COMMON BEAN RUST

Fig.1. Bean Rust on leaf (Photograph provided by H. F. Schwartz, AgImage - Colorado State University)

INTRODUCTION

The common bean rust disease (Figure 1) has a worldwide distribution and it occurs in most dry and snap bean productions areas of the world, and most especially in locations where humid to moderately humid conditions, long dew periods, and cool conditions prevail during the bean growing season. Bean rust rarely occurs under dry conditions in arid climates. Ideal conditions for bean rust are cool to moderate temperatures (17-22^{o}C) concurrent with high humidity (>95%) periods for at least 7-8 hours interspersed with dryer, windy periods that favor spore dispersal (Harter et al., 1935, Stavely and Pastor-Corrales, 1989). Recurrence of dew periods favors rust infection and progress of the rust disease.

[*Updated by Talo Pastor-Corrales and Merion Liebenberg – May 2010*]

Yield losses caused by bean rust depends on the degree of susceptibility of the dry or snap bean variety grown, the climatic conditions favoring rust infection and disease development, and earliness of the infection. Early infections occurring during the pre flowering and flowering stages of bean crop development usually result in higher yield losses. These losses can be extremely high, approaching 100%. Major losses caused by bean rust have been reported in many countries of Latin America and Eastern and Southern Africa.

CAUSAL ORGANISM OF COMMON BEAN RUST AND DISEASE CYCLE

The common bean rust disease is caused by the basidiomycete fungus *Uromyces appendiculatus* (Pers.: Pers.) Unger. It is an obligate parasitic fungus that cannot live independently of its common bean host. This fungus cannot be cultured on artificial media in the laboratory. The rust pathogen completes its entire life cycle on the common bean host; thus, this rust is autoecious (Harter & Zaumeyer, 1941). This pathogen is also macrocyclic; that is, it produces several different types of spores that include the urediniospores, teliospores, basidiospores, pycnyospores and aeciospores. See the sequence of the different spore stages of the bean rust pathogen in Fig. 2 below.

The rusty, cinnamon brown type of spores, named urediniospores, gives this disease its name. The urediniospores are contained within the reddish brown uredinia (known as pustules) which are observed on infected leaves, and sometimes on pods (Fig. 3), of bean plants during most of the bean crop growing season. The urediniospores are the most commonly observed type of spores of the bean rust fungus. Repeated infections by urediniospores occur during the summer (planting) season on dry or snap beans.

Toward the end of bean plant growth cycle, telia (dark pustules containing black teliospores) are usually seen on old infections. These teliospores are the overwintering, resting spores. When the teliospores germinate, they produce basidia and basidiospores that infect the leaf tissue of their bean host. Following these infection the next stage in the cycle of the rust pathogen is produced. These are the pycnia (the fruiting structure) that produce pycnyospores. Following cross fertilization of the bean host with the pycnyospores - some aeciospores are +, others are -; thus, the needed cross fertilization – an aecium (the fruiting structure) is produced. The aecium produces the aeciospores. When the aeciospores infect the leaf tissues of young bean plants during the spring, uredia pustules are produced, completing the cycle of the bean rust pathogen.

Basidiospores, pycnyospores, and the white aeciospores are not frequently observed under field conditions; they are rarely seen, but have been reported occurring in North Dakota and Colorado in the United States and other places. All stages of the complete Disease cycle have been observed under field conditions in Colorado and North Dakota (Stavely and Pastor-Corrales, 1989; Schwartz et al., 1990; Venette et al., 1978), as well as in Germany. The bean rust pathogen is not seedborne and thus it is not transmitted on or in the seed. Additionally, even though the bean rust pathogen does not grow in culture, viable urediniospores can be preserved for long periods in the laboratory either in liquid nitrogen or different type of freezers (e.g., -20, -80)

