est. Benteveo probably have *Lr14a*. Three families from Est. Pelón 90 were tested. One BCF_2 family derived from this cultivar had IT X^- to isolate B33, and IT 23 to B29. This family may have *Lr14a*. Eight BCF_2 families derived from Est. Federal were resistant to both B29 and B33, indicating that *Lr14b* may be present in this cultivar. Ten BCF_2 families derived from Est. Federal had IT 2^-1;c to B29, and high IT to B33, which were different from either of the *Lr14* alleles. Twelve BCF_2 families from Est. Halcón were tested. Three families had IT 3^+4 to B29 and B33. Six families had low IT to both B29 and B33, indicating that *Lr14b* may be present, although IT to B29 was different form Tc*Lr14b*. Two BCF_2 lines had IT 3^+4 to B29 and IT X to B33. These families may have *Lr14a*.

4.3. GENETICS OF ADULT PLANT RESISTANCE.

Thatcher lines with the Seedling genes present in the seven cultivars had field severity and response indicated in Table 13 in 1994 and 1995.

Table 13. Field severity and response of Thatcher lines with the leaf rust seedling resistance genes present in seven Uruguayan cultivars.

	Field severity and response	
Tc line	1994	1995
Tc*Lr1*	90[a] S[b]	80 S
Tc*Lr3*	90 S	60-70 S
Tc*Lr3bg*	--[c]	30-50 MSS
Tc*Lr10*	80 S	80 S
Tc*Lr14a*	80 S	80-60 S
Tc*Lr16*	40 R	20-60 MR
Tc*Lr17*	40 MRMS	40 MSS
Tc*Lr24*	T MR	5-40 MSS
Tc*Lr26*	70 MSS	50-60 MSS
Thatcher	90 S	70 S

[a] Peterson et al., 1948
[b] Stakman et al., 1962
[c] Data not available

Tc*Lr1*, Tc*Lr3*, Tc*Lr10*, TcLr*14a* and Tc*Lr26* had field severity and response similar to the susceptible Thatcher, and Tc*Lr16* and Tc*Lr24* were more resistant than Thatcher both years. Tc*Lr17* was more resistant than Thatcher in 1995, and had 40 MSS in 1995. Tc*Lr3bg* was only evaluated in 1995, when it had 30-50 MSS.

4.3.1. Evaluation of BCF_2 families in field tests.

BCF_2 families which were homozygous susceptible to race 1 in seedling tests, and most families which segregated for seedling resistance to race 1, were tested as adult plants in the field rust nursery at La Estanzuela in 1994. BCF_2 families

which segregated in single gene ratios for seedling resistance to race 1 were tested as adults in the rust nursery in 1995. Results from both years were combined (Table 14).

Table 14. Segregation of BCF_2 families from crosses involving seven Uruguayan wheat cultivars and the susceptible cultivar Thatcher for resistance to *Puccinia recondita tritici* in field tests.

Cultivars	BCF_2 seedling IT[a]	BCF_2 field reaction Seg[b]	HS[c]	Exp. ratio	N[d]	X^2	P
Est.Tarariras	HS	20	5	3:1	2	0.33	.70-.50
	Seg	24	8	3:1	2	0.00	1.00
	Total	44	13	3:1	2	0.15	.90-.70
	Homogen.[e]					0.19	.70-.50
Est.Benteveo	HS	3	15	1:1	1	8.00	<.01
	Seg	31	31	1:1	1	0.00	1.00
	Total	34	46	1:1	1	1.80	.20-.10
	Homogen.					6.20	<.05
Pelón 90	HS	2	1				
	Seg	35	6				
	Total	37	7	3:1	2	1.94	.20-.10
				7:1	3	0.47	.50-.30
INIA Boyero	HS	51	10	3:1	2	2.41	.20-.10
				7:1	3	0.85	.50-.30
	Seg	53	4	7:1	3	1.57	.30-.20
				15:1	4	0.09	.90-.70
	Total	104	14	3:1	2	10.86	<.001
				7:1	3	0.04	.90-.70
	Homogen.				2	1.38	.30-.20
					3	2.37	.20-.10
Est.Calandria	HS	1	4				
	Seg	54	5				
	Total	55	9	7:1	3	0.14	.90-.70
Est.Federal	HS	12	18	1:1	1	1.20	.30-.20
	Seg	15	16	1:1	1	0.03	.90-.70
	Total	27	34	1:1	1	0.80	.50-.30
	Homogen.					0.43	.70-.50
Est.Halcón	HS	0	11				
	Seg	30	14	2:1	1	0.05	.90-.70
	Total	30	25	1:1	1	0.45	.70-.50

[a] BCF_2 families classified according to seedling IT to race 1. HS: homozygous susceptible (IT 3-4), Seg: segregating (IT 0-2$^+$)

[b] Seg: segregating for APR, segregating for leaf rust rating lower than Thatcher

[c] HS: homozygous susceptible for APR, with leaf rust rating equal to Thatcher

[d] number of effective resistance genes

[e] Homogeneity X^2 test for segregation for field reaction of race 1 seedling susceptible and segregating BCF_2 families.

The cultivar Thatcher had 90% and 70% severity and

susceptible responses, respectively, in 1994 and 1995. BCF_2 families with severity and response similar to Thatcher were considered susceptible.

Est. Tarariras. BCF_2 families that segregated and were homozygous susceptible to race 1, segregated for APR according to expected two gene ratios, as did the combined BCF_2 families. The chi-square test for homogeneity indicated that BCF_2 families segregating and susceptible to race 1 did not segregate in different ratios for APR.

Est. Benteveo. Among the BCF_2 families that were susceptible to race 1, three segregated for field resistance, and 15 were homozygous susceptible, which did not fit an expected single gene ratio. BCF_2 families that segregated to race 1 segregated according to a single gene ratio for field resistance. The chi-square test for homogeneity indicated that BCF_2 families that segregated or were susceptible to race 1 segregated differently for field resistance. The segregation among the total BCF_2 families fit an expected single gene ratio.

Est. Pelón 90. Only segregation among the total number of BCF_2 families could be considered since only three families were homozygous susceptible to race 1. The total number of BCF_2 families segregated according to two and three gene ratios. Est. Pelón 90 appears to have at least two genes conditioning field resistance.

INIA Boyero. BCF_2 families that were susceptible to race

1 segregated for at least two resistance genes as adult plants in field tests. BCF_2 families segregating for seedling resistance to race 1 segregated as adults to fit a three gene and four gene ratio. The total number of BCF_2 families segregated to fit an expected three gene ratio.

Est. Calandria. Only five BCF_2 families were homozygous susceptible to race 1. The number of resistance genes expressing field resistance was estimated based on total number of BCF_2 families. The BCF_2 families segregated for field resistance according to a three gene ratio.

Est. Federal. BCF_2 families that were susceptible and segregated to race 1, and the combined families segregated for field resistance according to an expected single gene ratio.

Est. Halcón. BCF_2 families susceptible to race 1 were all susceptible as adult plants in the field test. BCF_2 families segregating for seedling resistance to race 1 segregated for field resistance in a two to one ratio, which would be expected for one field effective gene and one ineffective seedling gene. The total number of BCF_2 families segregated for field resistance according to a single gene ratio.

4.3.2. Segregation for field resistance in intercrosses of the selected Uruguayan cultivars and Thatcher lines with adult plant resistance genes Lr13 and Lr34.

Individual F_2 plants from Tc*Lr13* and Tc*Lr34* crossed with the seven Uruguayan cultivars were tested for leaf rust resistance in field rust nurseries in 1992-1995 (Table 15). F_2 plants with moderately susceptible to susceptible responses, and with high severity levels (50-80%), were marked and individually harvested. The F_2 derived-F_3 and E_4 lines were evaluated for field rust reaction in the following years. F_3 and F_4 lines with response and severity equal to Thatcher would indicate that the adult plant gene in the Thatcher line involved in the cross was segregating in the original F_2 population and was not present in the resistant cultivar.

Table 15. Total number of F_2 plants with susceptible response and high leaf rust severity in rust nursery tests and number of F_2-derived F_3 and F_4 lines from intercrosses of Thatcher lines with either *Lr13* or *Lr34* with seven Uruguayan wheat cultivars.

Intercross	Total No F_2 plants	F_3 lines		F_4 lines		
		N[a]	Max[c] reaction	N	Max reaction	
Year			**1993**		**1994**	
Tc*Lr13*/Est.[b]Tarariras	322	32	20-60 MS[d]	4	20 M-70 MSS	Res[e]
Tc*Lr34*/Est.Tarariras	412	14	50-70 MS	5	30-60 MSS	Res
Tc*Lr13*/Est.Benteveo	304	13	20-50 MSS	4	20 M-70 MSS	Res
Tc*Lr34*/Est.Benteveo	211	25	80 S	7	80 S	Seg[f]
Tc*Lr13*/Est.Pelón 90	266	10	60-70 S	3	90 S	Seg
Tc*Lr34*/Est.Pelón 90	222	14	60-70 MS	4	50 M-80 S	Seg?
Tc*Lr13*/Est.Calandria	269	5	5-60 MS	3	10 R-90 S	Seg
Tc*Lr34*/Est.Calandria	346	11	50-70 MS	4	T R-80 S	Seg?
Thatcher			80-90 S		80-90 S	
Tc*Lr13* RL 4031			2 MR-30 MRMS		5 MRR- 20 MS	
Tc*Lr34* RL 6058			50 MSS-60 S		5 M-40 MS	
Year			**1994**			
Tc*Lr13*/INIA Boyero	565	0				Res
Tc*Lr34*/INIA Boyero	568	11	20-90 MS			Seg?
Tc*Lr34*/Est.Federal	508	84	90 S			Seg
Tc*Lr13,34*/Est.Fed.	143	24	90 S			Seg
Tc*Lr13*/Est.Halcón	544	10	90 S			Seg
Tc*Lr34*/Est.Halcón	548	68	90 S			Seg
Tc*Lr13,34*/Est.Hal.	614	19	90 S			Seg
Thatcher			80-90 S			
Tc*Lr13* RL 4031			5 MRR-20 MS			
Tc*Lr34* RL 6058			5 M-40 MS			
Year			**1995**			
Tc*Lr34*/Est.Federal	442	11	90 S			Seg
Tc*Lr13,34*/Est.Fed.	494	4	80-90 S			Seg
Tc*Lr34*/Est.Pelón 90	394	12	70 MSS			Res
Thatcher			80-90 S			
Tc*Lr13* RL 4031			5-20 VR 20 S			
Tc*Lr34* RL 6058			5-20 M			

[a] Number of F_2-derived F_3 and F_4 lines
[b] Estanzuela, [c] Maximum
[d] Modified Cobb scale (Peterson et al, 1948).
[e] Homozygous resistant, [f] Segregating

The Thatcher near-isogenic line with *Lr13* (RL 4031) had a moderate resistant to moderate susceptible response with 2 - 30% severity in 1992 to 1995 (Table 15). The Thatcher line with *Lr34* (RL6058) had a mixed to moderately susceptible or susceptible response, with 5 - 60% severity. Severity levels were higher in 1993 (50MS-60MSS) on Tc*Lr34* compared to the other years.

Est. Tarariras. Selected F_2-derived F_3 and F_2-derived F_4 lines from Tc*Lr13* and Tc*Lr34*/Est. Tarariras all had resistant leaf rust field reaction. The lack of segregation for both APR genes indicates that Est. Tarariras has both *Lr13* and *Lr34*.

Est. Benteveo. Selected F_2-derived F_3 and F_2-derived F_4 lines from Tc*Lr13*/Est. Benteveo did not segregate for leaf rust severity and response; all F_3 and F_4 lines had resistant field reaction. F_2-derived F_3 and F_2-derived F_4 lines derived from Tc*Lr34*/Est. Benteveo had leaf rust severity and response levels equal to Thatcher. Lack of segregation for *Lr13* indicates that *L13* is present, and segregation for *Lr34* indicates that *Lr34* is absent in E. Benteveo.

Est. Pelón 90. F_2-derived F_3 and F_2-derived F_4 lines from Tc*Lr13*/Est. Pelón had leaf rust severity and response equal to Thatcher. F_2-derived F_3 and F_2-derived F_4 lines from Tc*Lr34*/Est. Pelón had leaf rust severity and response generally equal to Tc*Lr34*. In 1994, some F_3 and F_4 lines segregated for higher field response (80 S) but had leaf tip necrosis, and uredinia concentrated at the base of the flag

leaf, which is characteristic of the resistance response of *Lr34*. Lines from other F_2 population, tested in 1995, had maximum field response of 70 MSS. The segregation for *Lr13* and possible lack of segregation for *Lr34* indicate that Est. Pelón lacks *Lr13* and probably has *Lr34*.

INIA Boyero. No plants with high severity of infection and response were found among the 565 F_2 plants from Tc*Lr13*/INIA Boyero, indicating this cultivar has *Lr13*. Selected F_2-derived F_3 lines from Tc*Lr34*/INIA Boyero had a moderate susceptible response with severities between 5-20 and 90%. Some F_3 lines had plants with dead flag leaves due to leaf rust; these plants were probably susceptible. The presence of susceptible plants in F_3 lines indicates these lines probably are segregating for *Lr34* and that INIA Boyero does not have *Lr34*.

Est. Calandria. There were no homozygous susceptible F_2-derived F_3 and F_2-derived F_4 lines from Tc*Lr13* and Tc*Lr34*/ Est. Calandria. Selected F_3 and F_4 lines from Tc*Lr13*/Est. Calandria, however, appeared to segregate within lines for leaf rust severity and response equal to Thatcher, indicating that these lines segregated for *Lr13* and that Est. Calandria probably does not have this gene. Selected F_3 and $_4F$ lines from *TcLr34*/Est. Calandria, also appeared to segregate for leaf rust severity and response similar to Thatcher, but the leaves were more resistant at the leaf tip and generaly had leat tip necrosis, indicating *Lr34* might be present in Est. Calandria.

Est. Federal. Selected F_2-derived $_3F$ lines from Tc*Lr34*/Est. Federal and Tc*Lr13,34*/Est. Federal had severity and response equal to Thatcher. The segregation for leaf rust response and severity equal to Thatcher in the F_2 populations indicates that Est. Federal lacks both APR genes *Lr13* and *Lr34*.

Est. Halcón. Selected F_2-derived F_3 lines form Tc*Lr13*/Est. Halcón and Tc*Lr34*/Est. Halcón had response and severity levels equal to Thatcher. Est. Halcón thus does not have genes *Lr13* or *Lr34*.

4.3.3. Greenhouse progeny tests of selected field resistant, seedling susceptible BCF_2 plants.

Single plants that expressed field resistance were selected from BCF_2 and F_3 families susceptible to race 1 at the seedling stage. The BCF_3 and F_4 lines were tested in the adult plant stage in greenhouse tests with race 1, which is avirulent to adult plants with *Lr13*, and isolate B27 which is virulent to *Lr13*. For segregating progenies from heterozygous plants, only resistant ITs are presented in Table 16. The BCF_3 and F_4 lines also were tested as seedlings with race 1 and isolate B27 to confirm that these lines lack seedling resistance to these isolates (Table 16).

Table 16. BCF_3 and F_4 line seedling and adult plant infection types to *Lr13* avirulent isolate race 1, and *Lr13* virulent isolate B27.

Wheat line	Seedlings		Adult plant stage				
			Race 1		B27		Field
	R1	B27	IT	Severity	IT	Severity	res.[a]
Est.Tarariras							
BCF_3 15646-4-1	23+n[b]	33+	;1-		3+4		13
BCF_3 15654-3-2	33+n	3-3+	0;1-		3+4		13
BCF_3 15651-5-1	3-3+	3=3	2-3(Z)	30	23(Z)	40	34
BCF_3 15646-9-1	3-3	33+	23(Z)	20[c]	23(Z)	30	34
BCF_3 15647-1-1	12+n	3-	0;		23(Z)	20	13?[d],34
Est.Benteveo							
BCF_3 15704-9-1	2+3+n	33+	;1-		3+4		13
BCF_3 15704-9-2	2+3n	33+	;		3+4		13?
BCF_3 15713-6-2	3-3+	32;	33+(Z)	40	23(Z)	30	34
F_4 15632-128-1	3-2	33+	2-3-(Z)	10	23(Z)	20	34
Est.Pelón 90							
BCF_3 15727-2-1	23	3-3+	23(Z)	40	23+(Z)	20	34
F_4 15633-8-1	23-	33+	23(Z)	20	23+(Z)	50	34
INIA Boyero							
BCF_3 12635-6-1	2+3+n	2+3+	0;		3+4		13
BCF_3 12629-4-1	3-3	33+	23(Z)	20	33+(Z)	30	34
BCF_3 12629-9-1	3	33+	23-(Z)	5	2(Z)	5	34
BCF_3 12631-5-1	23cn	23	0;		23(Z)	30	13,34
BCF_3 12633-1-1	2+3+n	33+	0;		3+4		13,34?
BCF_3 12634-3-1	23n	Z-Z+	;		0;1-		13+[e]
BCF_3 12634-1-1	22+n	23;	0;1-		12(Z)	5	13,34+
Est.Calandria							
F_4 15628-37-2	34	33+	23+(Z)	30	3+(Z)	20	34
F_4 15628-37-3	23-	3-3+	23+(Z)	30	3+(Z)	50	34
Est.Federal							
BCF_3 12625-9-1	23+	33-	23c	40	2+3+(Z)	50	34
BCF_3 12618-10-1	23	23	2(Z)	30	2+3(Z)	30	34
BCF_3 12617-12-1	3=	Z-	;		0;12		dif[f]
BCF_3 12618-2-1	33+c	Z	13(Z)	20	0;1-		34?
Thatcher	3+4	3+	3+4	50	3+4	80	
Tc*Lr13*	1+3+n	3+	;		3+4	70	
Tc*Lr34*	12	3	2-3(Z)	10	2+3(Z)	10	

[a]: APR gene present according to field phenotypic response.
[b]: Infection type, Stakman et al, 1962.
[c]: Severity, modified Cobb scale (Peterson et al., 1948)
[d]: ?: Doubtful
[e]: +: Has additional resistance
[f]: Different from *Lr13* or *Lr34* phenotypic expression.

Adult plants of Tc*Lr13*, had IT ; to race 1, and seedling plants IT $1^{+}3^{+}$n (small to large uredinia associated with necrosis) (Table 16). Isolate B27 was virulent to adults and seedlings of Tc*Lr13*, producing IT 3^{+} on both. The resistant response of adult plants of Tc*Lr34* was characterized by larger uredinia at the base of the flag leaf, with smaller uredinia toward the tip of the leaf (Z response) and little or no chlorosis associated with the uredinia. Adult plants of Tc*Lr34* had IT $2^{-}3$(Z) to race 1 and lower severity of infection (10%) compared to Thatcher (50%). Seedlings of Tc*Lr34* had reduced pustule size (IT 12) without necrosis to race 1. Isolate B27 produced IT 3 on seedlings of Tc*Lr34*, and IT $2^{+}3$(Z) with 10% severity on adults of Tc*Lr34*.

Est. Tarariras. Twelve BCF_3 lines were tested. Of the lines listed in Table 16, two had IT 0;1^{-} to ;1^{-} to race 1, and IT $3^{+}4$ to isolate B27 as adults, which indicated that these lines have *Lr13*. Two lines had IT 23(Z) to both race 1 and B27, which indicates these lines have *Lr34*. One line had IT 0; to race 1, and IT 23(Z) to B27, which indicated the presence of both *Lr13* and *Lr34*.

Est. Benteveo. Of the four lines listed in Table 16, two had IT ;1 to race 1, and IT $3^{+}4$ to B27 as adults, which indicated the presence of *Lr13*. Two lines had IT 33^{+} (Z) or $2^{-}3^{-}$ (Z) and 23 (Z) to race 1 and B27, which indicated the presence of *Lr34*, or another APR gene with similar phenotypic expression.

Est. Pelón 90. Five lines had IT 23(Z) to both race 1 and B27, which indicates the presence of *Lr34*.

INIA Boyero. Twenty one lines were tested. Most lines had IT similar to Tc*Lr13* and/or Tc*Lr34* to both race 1 and isolate B27 which indicates the presence of *Lr13* and/or *Lr34*. BCF_3 line 12634-3-1 had IT 23n to race 1 and IT Z^-Z^+ to B27 in seedlings. Adult plants of this line had IT ; to race 1 and IT $0;1^-$ to isolate B27. This line may have *Lr13* plus an additional APR gene. BCF_3 line 12634-1-1 also had a lower IT as adult plants than either *Lr13* or *Lr34* to isolate B27, indicating this line probably has additional APR.

BCF_3 lines derived from BCF_2 families which segregated for IT Z in seedling tests with race 1 were tested with different leaf rust isolates to determine if the IT Z was due to the expression of *Lr13* in the seedling stage (Tables 17 and 18). These BCF_3 lines do not have *Lr26* since they had higher IT to *Lr26* avirulent isolates race 1, B39, B38 and B29 (Table 17), B26, B33, (Table 18) than Tc*Lr26*.

Table 17. Seedling infection types of selected BCF_3 lines derived from INIA Boyero to different *Puccinia recondita* isolates.

	Puccinia recondita isolates						
Wheat line	BBB Race1	MCR 19-3	CGT B39	SLG B37	TBD B38	LCG B25	TDT B29
INIA Boyero	0;[a]	2;3+	;	0;	0;	--[b]	0;1=
BCF_3 12631-18	Z	3+4	Z	1-;	3+	Z	2+3
BCF_3 12634-8	Z	3+4	3-3;	;1=	3+	--	13;cnZ
Lr26	;1-	33+	;	;1=	0;	3+4	1=;
Lr13	Z	Z+	Z	33+	3+4	4	4
Lr34	3-3+c	2+3+	3=3	2=3;	32-	3=3	2-3c

[a] Stakman et al., 1962; Roelfs, 1988a.
[b] Data not available.

BCF_3 lines 12631-18 and 12634-8 had high IT to isolate 19-3, which had IT Z^+ to *Lr13* (Table 18). Both lines expressed low or intermediate IT ($;1^=$ to 2^+3 or Z) to B37, B25 and B29, which had high IT on Tc*Lr13* in the seedling stage.

Table 18. Seedling infection types of selected BCF_3 lines derived from INIA Boyero to different *Puccinia recondita* isolates.

	Puccinia recondita isolates					
Wheat line	MBR B26	LBB B27	CBT B31	TGD B33	MCG B34	MFR 41-2
INIA Boyero	;[a]	12;	;	;1-	1-;	1;
BCF_3 12634-3	23	X	2n	3	X-	2n
BCF_3 12634-8	X	X	2n	3	X-	2-n
Lr26	;	2	1-;	1=;	3-	2+
Lr13	2n	3	2n	3	2+3-n	22-n
Lr34	3-3	23-	2-3	3-3	23-	32

[a] Stakman et al., 1962; Roelfs, 1988a.

BCF_3 lines 12634-3 and 12634-8 had similar intermediate (2n - 23) or X IT to isolates B26, B31, and 41-2 as the *Lr13*

line (Table 18). However, the lines also expressed IT X to B27, which is virulent to *Lr13*, and very low IT to B34 (X^-), which had IT 2^+3^-n to *Lr13*.

Resistance of BCF_3 lines derived from BCF_2 families with IT Z to race 1 was not clearly associated with *Lr13* resistance.

Est. Calandria. Three F_4 lines had IT 23^+(Z) to race 1 and IT 3^+(Z) to isolate B27 (Table 16), which indicates the presence of *Lr34*.

Est. Federal. Eleven BCF_3 lines were tested. Most lines had IT 2 to 33^- to isolates race 1 and B27 as adult plants, which were similar to the IT observed on Tc*Lr34*. Lines 12617-12-1 and 12618-2-1 had IT Z as seedlings to isolate B27. Line 12617-12-1 had IT ; and 0;12 to isolates race 1 and B27, respectively, as adult plants. Line 12618-2-1 had IT 13(Z) and IT $0;1^-$ to race 1 and isolate B27 respectively, as adult plants. Results from this test indicated that Est. Federal may have *Lr34* or a gene with similar phenotypic expression, plus an additional APR gene conditioning resistance to isolate race 1 and isolate B27.

Lines with *Lr13* generally had seedling IT 2^+3 to race 1 with necrosis associated with the uredinia. However, the resistance response of *Lr13* was most clearly seen in the adult plant tests.

4.3.4. Presence of genetic markers associated with Lr13 and Lr34 in selected Uruguayan cultivars.

F_1 plants of Spica/Est. Tarariras and Spica/INIA Boyero showed a premature gradual death of leaves and leaf sheaths (Table 19). This symptom resulted in slower plant development and complete death when the first tillers had formed. F_1 plans from Spica/Tc*Lr13* also had necrosis resulting in plant death.

Table 19. Expression of hybrid necrosis and presence of *Lr13* in selected Uruguayan cultivars, according to other tests.

Cultivars	Head N[a]	Hybrid necrosis	Progeny from intercrosses	Greenhouse BCF3 test	Presence of *Lr13*
Est. Tarariras	2	Yes	Resistant	*Lr13*	Yes
Est. Benteveo	2	No	Resistant	*Lr13*	Yes
Est. Pelón 90	4	No	Segregating		No
INIA Boyero	5	Yes	Resistant	*Lr13*	Yes
Est. Calandria	4	No	Segregating		No
Est. Federal	2	Yes	Segregating		No
Est. Halcón	2	No	Segregating		No

[a] Number of crossed heads

F_1 plants from Spica/Est. Federal died at three - five leaf stage, with severe hybrid necrosis at an earlier stage than F_1 plants of Spica/TcLr13. Hybrid necrosis was not detected in F_1 plants from crosses of Spica with Est. Benteveo, Est. Pelón 90, Est. Calandria, and Est. Halcón.