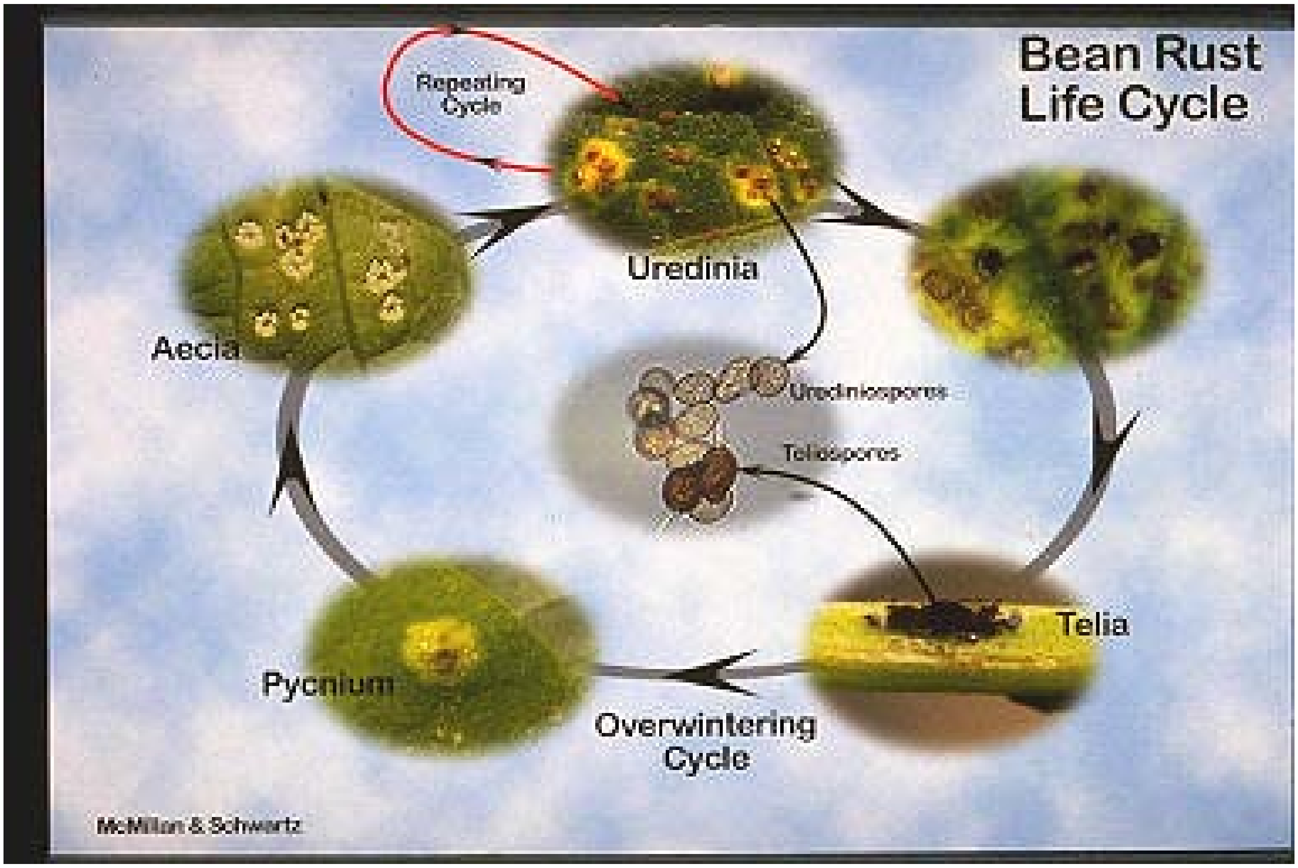


Fig. 2. Bean rust life cycle (Photograph provided by H. F. Schwartz Ag Image - Colorado State University)

SYMPTOMS

Symptoms of the bean rust disease can occur on most aerial parts of the common bean plant but are most often observed on the leaves (Fig. 1). These symptoms also occur on pods (Fig. 3) and sometimes on branches and stems (Fig. 4), albeit rarely. Bean rust symptoms do not occur on flowers. The most commonly observed symptoms are the rust-colored pustules which are the uredinia containing urediniospores, also called uredospores. This is known as the repeating summer cycle. The uredinia is <0.3 - <0.8 mm in diameter (Figs 5 and 6), often surrounded by a chlorotic halo (Figs.1 and 6).