The cultivars Est. Tarariras, Est. Pelón 90, and INIA Boyero had clear leaf tip necrosis (*Ltn*), which indicated that *Lr34* is most likely present in these wheats (Table 20).

Table 20. Expression of tip die necrosis and presence of *Lr34* in selected Uruguayan cultivars, according to other tests.

Cultivars	Tip die necrosis	Progeny from intercrosses	Greenhouse BCF3 test	Presence of *Lr34*
Est. Tarariras	Pronounced	Resistant	*Lr34*	Yes
Est. Benteveo	Little	Segregating	*Lr34*	Doubtful
Est. Pelón 90	Pronounced	Resistant?	*Lr34*	Yes
INIA Boyero	Pronounced	Segregating	*Lr34*	Possible
Est. Calandria	Some	Resistant?	*Lr34*	Yes
Est. Federal	Little	Segregating	*Lr34*	Possible
Est. Halcón	No	Segregating		No

Est. Calandria also expressed some leaf tip necrosis, although not as clearly as the other cultivars. Est. Benteveo and Est. Federal had little leaf tip necrosis, indicating these cultivars may not have *Lr34*. Est. Halcón did not have leaf tip necrosis which indicated the absence of *Lr34* in this cultivar.

4.4. SUMMARY OF RESULTS.

Table 21 summarizes most possible genotypes for leaf rust resistance in the selected Uruguayan cultivars.

Table 21: Probable leaf rust resistance genes present in seven Uruguayan wheat cultivars.

Cultivars	Seedling resistance	APR
Early maturity		
Est.Tarariras	*Lr 3bg*	*Lr 13, 34*
Est.Benteveo	*Lr 3, 26, 14a*	*Lr 13, 34?*[a]
Est.Pelón 90	*Lr 1,17, 26, 14a?*	*Lr 34*
INIA Boyero	*Lr 26* +[b]?	*Lr 13, 34* and/or+?
Late maturity		
Est.Calandria	*Lr 3bg, 16, 24*	*Lr 34*
Est.Federal	*Lr 10, 14b?* and/or +?	*Lr 34* and/or +?
Est.Halcón	*Lr 10, 16, 14a, 14b?,* +?	

[a] ?: doubtful
[b] +: unidentified

5. DISCUSSION.

5.1. LEAF RUST RESISTANCE GENES IN SELECTED URUGUAYAN CULTIVARS.

Seedling resistance genes *Lr1*, *Lr3*, *Lr3bg*, *Lr10*, *Lr14a*, *Lr16*, *Lr17*, *Lr24*, *Lr26*, and APR genes *Lr13* and *Lr34* were found in the selected Uruguayan cultivars. Seedling gene *Lr14b* may also be present. All these genes are in wheat cultivars that have been grown in the region: *Lr1*, *Lr3*, *Lr10*, *Lr16*, *Lr17*, *Lr23* and *Lr26* are frequent in Argentine germplasm (Antonelli, 1995). *Lr14b* is in María Escobar (Dyck and Samborski, 1970) and Rafaela MAG (Dyck and Kerber, 1977). Genes *Lr1*, *Lr3*, *Lr3bg*, *Lr10*, *Lr13*, *Lr14a*, *Lr16*, *Lr17*, *Lr26* and *Lr34* are found in CIMMYT germplasm (Singh and Rajaram, 1991, Singh, 1993).

Estanzuela Tarariras. A single incompletely dominant gene conditioned seedling resistance to race 1. This gene is probably *Lr3bg*, since the cultivar and derived BCF_3 lines were resistant to all isolates avirulent to this gene. Bagé, a parent of Est. Tarariras, has *Lr3bg* (Haggag and Dyck, 1973).

A seedling IT 23 to *Lr3bg* virulent isolates indicated that this cultivar probably has APR. The presence of *Lr13* and *Lr34* in Est. Tarariras was shown genetically, by the two-gene segregation of seedling susceptible BCF_2 families under field conditions and the absence of susceptible F_2 progeny in the intercrosses with Tc*Lr13* and Tc*Lr34*. The IT and rust severity of adult plants derived from adult plant resistant, seedling

susceptible BCF_2 plants to race 1 and isolate B27 corresponded with the IT and rust severity of Tc*Lr13* and Tc*Lr34*. The presence of *Ne2m* and *Ltn* also indicates, respectively, *Lr13* (Hawthorn, 1981) and *Lr34 (Singh, 1992a)*, are present in Est. Tarariras. Resistance gene *Lr13*, could have been derived from Surpresa or Frontana, and *Lr34* from Frontana (Appendix 1).

Estanzuela Benteveo. Seedling resistance to race 1 was conditioned by one partially dominant gene and another dominant gene. According to IT data of this cultivar and derived BCF_3 lines with single seedling genes, Est. Benteveo has *Lr3* and *Lr26*. Gene *Lr3* is most likely the partially dominant gene that expressed IT 0; to ;1^-. This gene was also shown to be partially dominant in a previous study (Haggag and Dyck, 1973). Gene *Lr26* is most likely the dominant gene that conferred IT 0;1 to ;1^-. The absence of gamma gliadin 45 indicates the 1BL/1RS translocation (Howes et al., 1989) and *Lr26* (Singh et al.,1990) are present in this cultivar. Both *Lr3* and *Lr26* were probably derived from Avrora (Appendix 2, Dyck, 1994b, Mettin et al., 1973, Zeller, 1973).

Leaf rust isolates with virulence to *Lr3* and *Lr26* have increased in Uruguay from 11.1% in 1989 (Germán and Kolmer, 1994) to 92.2% in 1994 (Germán, 1995). In Argentina, six new races isolated in 1991-1993 had virulence to both *Lr3* and *Lr26*. The increase of races with these virulences is probably due to the deployment of these genes in combination

(Antonelli, 1994).

Intermediate ITs $2^{-}2^{cn}$ to B34 (Table 6), IT 2 to race 15, and IT X to 63-88 (Appendix 8), indicate additional seedling resistance genes or that APR genes may be present. *Lr14a* is probably present in Est. Benteveo since one half of the BCF_2 families that were seedling susceptible to race 1 and also were susceptible in the field, expressed similar ITs to isolates B29 and B33, as did Tc*Lr14a* in seedling tests. *Lr14a* is present in Kalyansona (McIntosh et al., 1995), a progenitor of Est. Benteveo (Appendix 2).

Field resistance in BCF_2 families derived from Est. Benteveo was conditioned by one APR gene. The F_2 progeny from Tc*Lr13*/Est. Benteveo did not segregate for susceptibility, indicating the presence of *Lr13*. BCF_3 lines from selected field resistant BCF_2 plants had very low IT to *Lr13* avirulent isolate race 1 and high IT to *Lr13* virulent isolate B27. However, F_1 plants of Spica/Est. Benteveo did not have hybrid necrosis, indicating that Est. Benteveo does not have *Ne2m*. Singh and Rajaram (1991) found two cultivars which had *Ne2m* but lacked *Lr13*, which indicated that recombination between the two genes can occur. Anand et al. (1991) found a recombination value of 33.27 ± 4.12% between *Ne2m* and *Lr13*. This recombination frequency appears to be high since other reports confirmed that *Ne2m* and *Lr13* are closely linked (Hawthorn, 1981; Singh and Gupta, 1991; Singh, 1993). Gene *Lr13* is present in several wheats that comprise the pedigree

of Est. Benteveo: Frontana (Dyck et al., 1966), Kalyansona (Reedy and Rao, 1980), Klein Rendidor and Sinvalocho MA (Roelfs, 1988b).

Lr34 might also be present in Est. Benteveo, since two BCF_3 and two F lines had a phenotypic expression characteristic of *Lr34* in the greenhouse and field tests. However, F_2 plants of Tc*Lr34*/Est. Benteveo segregated for susceptibility, which would indicate that *Lr34* was not present in Est. Benteveo. BCF_2 families segregated for a single gene as adult plants in the field test. Est. Benteveo could carry *Lr34* at a different location than chromosome 7D. Dyck et al. (1994) demonstrated that RL 6077 carries *Lr34* on a translocation to a chromosome different from 7D, or has a different gene with phenotypic expression similar to *Lr34*. It is also possible that either *Lr13* or *Lr34* were not clearly expressed in BCF_2 families in field tests, resulting in a single gene segregation. Est. Benteveo had little leaf tip necrosis in the flag leaves, indicating it probably does not carry *Lr34*. The evidence for the presence of *Lr34* in Est. Benteveo is not conclusive. Segregation for susceptibility in F_2 populations from crosses of Est. Benteveo and/or BCF_3 lines probably carrying *Lr34* with RL 6077 should be studied. Single gene lines with the *Lr34* type resistance should be studied in greenhouse and field tests and further backcrossed to Thatcher. Progenitors of Est. Benteveo's have *Lr34*: Frontana (Dyck and Samborski, 1982), Bezostaja1 (Dyck, 1994b).

Alternatively, it is possible that Est. Benteveo has a different APR gene with phenotypic expression similar to *Lr34*.

Estanzuela Pelón 90. Seedling resistance to race 1 was conditioned by at least three genes. Genes *Lr1*, *Lr17* and *Lr26* were present in BCF_3 lines that segregated for single resistance genes. Est. Pelón 90 probably has *Lr1* and *Lr17*, inherited from Torim 73 (Singh, 1993), and *Lr26* from Kavkaz (which carries the 1BL/1RS translocation, Mettin et al., 1973, Zeller, 1973) and thus *Lr26* (Singh et al., 1990) (Appendix 4). The presence of the rye translocation and *Lr26* in Est. Pelón 90 was also demonstrated since it lacks gamma gliadin 45 (Howes et al., 1989).

The two dominant genes that conferred ITs 0; and 0; to ;1$^{=}$ probably were respectively *Lr1* and *Lr26*, as indicated by similar ITs for the Thatcher lines with these genes. Gene *Lr1* was reported to be dominant (Mains et al, 1926). The partially dominant gene expressing IT ;1$^{=}$ to ;1^{-} was probably *Lr17*. Dyck and Samborski (1968a) indicated that *Lr17* was partially dominant.

Gene *Lr14a* may also be present in Est. Pelón 90. To prove adequately this, all BCF_2 families should be tested with an *Lr14a* avirulent isolate. Families segregating for a single gene should be identified and progeny tested with isolates differing in virulence to *Lr14a*. Alternatively, lack of susceptible plants in a large F_2 population of Tc*Lr14a* x Est.

Pelón 90 tested with an *Lr14a* avirulent isolate would also demonstrate the presence of *Lr14a*.

In 1994 field tests, gene *Lr17* and one to two adult plant genes conditioned field resistance in Est. Pelón 90. BCF2 families with *Lr17* tested in 1995 were segregating for field resistance. Est. Pelón 90 lacks *Lr13*. Susceptible progeny were found in F_2 plants from Tc*Lr13*/Est. Pelón 90. None of the BCF_3 lines derived from field resistant BCF_2 plants had *Lr13*. Est. Pelón 90 also lacks *Ne2m*.

The APR of Est. Pelón 90 appears to be due to *Lr34*, which is probably present in one of its parents, Torim 73 (Singh, 1993a). A few F_3 and F_4 families from Tc*Lr34*/Est. Pelón 90 segregated for relatively high severity (80S). Flag leaves, however, were more resistant at the tip, which is typical of *Lr34* expression. Dyck (1979) described the resistance in PI 250413, considered to be due to *Lr34* (Dyck et al., 1994), as an IT Z, with the most resistance expressed near the tip of the leaf. The mesothetic reaction was variable, with some flag leaves showing little infection while others appeared to be susceptible, with only slight resistance near the tips of the leaves, as was observed for Tc*Lr34*/Est. Pelón 90 progenies. Further evidence for the presence of *Lr34* in Est. Pelón 90 were *Ltn* in the cultivar, and similar phenotypic expression as Tc*Lr34* of BCF_3 lines derived from field resistant BCF_2 plants.

INIA Boyero. BCF_2 families segregated for one dominant

gene with IT ;1⁼ to ;1⁻ when tested with race 1. This gene should be *Lr26* as indicated by IT data from the cultivar and BCF_3 lines, and the presence of the 1BL/1RS translocation in INIA Boyero. *Lr26* was probably inherited from Bobwhite "S" (Appendix 2). INIA Boyero may have additional seedling resistance, as shown by the low IT to isolate 41-2. This resistance probably was inherited from MN 72-131. This line is derived from the cross Aepoglon/Angus. Aepoglon is resistant at the seedling stage to all North American leaf rust isolates (Alan P. Roelfs, personal communication).

INIA Boyero had intermediate IT to some *Lr26* virulent isolates indicating the presence of APR in this cultivar. INIA Boyero probably has three genes conferring field resistance. These must be APR genes since *Lr26* does not condition effective resistance to the current leaf rust population.

There were no susceptible F_2 plants or F_3 families in progenies from intercrosses with Tc*Lr13*. There was only one F_3 family from Tc*Lr34*/INIA Boyero with infection 20 to 90 MS, but others had dead leaves due to leaf rust. This evidence does not eliminate the possible presence of *Lr34* in INIA Boyero, since *Lr34* may be located in another chromosome (Dyck et al., 1994). BCF_3 lines from selected field resistant BCF_2 plants had the same phenotypic expression as Tc*Lr13* or/and Tc*Lr34* to isolates avirulent and virulent to *Lr13*. INIA Boyero also has *Ne2* and *Ltn*, genetic markers for *Lr13* and *Lr34*. Therefore, INIA Boyero should have has *Lr13* and probably *Lr34*.

INIA Boyero probably has a third APR gene in addition to *Lr13* and *Lr34*. In previous years virulence to *Lr13* and *Lr26* has been high since the Uruguayan cultivar Est. Cardenal (Veery 3 - CIMMYT), with *Lr13* + *Lr26* (Singh and Rajaram, 1991) had high leaf rust severity. INIA Boyero was highly resistant in the same years, while Est. Tarariras (*Lr3bg*, *Lr13* + *Lr34*) had up to 60 S leaf rust infection (Verges et al., 1991). INIA Boyero appears to have APR in addition to *Lr13* + *Lr34*.

Four BCF_3 lines with IT Z to race 1 that did not have *Lr26*, had intermediate or mesothetic ITs to other isolates in seedling tests. Mesothetic or Z IT in the seedling stage can indicate the presence of APR. Tc*Lr13* also expressed Z or X IT to isolates which are probably avirulent to adult plants with this gene. Isolates B27, B25 and B29 caused high IT to *Lr13* as seedlings, but produced mesothetic IT to BCF_3 lines from INIA Boyero. The X or Z IT expressed by these lines to these isolates was not conditioned by *Lr13*. *Lr34* does not condition Z or X IT at the seedling stage and does not express necrosis (Dyck, 1977; Drijepond and Pretorius, 1989). These lines thus appear to carry a different resistance gene and should be studied further. BCF_2 families should be tested with one or more *Lr26* virulent isolates that are avirulent to INIA Boyero. This test would verify if only one gene in addition to *Lr26*, is segregating in the BCF_2 families. The resistance should be isolated in a single gene line and the infection types to different leaf rust isolates compared to previously identified

seedling resistance genes.

The BCF_3 line derived from a field resistant BCF_2 12634-3 plant was tested in adult plant stage with race 1 and B27. All plants of BCF_3 12634-3-1 had Z IT in the seedling stage and 0;1⁻ IT in the adult plant stage to *Lr13* virulent isolate B27. The field reaction of the BCF_3 line was not similar to either Tc*Lr13* or Tc*Lr34*. BCF_3 line 12634-3-1 thus may have a different APR gene than *Lr13* or *Lr34*. This gene cannot be *Lr12* or *Lr22b* since these genes do not confer field resistance. The possibility that this gene is different from previously described APR genes needs to be further tested for inheritance and independence to *Lr13* and *Lr34*.

Gene *Lr13* in INIA Boyero was probably derived from Bobwhite "S" (Mohan M. Kohli, personal communication). Other APR factors may have been derived from MN 72-131. This line from Minnesota was released in Paraguay as Cordillera-4 (Kohli, 1986), and has remained resistant to leaf rust since release in 1984 (M.M. Kohli, personal communication). Angus, a parent of MN 72-131, was released in Minnesota in 1978 and it is still resistant to leaf rust in North America. Angus was selected from the cross Thatcher / *2Surpresa /3/ Frontana /2/ Kenya 58 / Newthatch /7/ Pembina / Frontana / 5*Thatcher /6/ Mida / Kenya 117A / *2Thatcher /3/ Frontana / 4*Thatcher /4/ (III-58-4, MT Semidwarf #839, (Norin 10 / Brevor, Sel. 14) /2/ ?*Centana) /5/ Kenya 58 / Newthatch /2/ 3*Lee and may derive its APR from Frontana (Dyck et al., 1966; Dyck and Samborski,

1982, Singh and Rajaram, 1992) or Surpresa (Roelfs, 1988b). Angus has a different leaf rust resistance gene(s) than Chris and Era (D.V. McVey, personal communication).

Estanzuela Calandria. Seedling resistance to race 1 is probably conditioned by 3 genes. BCF_2 families with single resistance genes probably had *Lr3bg*, *Lr16* and *Lr24*, according to IT data to different leaf rust isolates. The dominant gene with IT 1n was probably *Lr16* which also was found to be dominant to certain races by Anderson (1961). The second dominant gene with IT 0; was probably *Lr24*, which has previously been reported to be dominant (Gough and Merkle, 1971). The partially dominant gene expressing IT 0; was probably *Lr3bg* (Haggag and Dyck, 1973). A parent of Est. Calandria is Est. Tarariras, which probably *has Lr3bg*. *Lr16* and *Lr24* could have been inherited from L10, which is a CIMMYT line. The combination of *Lr3bg*, *Lr16* and *Lr24* conferring seedling resistance in Est. Calandria to race 1 explains the IT characteristic of *Lr16* expressed by this cultivar when tested with isolates virulent to *Lr3bg* and *Lr24* (B29, 41-2, Table 6).

The BCF_2 families segregated to fit a two gene ratio to isolate 19-3. This isolate is virulent to *Lr3* and causes IT 32; (Y) to Tc*Lr3bg*. Since the IT 32; was difficult to distinguish from IT 3^+, six families expressing the 32; IT were considered susceptible to isolate 19-3 and may have

Lr3bg. The dominant gene with IT 0; to ; to isolate 19-3 probably was *Lr24*. The second gene expressing IT 1 to 19-3 probably was *Lr16*. *Lr16* was dominant to isolate race 1 and recessive to isolate 19-3. Anderson (1961) also found that *Lr16* was dominant to certain leaf rust isolates and recessive to other isolates. Kolmer and Dyck (1994) demonstrated that certain *Lr* genes changed dominance relationships when tested with homozygous or heterozygous avirulent leaf rust isolates. Probably race 1 is homozygous and 19-3 is heterozygous avirulent at the locus corresponding to *Lr16*.

BCF_2 families from Est. Calandria segregated for three genes conditioning resistance in the field. *Lr16* and *Lr24* in Est. Calandria were more resistant than Thatcher in 1994 and 1995. Tc*Lr3bg* was not tested in 1994 and in 1995 had 30-50 MSS infection in field tests, when Thatcher had 70 S. Although the severity and response of the Tc*Lr3bg* was lower than that on Thatcher, infection on Tc*Lr3bg* increased to 70-80 MSS in a later reading. BCF2 families segregating for *Lr3bg* may have been missclassified as homozygous susceptible. Two of five BCF2 families with only *Lr3bg* tested in 1995, were homozygous susceptible and three were segregating for field resistance. BCF2 families from Est. Tarariras, segregated for two APR in BCF2 families that were susceptible and segregating for seedling resistance, indicating *Lr3bg* was not detected in BCF2 families from this cultivar. The third field effective gene in Est. Calandria is probably an APR gene. Two BCF_2 families from

Est. Calandria carrying only *Lr3bg* segregated for field severity and response of 2M to 5M, while *Lr3bg* was 30 to 50 MSS. This further indicates the presence of APR in this cultivar.

There were no homozygous susceptible F_3 or F_4 lines from Tc*Lr13*/Est. Calandria, but some lines segregated for *Lr13*. Homozygous susceptible F_2 plants may not have been identified because only one plant in 256 would be susceptible if three genes from Est. Calandria (*Lr16*, *Lr24*, one APR gene) were segregating in addition to *Lr13*. F_4 lines from field resistant BCF_2 families had different ITs as compared to Tc*Lr13* to race 1 and isolate B27 in adult plant greenhouse tests. This cultivar also did not have *Ne2m*, indicating Est. Calandria does not have *Lr13*.

There also were no homozygous susceptible F_3 or F_4 families from Tc*Lr34*/Est. Calandria. The F_3 families with highest infection in 1993 had severity and response of 50 to 70 MS which was similar to the relatively high infection on Tc*Lr34* (50 MSS to 60 S) observed that year. Tc*Lr34* was 5M to 40 MS in 1994 and three F_4 lines from Tc*Lr34*/Est. Calandria were mostly resistant but there were a few plants with 80 S. Leaves from these plants also had leaf tip necrosis and were more resistant at the leaf tip, which is typical from *Lr34* phenotypic expression. BCF_3 lines derived from field resistant BCF_2 selections had *Lr34* phenotypic expression in greenhouse adult plant tests. Est. Calandria has leaf tip necrosis,

although not as clearly expressed as in other cultivars. *Lr34* is most likely present in Est. Calandria, and may have been inherited from Est. Tarariras.

Estanzuela Federal had been very resistant to the prevalent leaf rust population in Uruguay since release in 1989. In 1993, low to intermediate field severities were observed. Est. Federal had high early leaf rust severity in 1994, due to infection by race MCR-10. Est. Federal is seedling susceptible to MCR-10 (isolate 19-3), but it is not uniform for rust reaction in field tests. In 1995, 130 head rows were observed for field reaction, 31% had 80 to 90 MSS or S, 49% had intermediate infections of 50 to 70% MSS and 20% had infections lower than 40 MSS, usually 5 to 20 M. The plant of Est. Federal used for crossing was of the resistant type.

Seedling resistance to race 1 in Est. Federal was conditioned by a single partially dominant gene with IT ; to 1⁻;. Infection type data of this cultivar and derived lines indicated that this gene is *Lr10*. Anderson (1961) found that *Lr10* was recessive and dominant in progenies from the same cultivars inoculated with the same isolates in different tests, due to variable expression of heterozygous plants under different environmental conditions. Heterozygous BCF_2 plants from Est. Federal expressed an intermediate IT in this study. Est. Federal probably inherited *Lr10* from Lee (Anderson, 1961), through ND 84 (Appendix 5).

Gene *Lr10* does not condition effective field resistance in Uruguay (Germán and Kolmer, 1994), thus Est. Federal must have additional resistance. Additional seedling resistance in Est. Federal was indicated by IT ; to ;1^{-} to *Lr10* virulent isolates B34 and R9 (Table 6), PNM (Appendix 10) and low mesothetic IT to B25 and B27 (Table 6). BCF_3 lines 12617-7 and 12619-3 also had IT Z to B25 and IT 0;1^{-} and IT 0;12 to B34 (Table 9). These lines appear to carry the same additional resistance. This resistance is different from any of the known seedling genes tested. Race 1 had high IT on lines with the additional resistance gene(s). BCF_2 families susceptible as seedlings to isolates B29 and B33 indicated that Est. Federal may carry *Lr14b*, assuming some families were misclassified for susceptibility to B33. However, the IT of Est. Federal derived BCF_3 lines was different from the IT of Tc*Lr14b*. Est. Federal may have seedling resistance that has not previously been characterized. This gene did not confer resistance to the prevalent leaf rust population, since BCF_3 lines tested with B29 and B33 were susceptible in field tests. The seedling resistance in Americano 44d (Antonelli, 1994) could be this gene in Est. Federal since this cultivar is in the pedigree of Est. Federal (Appendix 5). Further tests are required to study the additional seedling resistance in the cultivar. *Lr10* virulent isolates that are avirulent to Est. Federal should be used to test BCF_2 families.

The plant selected from Est. Federal for crossing had one

gene conditioning field resistance. This gene must be an APR gene since Est. Federal was susceptible to race MCR-10 in the seedling stage. Est. Federal does not have *Lr13*. There were susceptible F_3 lines among the progeny of Tc*Lr13*/Est. Federal, and BCF_3 lines derived from field resistant BCF_2 plants had low IT as adults to *Lr13* virulent isolate B27. The severe hybrid necrosis of F_1 plants from Spica/Est. Federal indicated that Est. Federal has *Ne2s*, which is a different allele at the *Ne2* locus (Hermsen, 1963) linked in repulsion with *Lr13*.