In the field, different types of uredinial pustules (large and small pustules) have been observed on the same plant (Fig. 7), suggesting that different races of this pathogen are present on the same bean plant. Pustules on pods and stems are often elongated. As the summer or growing season advances and the bean plants get older, especially near the end of the growing season, the uredinia can be gradually replaced by the dark telia (dark, almost black pustules) containing the also dark brown to black teliospores (Zaumeyer and Thomas 1957), (Fig. 8). A hypersensitive reaction, typical of some host-pathogen genotype reactions is often observed under greenhouse conditions. This type of reaction is also observed in the field. In some cases this necrotic lesion can contain a sporulating pustule (Fromme & Wingard 1921; Harter & Zaumeyer 1941).

Evaluating the reaction of common bean plants to the rust pathogen

Evaluations of the reactions of common bean plants to the rust pathogen can be performed under greenhouse or field conditions.

Most evaluations under greenhouse conditions are usually conducted with the objective of identifying new races of the rust pathogen, perform virulence diversity studies, identify bean plants with certain gene or genes for rust resistance, study the inheritance of resistance of a new rust resistance gene, and other studies involving the interaction between the rust pathogen the and its bean plant host.

These evaluations require systems of evaluation that clearly distinguish the different phenotypes or types of reactions resulting from the interactions that occur between these two organisms, the rust pathogen and its host the bean plant.

Stavely et al. (1983) reported the evaluation system proposed during the 1983 Bean Rust Workshop held at Mayaguez, Puerto Rico. This “Standard Bean Rust Grading Scale” included two attributes, the “Grade or reaction Classifications” and the “Intensity” of the infection (Table 1).

The grade or reaction classifications are evaluated using a 1-6 scale as follows: Grade 1 = immune, no visible symptoms; 2 = necrotic spots without sporulation -this highly resistant reaction is the so called hypersensitive reaction or HR, where 2 = necrotic spots less than 0.3 mm in diameter, 2^{+} = necrotic spots 0.3 - 1.0 mm in diameter, 2^{++} = necrotic spots 1.0 - 3.0 mm in diameter, 2^{+++} = necrotic spots greater than 3.0 mm in diameter, respectively; 3 = resistant; uredinia - sporulating lesions - less than 0.3mm in diameter; 4 = uredinia 0.3 – 0.5 mm in diameter; 5 = uredinia 0.5 - 0.8 mm in diameter; and 6 = uredinia larger than 0.8mm in diameter. When several pustule grades are present, they are recorded in order of predominance with the most prevalent type listed first.

Intensity is evaluated using a modified Cobb scale (1 - 7) for estimating percent of the leaf area affected including the area occupied by the halo surrounding the pustules (Stavely, 1985). For rust evaluations under field conditions, it is suggested to use the Standard System for the Evaluation of Bean Germplasm developed by van Schoonhoven and Pastor-Corrales (1987). Bean researchers working with bean rust consider the following reactions grades as resistant: grade 1 (grade 1, immunity with no visible rust symptoms), grades 2, 2^{+}, 2^{++}, and 2^{+++} (chlorotic or necrotic non-sporulating spots of various diameters; HR), and grade 3 (tiny, sporualting uredinia, less than 0.3 mm in diameter.