Susceptible F_3 lines were also found among the progeny of Tc*Lr34*/Est. Federal, indicating the absence of *Lr34* in this cultivar. However, BCF_3 lines 12625-9-1 and 12618-10-1 derived from field resistant BCF_2 plants had resistant phenotypic expression similar to *Lr34* in adult plant greenhouse and field tests. Est. Federal also expressed little leaf tip necrosis. As for Est. Benteveo, it is possible that *Lr34* in Est. Federal is located on a chromosome other than 7D, or thatEst. Federal has a different gene with resistant phenotypic expression similar to *Lr34*, as suggested for RL 6077 (Dyck et al., 1994). Cultivars which have *Lr34* in the pedigree of Est. Federal are Frontana (Dyck and Samborski, 1982) and probably Americano 44d (Roelfs, 1988b).

Est. Federal may also have an additional APR gene. BCF_3 lines BCF_3 12617-12-1 and 12618-2-1 had high and Z IT to race 1 and B27, respectively, in the seedling stage and low IT to both isolates in the adult plant stage. Line 12617-12-1 had a

field reaction of 30-60 MRMS and line 12618 50 MS to 70 MSS, compared to 2 to 10 M for *Lr34* field reaction. *Lr34* is probably absent in lines 12617-12-1 and 12618-2-1, and these may have a different APR gene.

Est. Federal may have *Lr34* alone, or *Lr34* plus another APR gene for adult plant field resistance. However the BCF_2 families segregated according to a single gene ratio. If Est. Federal has *Lr34*, this was probably the gene that segregated for field resistance. If Est. Federal does not have *Lr34*, additional testing will be required to determine which gene conditioned the field resistance.

The resistance of Est. Federal selection used for this study needs to be further tested to determine if it is sufficient to prevent yield losses. If this has an acceptable level of leaf rust resistance, it could be released as a new cultivar.

Estanzuela Halcón has the seedling genes *Lr10* and *Lr16*, according to IT data of the cultivar and single gene-derived lines. The dominant gene conferring IT 1n to race 1 was probably *Lr16*. The gene expressing incomplete dominance and IT ; to 1⁻; was probably *Lr10*.

Some BCF_2 families derived from Est. Halcón that were susceptible to race 1 may have *Lr14a*. BCF_3 lines resistant to isolate B29 (IT 2⁼c and 1⁻;n) and B33 (IT X) indicated that additional seedling resistance was present. This resistance

could be an unidentified gene or might be *Lr14b*, although the IT of these lines to isolate B29 was different from IT ; of Tc*Lr14b*. The presence of both *Lr14a* and *Lr14b* in Est. Halcón, although unlikely, is possible since the genes are not true alleles, but are very closely linked genes which have been combined in a single line (Dyck and Samborski, 1970).

The pedigree of the parents of Est. Halcón is not known, therefore the origin of the leaf rust resistance genes cannot be traced back. Buck 6 is a line from Buck Breeding Program, which may be the origin of *Lr16*, since this gene is present in Buck germplasm: Buck Manantial (Dyck, 1989), Buck Patacón, Buck Fogón and Buck Cimarrón (Antonelli, 1995). MR 74507 is a line from Rio Grande do Sul, Brazil. There is no information available about the type of germplasm used in this program.

Est. Halcón does not have any APR genes. Seedling susceptible families also were susceptible in field or adult plant greenhouse tests. *Lr13* and *Lr34* are not in Est. Halcón since there were susceptible F_2 plants and F_3 families from the intercrosses with the Thatcher lines with these APR genes.

Field resistance in Est. Halcón is due to only *Lr16*. The Thatcher line with this gene had a field leaf rust severity and response similar to Est. Halcón. If *Lr13* and/or *Lr34* were also present in Est. Halcón, a higher level of resistance would be expected since *Lr16* interacts with *Lr13* and *Lr34* for enhanced resistance (Samborski and Dyck, 1982; Kolmer, 1992; Germán and Kolmer, 1992).

Under heavy inoculum pressure, Est. Halcón does not have sufficient resistance to prevent yield losses. Reductions of 17% were measured at La Estanzuela (R.P. Verges, M.M. Kohli and G. Bernheim, unpublished data). Samborski and Peturson (1960) measured yield losses up to 28% in lines with genes conferring intermediate resistance.

Est. Halcón was released in 1991, but was never grown over a large area. It was not widely adopted by farmers because of inferior yield potential compared to Est. Federal. Reduced exposure may be the reason why isolates virulent to *Lr10* and *Lr16* have not yet appeared.

To confirm the presence of postulated seedling resistance genes in the cultivars analyzed, intercrosses of the cultivars or derived lines with the corresponding Thatcher lines should be done. Absence of susceptible plants in the F_2 progenies tested with avirulent isolates will be the final evidence for the presence of the resistance genes in these cultivars.

Other genes may also be present. Detection of *Lr12* was attempted but this APR gene could not be distinguished from the susceptible check Thatcher in field tests. Adult plant gene *Lr22b* is in Thatcher but is ineffective to the local leaf rust population. Seed of Tc*Lr15* and Gatcher (*Lr27* + *Lr31*) was not available.

5.1.1. General comments on field tests.

It was not always clear which BCF_2 families were homozygous susceptible in field tests, mainly because of differences in maturity among the families. Differences in maturity among families were greater in crosses with the late maturity cultivars Est. Calandria, Est. Federal and Est. Halcón, and CIMMYT materials Est. Benteveo and Est. Pelón 90, which are both derived from spring/winter wheat crosses. Early maturity families were more advanced when evaluated for leaf rust and the resistance may have been underestimated. Late maturity families were in an earlier stage of plant development when evaluated and the resistance may have been overestimated. The problem is only partially solved when readings are taken at different dates. The APR genes may have variable expression, such as *Lr34*. Adult plant resistance may be conditioned by genes which have a small effect individually but act in additive manner, conferring a higher degree of resistance when three or more are present in a wheat line (Singh and Rajaram, 1992). Plants or families with a single APR gene may be difficult to distinguish from homozygous susceptible families. Segregation for APR and maturity within BCF_2 or $_3F$ families can make the distinction between resistant/segregating and susceptible families difficult.

When *Lr13* or *Lr34* were present, the progeny of the intercrosses with Tc*Lr13* and Tc*Lr34* were homozygous resistant for the APR genes. All plants should express equal or higher

resistance than Tc*Lr13* or Tc*Lr34* respectively. However, some F_2 plants or F_3 families often had higher infection than the corresponding Tc line. This might be explained by differences in maturity and differential expression of the genes in various genetic backgrounds.

5.2. GENETIC VARIABILITY AMONG CULTIVARS.

Nine known seedling resistance genes and probably unknown genes in INIA Boyero, Est. Federal and Est. Halcón were identified in the selected Uruguayan cultivars. Adult plant genes *Lr13* and *Lr34* and probably unidentified APR genes in INIA Boyero and Est. Federal also were identified.

Virulence to most seedling genes in the cultivars tested and *Lr13* is found in the *P. recondita* population in Uruguay. Virulence to *Lr1*, *Lr3*, *Lr10*, *Lr14a* and *Lr14b* was high during 1989 to 1994 (Germán and Kolmer, 1994; Germán, 1995). These genes do not condition effective levels of resistance in Uruguay. Virulence to *Lr16* is currently low (Germán and Kolmer, 1994; Germán, 1995). Virulence to *Lr16* was common in Canada 10 years after the release of Selkirk (Martens and Dyck, 1988), which has *Lr10* and *Lr16* (Anderson, 1961). In Uruguay, virulence to *Lr26* increased from 17.2% in 1989 to 94.8% in 1994, due to widespread use of CIMMYT germplasm with the 1BL/1RS translocation. Virulence to *Lr17* has been intermediate (15.2 to 53.6%, Germán and Kolmer, 1994) except in 1994 when it was at 0% (Germán, 1995). Virulence to *Lr24*

was high in 1982 when Cargill Trigal 800, an Agent derivative with *Lr24* (Antonelli, 1995), was severely damaged in Argentina and Uruguay. After Trigal 800 was withdrawn from cultivation, virulence to *Lr24* declined. In 1994, when a race with virulence to *Lr24* and *Lr26* was first isolated, virulence to *Lr24* increased to 32.5 % (Germán, 1995). Virulence frequency to Lr3bg is not known since this gene is not included in surveys; many races found in the region are virulent on this gene.

Frequency of virulence to APR gene *Lr13* has not been regularly tested, although virulence is present in the local leaf rust population. Tc*Lr13* has had varying leaf rust severity with a susceptible response in field tests. Tc*Lr34* has expressed a similar response in Uruguay as in North America, where no virulence to *Lr34* has been found (J.A. Kolmer, unpublished data). Therefore, there is probably no specific virulence to *Lr34* in the leaf rust population in Uruguay.

The genetic basis for leaf rust resistance in Uruguayan cultivars needs to be more diverse. Several seedling genes are common to various cultivars. *Lr3bg* is present in Est. Tarariras and Est. Calandria. Est. Benteveo and Est. Pelón 90, selected from CIMMYT germplasm, have *Lr26,* which is also present in INIA Boyero; *Lr10* is present in Est. Federal and Est. Halcón. *Lr16* is in Est. Calandria and Est. Halcón.

Leaf rust resistance gene *Lr26* and stem rust resistance

gene *Sr31* are both on the 1BL/1RS translocation (Singh et al., 1990). Gene *Lr26* is present in combination with other seedling and/or APR genes, which were selected together since *Lr26* does not condition effective resistance. However, virulence to *Sr31* has not been reported (McIntosh et al., 1995). Since *Sr31* conditions a very low IT, it is not possible without further genetic tests to determine if there is additional stem rust resistance in cultivars carrying *Sr31*. As many cultivars grown in the region carry the 1BL/1RS translocation, the basis for stem rust resistance may be very narrow.

Resistance genes present in Uruguayan cultivars selected from CIMMYT germplasm but not present in cultivars developed at La Estanzuela were *Lr1*, *Lr17* in Est. Pelón 90, *Lr3* in Est. Benteveo and *Lr14a*, which may be present in both cultivars. *Lr3*, *Lr17* and *Lr26* are present only in early maturity cultivars Est. Benteveo, Est. Pelón 90 and INIA Boyero. *Lr10*, *Lr16* and *Lr24* are present only in late maturity cultivars Est. Calandria, Est. Federal and Est. Halcón. The appearance of leaf rust isolates virulent to more than one cultivar is more likely when different cultivars have the same resistance genes. Therefore the release of cultivars with identical resistance genes should be avoided and genetic diversity of leaf rust resistance maintained.

In 1994, a severe epidemic on Est. Federal, the most widely grown late maturity cultivar in Uruguay, also caused yield losses of 30% or more (Díaz and Kohli, 1995). An early

planted late maturity cultivar allows early primary infections during the fall from oversummering inoculum. In 1995, infections at the beginning of April were observed on volunteer plants. These early infections provide inoculum which can increase over many infection cycles for nine months during the crop season. It is, therefore critical to maintain genetic diversity for leaf rust resistance between late and early maturity cultivars.

5.3. ADULT PLANT LEAF RUST RESISTANCE.

All cultivars except Est. Halcón have at least one APR gene. *Lr13* is present in three cultivars and *Lr34* in four cultivars and probably in two more. Only early maturity cultivars Est. Tarariras and INIA Boyero developed at La Estanzuela had both *Lr13* and *Lr34*. Cultivars selected from CIMMYT germplasm had either *Lr13* or *Lr34*. Late maturity cultivars had none or only one APR gene.

Adult plant leaf resistance has probably been maintained in germplasm developed in Uruguay since the first land race selections were made by Boerger. Climatic conditions and crop management practices (long planting time) in Uruguay make leaf rust an annual and highly destructive disease. Genotypes with no resistance probably cannot survive under these conditions and only resistant genotypes with complex resistance of two or more effective genes would be selected.

Some of the most widely used sources of resistance to

barley leaf rust and oat crown rust in addition to wheat leaf rust originated in Uruguay, Argentina and Brazil. Barley cultivars Cebada Capa and La Estanzuela have *Rph7* (Parlevliet, 1976) and high levels of partial resistance to barley leaf rust (Parlevliet, 1977). Barley leaf rust races with virulence to *Rph7* were not reported until 1976 (Parlevliet, 1976). Parlevliet (1977) suggested that Cebada Capa and La Estanzuela are identical. These cultivars probably were originally selected in Uruguay. The Uruguayan oat cultivar Victoria (*Pc2*, *Pc11*) was the first highly effective source of crown rust resistance that was widely used by plant breeders in North America (Martens and Dyck, 1989). The Victoria resistance could not be utilized for long because of the associated Victoria blight susceptibility. Later Landhafer (*Pc5*), also from Uruguay, and the Argentine cultivar Santa Fe (*Pc6* and *Pc9*) were also used (Martens and Dyck, 1989).

Under the extremely favorable conditions for leaf rust development, *Lr34* and probably other APR genes may have been selected in the land race cultivars, which were extremely heterogeneous (Boerger, 1928). Dyck (1991) considered the possibility that *Lr34* may also have been introduced to South American germplasm through the wheat cultivar Chino, which may be Chinese Spring (*Lr12* + *Lr34*, Dyck, 1991) or a selection. The cultivar 38 MA, selected from the cross of Barleta/Chino, was resistant for a long period of time, indicating it may have APR.

Gene *Lr34* may have been selected and maintained in wheats from the Southern Cone of South America through indirect selection for stripe rust resistance gene *Yr18* (Kolmer, 1996; Dyck, 1991), which is tightly linked with *Lr34* (Singh, 1992b; McIntosh, 1992). There is no record of *Puccinia striiformis* in Uruguay until 1929 (Ribeiro, 1953). In 1930, a very severe stripe rust epidemic in Argentina, Rio Grande do Sul in Brazil, and Uruguay, caused significant yield losses in many wheat cultivars. Selection for *Yr18* may have occurred then. Stripe rust is a sporadic disease that occurs in restricted areas of the region. Leaf rust was the most common rust in Uruguay early this century (Boerger, 1928) as it is presently (Germán, 1995). Direct selection for leaf rust resistance is most likely the reason why *Lr34* has been maintained in Uruguayan germplasm. Selection under field conditions for high levels of resistance in progenies from crosses including at least one adapted parent, probably resulted in combinations of seedling genes and *Lr34*, *Lr13* and/or other APR genes.

Most durable resistance in wheat germplasm has been conferred by combinations of APR resistance genes *Lr12* + *Lr34* and *Lr13* + *Lr34* (Roelfs, 1988b). The absence of virulence to *Lr34* on a worldwide basis, even though this gene is widespread (Dyck and Samborski, 1982; Shang et al., 1986; Dyck, 1994a and 1994b) does not ensure that virulence will not eventually develop and be selected. Therefore, there is a continuing need to identify new APR genes which may be similar to *Lr34*. Adult

plant resistance genes other than *Lr13* or *Lr34* in INIA Boyero and probably in Est. Federal add to reports of probably different APR genes in wheat cultivars (Dyck, 1994a; Kolmer, 1994; Barcellos, 1994; Singh and Rajaram, 1992).

Effective APR genes can also prevent high yield losses when isolates virulent to seedling resistance genes in cultivars become prevalent. Cultivars such as La Paz INTA, which only had *Lr9*, can suffer yield losses of 50% in Uruguay when virulent races increase in frequency (Germán et al., 1986).

Currently, only Est. Pelón 90 (*Lr1,14a?,17,26,34*), INIA Boyero (*Lr26,+,13,34*+APR) and Est. Calandria (*Lr3bg,16,24, 34*), have acceptable levels of leaf rust resistance. Resistance in Est. Tarariras (*Lr3bg,13,34*), Est. Benteveo (*Lr3,13,14a,26,34?*), and Est. Halcón (*Lr10,14a, 14b?,16,+?*) is not adequate to prevent yield losses. Higher levels of leaf rust resistance will be needed in future cultivars to avoid yield losses. The resistance of the Est. Federal selection used for this study needs to be further tested.

Breeding for leaf rust resistance at INIA La Estanzuela Wheat Breeding Program should be based on the knowledge of the basis of leaf rust resistance in cultivars being currently grown, which select the leaf rust isolates which will become prevalent (McIntosh, 1992b), and in new cultivars, which should have adequate resistance to these isolates.

Wheat breeding for effective and durable leaf rust

resistance in INIA should be based on developing strategies of maintaining adequate levels of APR in the wheat germplasm. The genetic basis of APR should be widened by incorporating new genes that are not used in other breeding programs in the region. The combination of *Lr13* and *Lr34* does not condition adequate levels of resistance to avoid yield loss in many years. Additional APR as described in INIA Boyero should be used.

Seedling resistance can also be used but should always be combined with effective APR to avoid release of cultivars with only seedling resistance like La Paz INTA. Combinations of seedling and field tests can be used to identify which wheat lines have seedling resistance, and also APR. Inoculation of breeding nurseries with diverse collection of races can help select more complex resistance genotypes.

Seedling genes conferring very low IT, with no specific virulence frequency in the pathogen population, could be used if appropriate breeding strategies to maintain APR are followed. The presence of these genes singly will mask the presence of any other resistance genes in wheat lines. When this type of resistance is used, it could be backcrossed to wheat genotypes with known APR genes, or advanced lines from crosses with genotypes with APR should be genetically analyzed before release to ensure complex resistance is present in the cultivars.

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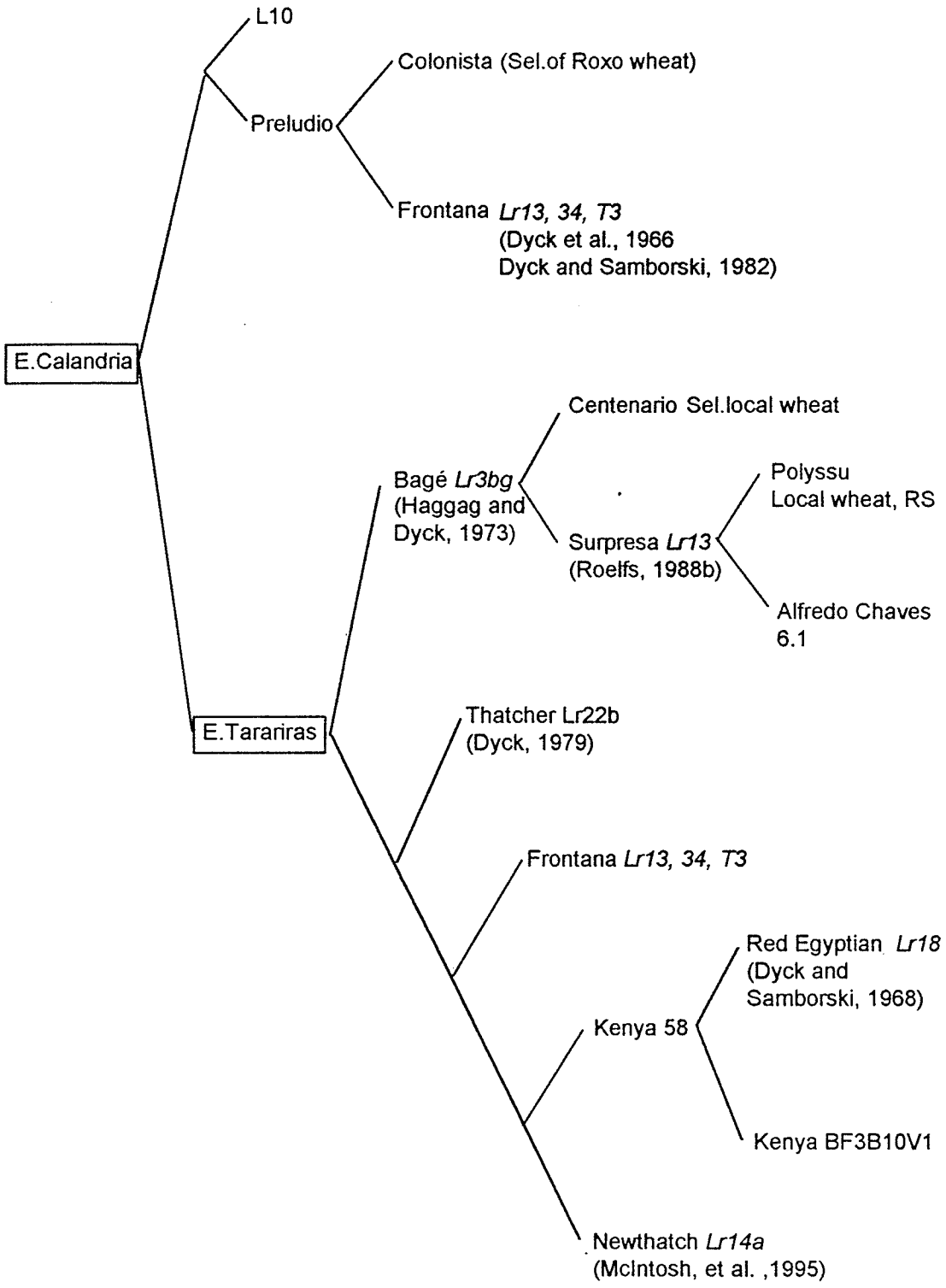
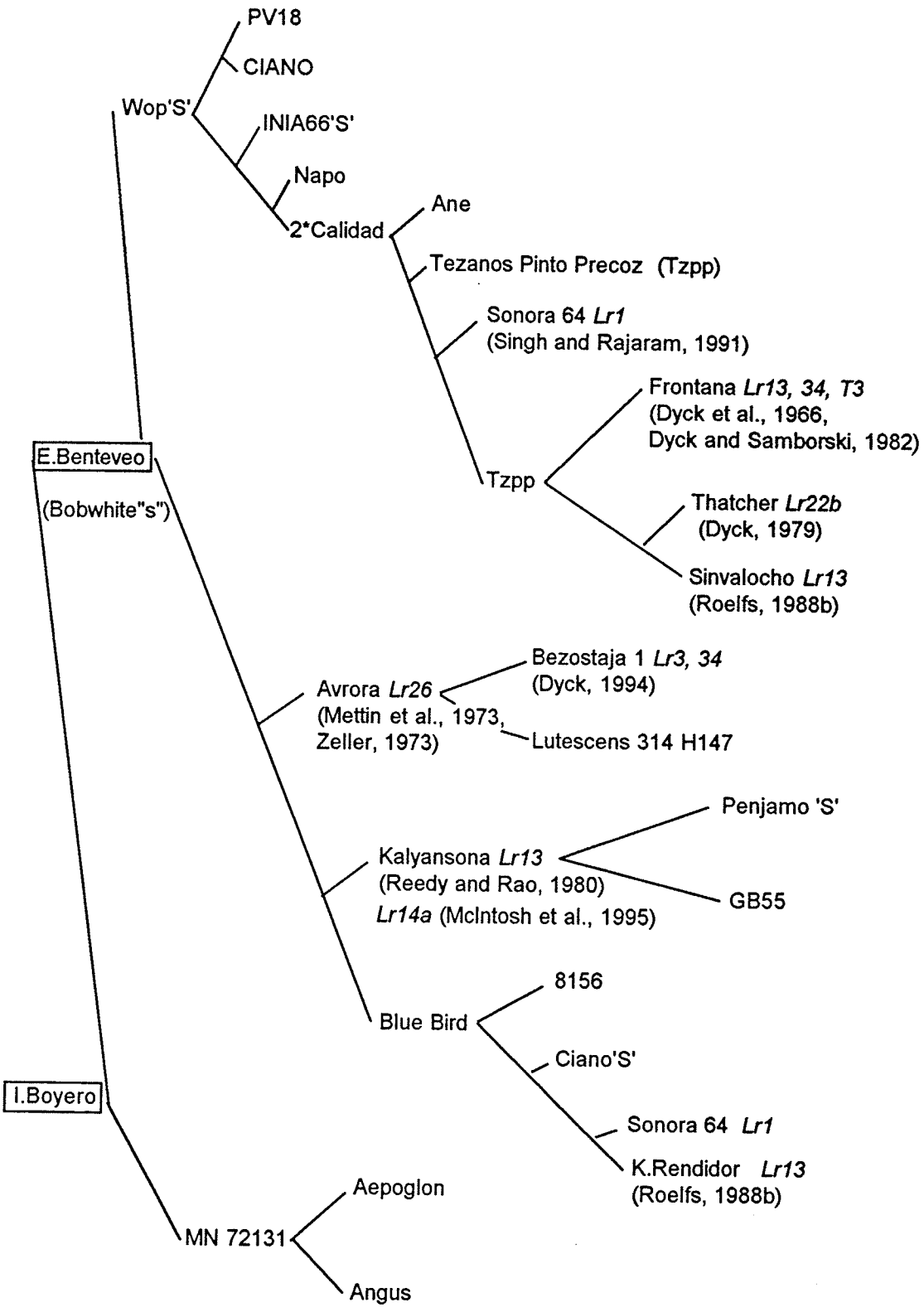
7. APPENDIX.