Table 1. Standard bean rust grading scale for the evaluation of the reactions resulting from the interaction between the bean plant and the bean rust pathogen. This evaluation includes rust pustule size and intensity of infection

Grade or reaction classifications (1-6 scale)	Type of reaction	Description of interaction	Lesion size (diameter)
1	Immune	No visible symptoms	
2	Resistant (HR)	Necrotic lesions without sporulation	0.3 mm
2+	Resistant (HR	Necrotic lesions without sporulation	0.3 – 1 mm
2++	Resistant (HR	Necrotic lesions without sporulation	1 – 3 mm
2+++	Resistant (HR	Necrotic lesions without sporulation	>3 mm
3	Resistant	Tiny sporulating pustules	<0.3 mm
4	Susceptible	Sporulating pustules	0.3 - 0.5 mm
5	Susceptible	Sporulating pustules	0.5 - 0.8 mm
6	Susceptible	Sporulating pustules	> 0.8 mm

Intensity of infection
Use the 1 – 7 modified Cobb scale for estimating percent leaf area infected including the area occupied by the halos. Stavely, 1985.

Scale (1-9) developed at CIAT for the evaluation of the reaction of bean plants to rust under field conditions. Van Schoonhoven & Pastor-Corrales, 1987. This is a scale to estimate rust severity

Grade	Category	Description
1	Immune	No visible rust pustules
3	Resistant	Presence of only a few and small or intermediate pustules covering less than 2% of foliar area
5	Intermediate	Presence of small and intermediate pustules covering approximately 5% of foliar area
7	Susceptible	Presence of mostly large pustules often surrounded by chlorotic halos covering approximately 10% of foliar area causing some premature defoliation
9	Highly Susceptible	Presence of large and very large pustules with chlorotic halos covering more than 25% of foliar area and causing severe premature defoliation

VIRULENCE DIVERSITY

The bean rust pathogen (*Uromyces appendiculatus*) is considered among the most virulence variable of plant pathogens. Often, individual field collections of spores of the bean rust pathogen contain several different virulence strains. Different strains of the bean rust pathogen once characterized for their virulence spectrum by inoculating them on a set of bean rust differential cultivars are called races.

Numerous races of *U. appendiculatus* from many bean producing areas of the world have been reported in the literature. These races are defined by the reaction grades they elicit on each cultivar of a differential set. In essence, each race of the bean rust pathogen is a virulence phenotype.

Plant pathologist working with common bean realized in the first quarter of the 20^{th} century that the bean rust pathogen had high virulence diversity. To understand and estimate this diversity, different bean scientists generated many different sets of differential cultivars to characterize their rust isolates into races. Many races of the bean rust pathogen were published from different countries including the United States, Australia, Brazil, Colombia, Mexico, Peru, and many others.

Each of these researchers used their own set of differential cultivars, their own grading scale to score the host reactions, and their own system of naming these races. As a result many of the named and published races of the bean rust pathogen found on dry and snap beans could not be compared with each other. Thus, there was a need to create a uniform set of differential cultivars for the systematic evaluation of pathogen variability and naming of distinct races.

During the 1983 Bean Rust Workshop held at Mayaguez, Puerto Rico, a uniform set of 20 differential common bean cultivars was proposed to characterize the virulence diversity of the bean rust pathogen (Stavely et al. 1983). At the same meeting, a standard grading scale was also proposed and adopted. Soon after, the set of differentials was reduced to only 19 cultivars when Mountaineer White Half Runner was abandoned as a bean rust differential cultivar (Table 2).

Using this set of 19 differential cultivars and the rust rating system (Table 1), more than 90 races of this pathogen from the United States and other parts of the world were isolated, identified, and maintained in storage at the USDA-ARS Beltsville Agricultural Research Center in Maryland since 1980 (Stavely, 1984; Mmbaga and Stavely, 1988; Stavely and Pastor-Corrales, 1989a; Stavely et al, 1989c; Pastor-Corrales, 2001).

Many of the differential cultivars from this set have been used throughout the world as sources of rust resistance genes for the development of rust resistant dry and snap beans. Among these are Aurora, Early Gallatin, Golden Gate Wax, Olathe, Mexico 299, NEP 2, Mexico 309, Redlands Pioneer, CNC, and others.