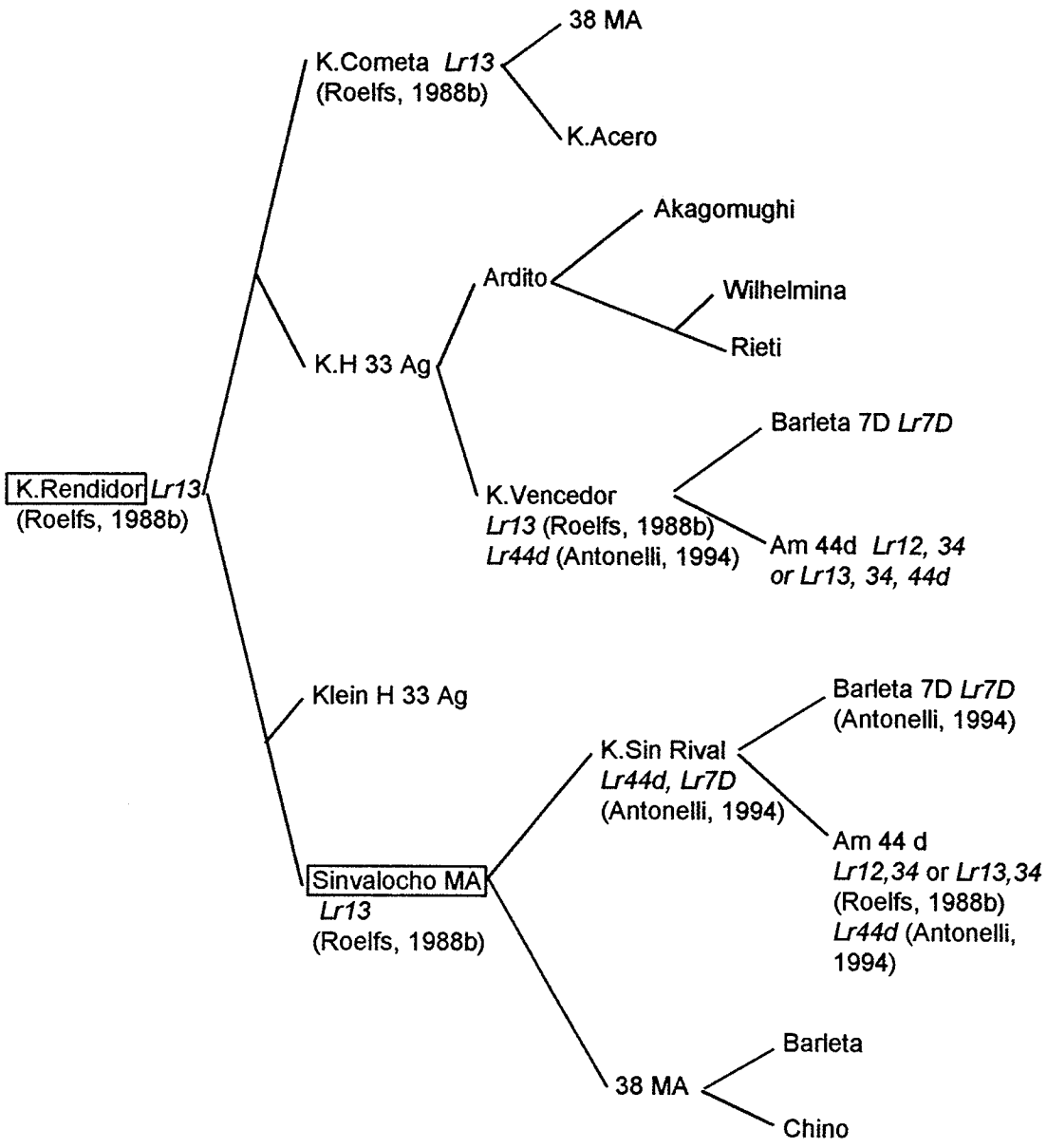
Appendix 1: Pedigree of E. Tarariras and E. Calandria



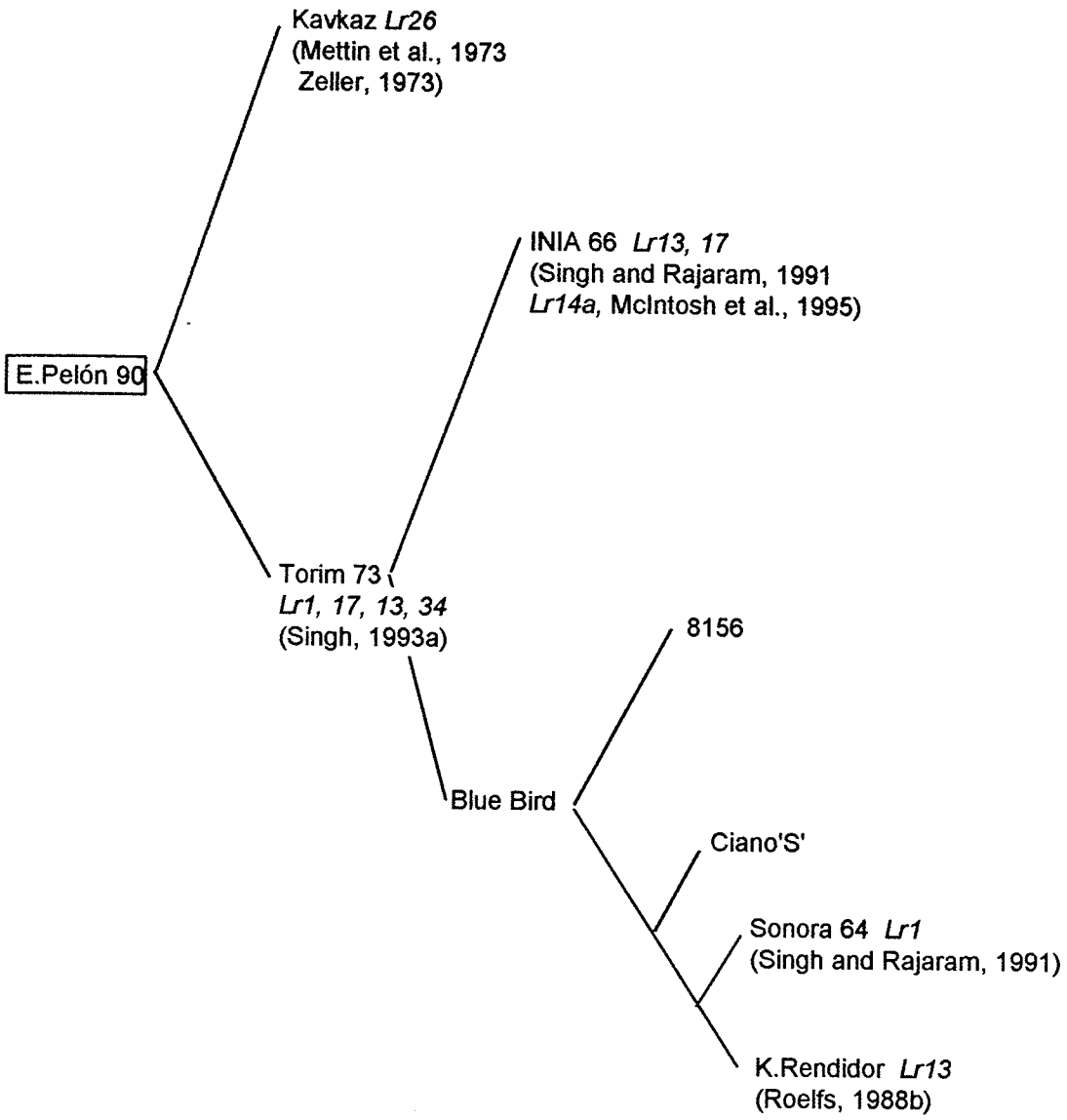
Appendix 2: Pedigree of E. Benteveo and I. Boyero.



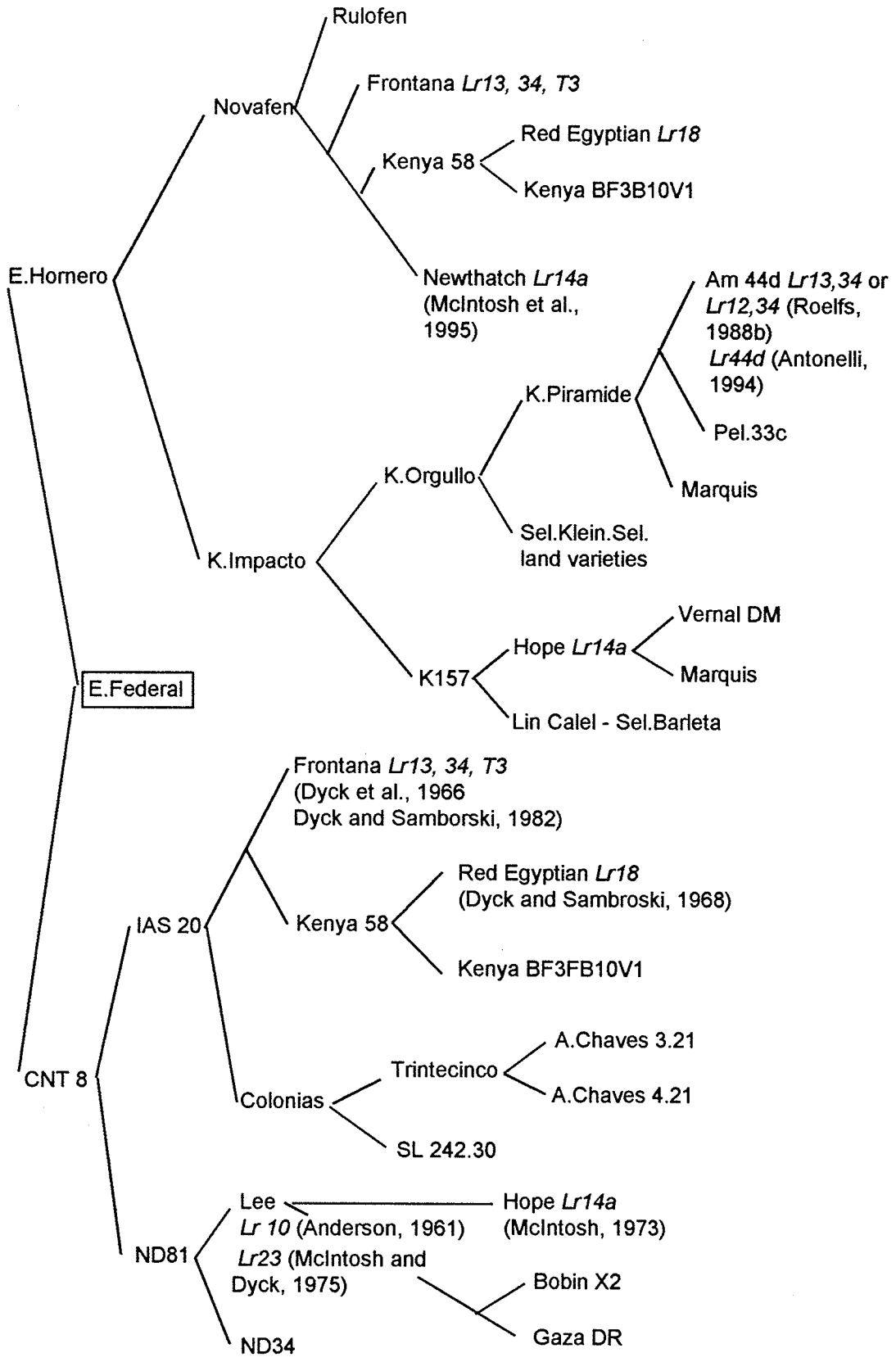
Appendix 3: Pedigree of Klein Rendidor and Sinvalocho MA.



Appendix 4: Pedigree of E. Pelón 90.



Appendix 5: Pedigree of E. Federal.



Pedigrees were obtained from Kohli (1986), Villareal and Rajaram (1988) and Zeven and Zeven-Hissink (1976).

Appendix 6. Virulence formula of selected *Puccinia recondita* isolates.

Isolate	Ptr code[a]	Origin	Avirulence/Virulence formula.
R35	TBB	Canada	3ka,9,10,11,16,17,18,24,26,30,B / 1,2a,2c,3,14a,14b,20,23
R58	FBB	Canada	1,2a,3ka,9,11,16,17,18,24,26,30 / 2c,3,10,14a,14b,20,23,B
63-88	MFB	Canada	2a,2c,3ka,9,11,16,17,18,30,B / 1,3,10,14a,14b,20,23,24,26
159-71	CGB	Canada	1,2a,2c,3ka,9,11,17,18,24,26,30,B / 3,10,14a,14b,16,20,23
215-88	TBJ	Canada	3ka,9,16,24,26,30,B / 1,2a,2c,3,10,11,14a,14b,17,18,20,23
269-88	MBG	Canada	2a,2c,3ka,9,16,17,18,23,24,26,30,B / 1,3,10,11,14a,14b,20
358-88	PBP	Canada	2a,9,11,14a,16,18,23,24,26,B / 1,2c,3,3ka,10,14b,17,20,30
366-88	PLM	Canada	2a,11,14a,16,17,18,23,24,26 / 1,2c,3,3ka,9,10,14b,20,30,B
394-88	PBL	Canada	2a,9,11,14a,16,17,18,23,24,26,30 / 1,2c,3,3ka,10,14b,20,B
Ae48-2	MBT	Canada	2a,2c,9,14a,16,18,23,24,26 / 1,3,3ka,10,11,14b,17,20,30,B
	PBL	Canada	2a,9,11,16,17,24,26,30 / 1,2c,3,3ka,10,14a,18,B
	MBM	Canada	2a,2c,9,16,17,18,24,26,B / 1,3,3ka,10,11,14a,30
	TBD	Canada	3ka,9,11,16,24,26,30,B / 1,2a,2c,3,3bg,10,14a,14b,17,18,20,23
	TFB	Canada	3bg,3ka,9,11,16,17,18,30,B / 1,2a,2c,3,10,14a,14b,20,23,24,26
	CBB	Canada	1,2a,2c,3ka,9,10,11,16,17,18,24,26,30,B / 3,14a
	MBG	Canada	2a,2c,3ka,9,16,17,18,24,26,30,B / 1,3,10,11,14a
	TDT	Canada	9,16,18,26,B / 1,2a,2c,3,24,3ka,10,11,14a,17,30
	MBB	Canada	2a,2c,3ka,9,11,16,17,18,24,26,30,B / 1,3,10,14a
	MFM	Canada	2a,2c,3bg,9,11,16,17,18,B / 1,3,3ka,10,14a,14b,20,23,24,26,30
	MBR	Canada	2a,2c,3bg,9,16,17,18,24,26,B / 1,3,3ka,10,11,14a,14b,20,23,30
	PBG	Canada	2a,3ka,3bg,9,14a,16,17,18,24,26,30 / 1,2c,3,10,11,14b,20,23,B
	PNM	Canada	2a,3bg,11,14a,16,17,26 / 1,2c,3,3ka,9,10,14b,18,20,23,24,30,B
U2-1	LCG	Uruguay	2a,2c,3,3ka,9,16,17,20,24,30,B / 1,10,11,14a,14b,18,23,26
U8-1	MCR	Uruguay	2a,2c,9,10,16,17,18,20,23,24,B / 1,3,3ka,11,14a,14b,26,30
U23-4	CBT	Uruguay	1,2a,2c,9,10,16,18,24,26,B / 3,3ka,11,14a,14b,20,17,23,30
U30-1	SBJ	Uruguay	3,3ka,9,16,18,20,23,24,26,30,B / 1,2a,2c,10,11,14a,14b,17

[a] Long and Kolmer, 1989.

Appendix 7. Infection types produced by physiologic races of *Puccinia graminis* var. *tritici* on standard differential varieties of *Triticum* spp. (Stakman et al., 1962).

Infection type[a]	Varietal reactions and reaction clases[b]
	Resistant
0	IMMUNE. No uredia nor other indications of infection.
0;	NEARY IMMUNE. No uredia but hypersensitive flecks present.
1	VERY RESISTANT. Uredia minute; surrounded by distinct necrotic areas.
2	MODERATELY RESISTANT. Uredia small to medium; usually in green islands surrounded by a decidedliy chlorotic or necrotic border.
	Susceptible
3	MODERATELY SUSCEPTIBLE. Uredia medium in size; coalescence infrequent; no necrosis, but chlorotic areas may be present, especially under unfavourable growing conditions.
4	VERY SUSCEPTIBLE. Uredia large, and often coalescing; no necrosis, but chlorosis may be present under unfavourable conditions.
	Mesothetic
X	HETEROGENEOUS. Uredia variable, sometimes including all infection types and itergradations between them oh the same leaf; no mechanical separation possible; on reinoculation small uredia may produce large ones, and vice versa.

[a] Plus and minus signs are used to indicate variation within a given IT: ++ and = indicate the upper and lower limits, respectively of each type. The symbol +- indicates a variation between + and - for the type. The symbol c indicates exceptionally pronounced chlorosis; b indicates browning with a tendency toward necrosis; n indicates a tendency toward necrosis.

[b] These classes were established primarily to facilitate the identification of rust races rather than to indicate the degrees of resistance of wheats varieties. Thus, IT 2 is considered to indicate resistance and type 3 to indicate susceptibility, although a variety with IT 2++ may appear more susceptible for practical purposes than one with IT 3=.

Moreover, the mesothetic class is based solely on the presence of IT X, and there can be a wide range of susceptibility and resistance within the class, as indicated by the plus and the minus signs after the X.

Appendix 8. Seedling infection type of Uruguayan cultivars and Thatcher lines with single resistance genes tested with different leaf rust isolates.

GENOTYPE	BBB R1	CHB R15	TBB R35	FBB R58	MFB 63-88	CGB 159-71	TBJ 215-88	LCG U2-1	CBT U23-4	SBD R9	MBG 269-88	PBP 358-88	PLM 366-88	PBL 394-88	MCR U8-1	SBJ U30-1	MBT Ae48-2
Est. Tarariras	0;[a]	33+	33+	33+c	X	3+	23	0;	X	0;	0;12-	;12	;	23;	X	0;	0;1
Est. Benteveo	0;	2	0;	0;	X	;1-	0;	;1=	;	0;	;	;	;	;	--[b]	0;	0;
Est. Pelón 90	0;	0;	0;	0;	;	0;	0;	;	0;	0;	0;	;	0;	0;	;1-	;	0;
Est. Calandria	0	0;	0;	;	;1-	0;	;	0;	0;	0;	0;	0;	0;	;	;	0;	0;
Tc	3	3	3+	4	3	4	4	3+	4	4	3+	3	3+	3+	3+	4	4
Lr1	0;	0;	3+	0;	4	0;	4	4	0;	3+	3+	3+	3	4	3+	4	3+
Lr2a	0	0;	3	;1	0;	0;	4	0;	0;	3+	0;	2;	2+;	;2	0;	4	0;
Lr2c	;1=	;1-	3+	4	;1-	;1	4	;1-	0;1-	3+	0;1-	4	3	4	;1-	4	2
Lr3	;1-	33+	3+	3+	3+	4	4	;1	3+	;1-	4	4	3+	4	4	;1-	3+
Lr9	0	0;	0;	0;	0;	0;	0;	0;	0	;	0	0;	3+	0;	0;	;n	0;
Lr16	1-n	3	1n	1n	;1-n	23c	1;n	1n	1n	;1-	1n	;1-	1n	1n	1	1+	1n
Lr24	0;	;	;	;1-n	3+	;	;	;	0;	0;	0;	0;	;	;	0;	;	0;
Lr26	;1-	33+	;	0;	33+	2n	;	4	;1-	;1-	;	;1	;	;	4	;1-	0;
Lr3ka	;1-	12;	2	2	2	12	12;	1;	33+	;12	2	3+	4	3+	4	;1	4
Lr11	2	11+	1+n	2	2	;11+	3+	3+	33+	1	4	2;	2	2c	4	4	4
Lr17	1-;	1;n	1;	12	12;	11+	3+	;1n	3+4	3+	2	3	;1	2c	2	3+	4
Lr30	12-	1;c	12;c	2	1;n	1	1;	1	33+	;1-	1;	3	3+	2	3	;1	3+
LrB	1-n	1+c	2c	4	2c	1n	1n	1+c	1n	1-;	1n	2c	3	3	1n	;1-	4
Lr14a	4	3	3+	X+	3	4	3+	4	3+	1;	3+	X-	X-	X-	4	3+	X+
Lr18	1-;	1;	12n	3+	11+	1n	3+	3+	1;n	1-;	1n	1-;	23	2-	1	;1n	23+
Lr21	1-;	1;	12;	2	12-;	11+;	12;	12-;	2;	;1-	1;	1;	2-;	;1	2;	;12-	1;
Lr10	;1-	3	1;	3	3	4	3+	3+	1;	3+	3	3	3+	3+	1-;	4	4
Lr14b	3+	3	3+	3+	3	3+	3+	3+	4	4	3	3	3+	3+	3	3	4
Lr33	1-;	1;	1+	2-	1;	1	11+;	2	1+	1;	1;	1;	1;	2	1;	1	12
Lr20	4	4	3+	3+	3	4	4	;	;	4	4	3+	3+	4	;	;	4
Lr23	2+	4	4	3	3+	4	3+	3+	4	;1-	22+	2	23	23	23	;1-	22+
Lr13	33+	3+4	3	3c	3n	34n	3+	3+	13+	33+	;12n	12+;c	;1-3	23	23	3	3;
Lr34	13	23+	23+	3+	2+3+	33+	13;	3	3+	12;	0;12	2;	2	2;	23	012+;	12-

[a]: Stakman et al., 1962; Roelfs, 1988a.
[b]: Data not available.

Appendix 9. Seedling infection type of Uruguayan cultivars and Thatcher lines with single resistance genes with different leaf rust isolates (J.A. Kolmer, unpublished data).

Wheat line	PBL	MBM	TBD	TFB	CBB	MBG	TDT	MCB
Est.Tarariras	2+3a	1+2	33+	;2-	;2-3	;2+	;3-	;2
Est.Benteveo	;	;	;	;	;1-	;	;	;1-
Est.Pelón	;	;	;	;	0;	;	;	0;
INIA Boyero	;	;	;	;12	;3	;	;	;
Est.Calandria	;1-	;	;	;	;	;	2-	;
Est.Federal	2+3	33+	2	3+	2+3	3	;3+	22+
Est.Halcón	11+	2-	2-	2-	2+3	;1	;1	1
Tc	4	4	4	4	4	4	4	4
Lr1	4	4	4	4	0;	4	4	4
Lr2a	;12-	0;	4	4	;	0;	4	0;
Lr2c	4	;	4	4	;	;	4	;
Lr3	4	4	4	4	4	4	4	4
Lr9	0	0	0	0	0	0	0	0
Lr16	1+2-	1	;1-	1	1	;1-	;1	;1-
Lr24	;	;	;1-	3+	;	;	3+	;
Lr26	;	;1-	;	2+3	0;	;	;1	;1
Lr3ka	3+	3+	22-	;1	;1+	;1	3+	;1
Lr11	2	3+	22-	;1	;2-	3+	3+	;1-
Lr17	;1	;1-	3+	;1-	;	;	3+	;1+
Lr30	2	3+	;2-	;1	;1=	;1	3	;1-
LrB	3+	22-	2c	22+	2	2+c	2-c	2c
Lr14a	;3+	4	4	4	4	4	4	4
Lr18	3+	;12-	3+	2=	;12-	;1-	;1-	;1-
Lr10	3+	3+	3+	3+	;1-	3+	3+3+	3

a: Stakman et al., 1962; Roelfs, 1988a.
b: Data not available.

Appendix 10. Seedling infection type of Uruguayan cultivars and Thatcher lines with single resistance genes tested with different leaf rust isolates (J.A. Kolmer, unpublished data).

Wheat line	CHB	MFM	TFB	MBR	PBG	TBD	PNM
Est.Calandria	;a	;1-	;2	;1=	;	;	22+3
Est.Federal	2+3	2+3	;3	3	2+3	2+3	;
Est.Halcón	3	;1-	;2-	22-	;1-	1	;1-
Lr1	;	3+	4	4	3+	4	4
Lr2a	;	;	4	;	;2	3+	;22
Lr2b	;	;	4	;	2	3+	3
Lr2c	;1=	;	4	;	3+	3+	3+
Lr3	3+	3+	4	3+	3+	3+	3+
Lr9	0	0	0	0	;	;	3+
Lr16	2+3	;1-	;1	;1	;1	;1	1
Lr24	;	3+	3+	;	;	;	3+
Lr26	3+	3+	3+	;1	;	;	;
Lr3ka	;1	3+	;12-	3+	;2	;1-	3+
Lr11	;1	;2	;2	3+	3+	2-	2
Lr17	;	;1	;1	;12	;1	3+	;1-
Lr30	;1	3+	;2	3+	;2-	;12-	3+
LrB	1+c	1+c	2c	1c	3+	2c	3
Lr3bg	3+	;2	;12	;12	;12	3+	12
Lr10	3+	3	3+	3+	3+	3+	3+
Lr14a	3+	3+	3+	3+	X	3+	X
Lr14b	3+	3+	3+	3+	3+	3+	4
Lr15	3+	3+	3+	3+	3+	3+	3+
Lr18	;1	;1	;1	;1	;1	3+	3+
Lr19	;	;	;	;	;	;	;
Lr20	3+	3+	3+	3+	3+	3+	3+
Lr21	;1	;1-	;1-	;1-	;1-	;1-	;1
Lr23	3+	3+	3+	3+	3+	3+	3+
Lr25	;	;	;	;	;	;	;
Lr28	3+	3+	3+	3+	3+	3+	3+
Lr29	;	;	;	;	;	;	;
Lr32	;1-	;1-	;1	;1-	;1	;1-	;1-
Lr21	;12-	;1=	;1-	;1	;12-	;1=	;2-
Lr39	;12-	;1=	;1-	;1-	;12-	;1=	;2-
Lr40	;12-	;1=	;1-	;1=	;12-	;1=	;2-

a: Stakman et al., 1962; Roelfs, 1988a.