Despite the utility of this set of differential cultivars to characterize races of the rust pathogen, after some 20 years of use, it required updating. Four of the 19 differential cultivars (Aurora, Mexico 235, Ecuador 299, NEP 2, and 51051) have the *Ur-3* rust resistance gene. Similarly, Early Gallatin and Brown Beauty have the *Ur-4* gene, and Golden gate Wax and Olathe have the *Ur*-6 rust gene; indicating too much duplication for the set of 19 differentials. Moreover, as knowledge of the common bean origin and diversity increased, it became quite obvious that that this set of differentials consisted primarily of bean cultivars from the Middle American gene pool.

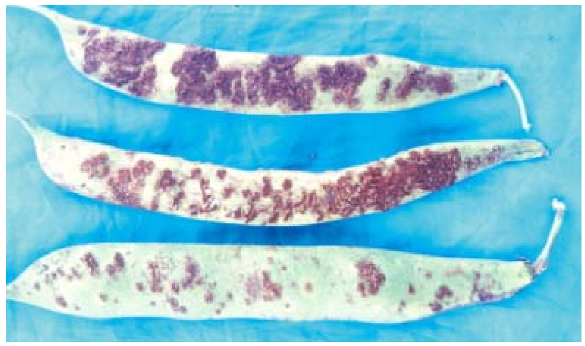
In addition, new information about the diversity of the bean rust pathogen revealed that this diversity could also be separated into two different groups, one Andean and another Middle American, which corresponded to the Andean and Middle American gene pools of the common bean host. Andean races of the rust pathogen are found under field conditions infecting mostly or only Andean bean cultivars. These races are common in Andean countries of South America and in Eastern and Southern Africa where they grow Andean beans. Conversely, Middle American races of the rust pathogen infect bean from both gene pools. These races are prevalent in Brazil, Central America and Mexico, and many locations where Middle American beans are planted. These results, suggested the need for more Andean bean differential cultivars to better separate Andean from Middle American races of the rust pathogen.

During the Third International Rust Workshop in South Africa in 2002 (Steadman et al., 2002b), a new set of differential cultivars was proposed. Several of the most useful differential cultivars from the 1983 set were included in the new 2002 set of bean rust differential cultivars proposed. At this meeting it was agreed that the new 2002 set would comprise of 12 differential bean cultivars; six Andean and six Middle American. It was also agreed that the six Andean bean cultivars will be listed first in the following order: 1. Early Gallatin; 2. Redlands Pioneer; 3. Montcalm; 4. Pompadour Checa 50 (PC 50); 5. Golden Gate Wax; and 6. PI 260418. The second group of Middle American cultivars would be listed in the following order: 1. Great Northern (GN) 1140; 2. Aurora; 3. Mexico 309; 4. Mexico 235; 5. Compuesto Negro Chimaltenango (CNC); and 6. PI 181996 (Table 3). It was also agreed to continue using the same standard grading scale accepted in the 1983 Puerto Rico Meeting.

In addition it was agreed at the South African meeting to name the new races of *U. appendiculatus* using a “Binary System”. In this system each cultivar was assigned a numeric value based on the binary system. The value for each of the six Andean and Middle American cultivars from 1 to 6 would be: 1, 2, 4, 8, 16, and 32, respectively (See Table 3). The designation of each rust race of the rust pathogen would have two digits separated by a hyphen. The first digit would be obtained from the addition of the binary values for each of the susceptible Andean differential cultivars. The second digit would be the result of adding the binary values of each of the susceptible Middle American differential cultivars. For instance, if a newly found rust isolate was compatible with the Andean cultivars Early Gallatin (Binary value is 1), Redlands Pioneer (2) and Golden Gate Wax (16) and with the Middle American cultivars GN 1140 (1) and Aurora (2) and incompatible (resistant) with the other cultivars, the “new” race would be named 19-3. This first digit resulted from the addition of the binary values of the susceptible Andean cultivars Early Gallatin, Redlands Pioneer and Golden Gate Wax (1 + 2 + 16 = 19). The second digit resulted from the addition of the binary values of the susceptible Middle American bean cultivars GN 1140, and Aurora (1 + 2 = 3), respectively. The names of these races are unique and easy to discern. If an isolate of the rust pathogen is named race 22-2, it is because it is compatible only with Andean bean cultivars Redland Pioneer (2), Montcalm (4), and Golden gate Wax (16), as well with Middle American cultivar Aurora (2). This is the only way this new isolate could be named 22-2 (Pastor-Corrales et al. (2010).

Steadman et al. (2002a) recommended a mobile nursery of bean lines with different rust resistance genes to determine which combination of rust resistance genes would be effective when incorporated into widely grown cultivars (Table 4).

An effective field screening technique was developed at the Escuela Agrícola Panamericana. Accessions growing in pots on benches are inoculated with a mixture of virulent pathotypes of bean rust, followed by frequent moistening of the leaf canopy using micro-irrigation (Beaver et al., 2003).



Photograph provided by M. M. Liebenberg (above)

Photograph provided by Talo Pastor-Corrales (right)

Fig. 3. Pustules (uredinia) of the bean rust pathogen on pods

Fig. 4. Pustules (uredinia) of the rust pathogen on stem branch
(Photograph provided by Howard F. Schwartz)

Table 2. Standard set of 19 rust differential bean cultivars adopted in Puerto Rico in 1983 to study the virulence diversity of *Uromyces appendiculatus*					
	Differential Bean Cultivars[1]	Seed color	Weight (100 seeds)	Gene Pool Origin[2]	Rust resistance Gene
1	U.S. 3	White	30.1	A/MA	Unknown
2	C.S.W. 643	White	17.2	MA	Unknown
3	Pinto 650	Pinto	29.4	MA	Unknown
4	K.W. 765	Dark Brown	24.7	A/MA	Unknown
5	K.W. 780	White	18.3	A/MA	Unknown
6	K.W. 814	Brown	28.7	MA	Unknown
7	Golden Gate Wax	Brown	31.00	A/MA	*Ur-6*
8	Early Gallatin	White	24.3	A/MA	*Ur-4*
9	Redlands Pioneer	Brown	35.6	A	*Ur-13*
10	Ecuador 299	Red	25.3	MA	*Ur-3+*
11	Mexico 235	Red	29.3	MA	*Ur-3+*
12	Mexico 309	Black	29.4	A/MA	*Ur-5*
13	Brown Beauty	Brown	39.00	A	*Ur-4*
14	Olathe	Brown	34.00	MA	*Ur-6+*
15	A x S 37	White	12.7	MA	Unknown
16	NEP-2	White	9.4	MA	*Ur-3+*
17	Aurora	White	18.7	MA	*Ur-3*
18	51051	Black	18.9	MA	*Ur-3*
19	CNC	Black	28.5	MA	Unknown

[1]U.S. = United States, CSW = California Smal White; KW = Kentucky Wonder, A x S 37 = Actopan x Sanilac Selection 37, CNC = Compuesto negro Chimaltenango.
[2]Gene pool, origin, of bean cultivars: A = Andean, MA=Middle American, A/MA = mixed

Fig. 5. Small pustules (uredinia) of bean rust pathogen on leaves (Photograph provided by M. M. Liebenberg)

Table 3. Set of 12 common bean differential cultivars proposed at the Third International Bean Rust Workshop held in South Africa in 2002 and used in the characterization of the virulence diversity of *Uromyces appendiculatus*

	Bean Differential Cultivars[1]	Rust R Gene	Gene Pool[2]	Binary Value[3]	Linkage Group where rust resistance gene is mapped
	Andean Beans				
1	Early Gallatin	*Ur-4*	A/MA	1	Pv 06
2	Redlands Pioneer	*Ur-13*	A	2	Pv 08
3	Montcalm	Unknown	A	4	
4	PC 50	*Ur-9*, *Ur-12*	A	8	Pv 01 (*Ur-9*), Pv 7 (*Ur-12*)
5	Golden Gate Wax	*Ur-6*	A/MA	16	Pv 11
6	PI 260418	Unknown	A	32	
	Middle American Beans				
7	GN 1140	*Ur-7*	MA	1	Pv 11
8	Aurora	*Ur-3*	MA	2	Pv 11
9	Mexico 309	*Ur-5*	MA	4	Pv 04
10	Mexico 235	*Ur-3+*	MA	8	
11	CNC	Unknown	MA	16	
12	PI 181996	*Ur-11*	MA	32	Pv 11

[1]PC 50 = Pompadour Checa 50; GN 1140 = Great Northern 1140; CNC = Compuesto Negro Chimaltenango.
[2]Gene pool, origin, of bean cultivars: A = Andean, MA=Middle American
[3]Example of how races of the bean rust pathogen are named using this set of six Andean and six Middle American differential cultivars and the binary system. If a new isolate of the rust pathogen is compatible with Andean bean cultivars Montcalm and Golden Gate Wax, and with Middle American cultivars GN 1140 and Aurora, the new race would be named 20-3. The first digit (20) is obtained from the addition of the binary values of the Andean bean cultivars Montcalm (4) and Golden Gate Wax (16). The second digit (3) is obtained from the addition of the binary values of the Middle American bean cultivars GN 1140 (1) and Aurora (2).

Table 4. Procedures for conducting the bean rust mobile nursery (Steadman et al., 2002a)

1. The bean rust differentials (Tables 2 and 3) and other sources of rust resistance can be used for the mobile nursery.
2. Because the state of development of the leaf affects the size of the pustule, all plants should have the same degree of leaf expansion. The seed of accessions which take longer to emerge can be pre-germinated in order to obtain more uniform germination. Scarification of the testa can also be used to promote germination. Plant two seeds per pot, with extra pots to allow for poor or late germination. Place pots (one per accession) in a tray for easy transportation. Replicate as required.
3. Seedlings are generally ready to take to the field approximately one week after planting, when the primary leaves are approximately ½ to ⅔ expanded.
4. Place the tray near a focus of infection, i.e. bean plants with fresh urediniospores). Dry and windy conditions favor spore dispersal to the seedlings.
5. After 3 to 4 h, remove to a mist chamber (>95% humidity) for 15 – 24 h at 18-24 º C. Use the longer dew period in drier climates. It is important to avoid temperatures > 30º C. The plants can then be placed in a greenhouse maintained at 18/24 º C night/day.
6. Score 14 days after exposure to rust, using the scale established at the First International Bean Rust Workshop (Table 1).

BEAN RUST MANAGEMENT

Although several strategies exist for the management of the common bean rust disease, rust management (control) under field conditions in most bean producing countries of the world is accomplished using disease resistant cultivars and fungicides. Several fungicides are available for the effective management of bean rust; however, use of fungicides invariably increase production costs. Fungicides are used mostly for the control of rust in snap beans. As indicated earlier, snap beans in many parts of the world (e.g., Eastern and Southern African countries) are notoriously susceptible to rust. Fungicides for bean rust management are most effective when used in the very early stages of the epidemic and preventatively. Effective fungicides include protectants such as chlorothalonil and dithiocarbamates, and systemic chemicals such as triazoles and carboxins (summarized in Liebenberg & Pretorius, 2010). Because the bean rust pathogen is not transmitted with the seed, seed treatments for bean rust control are not usually used or needed. Other effective control measures include crop rotation, removal of volunteer plants, deep plowing to remove bean debris from the soil surface and encourage rotting and avoidance by choice of planting time.

Host resistance is the most effective bean rust management strategy. Resistance to bean rust is controlled by a series of several genes that - to date - all are single and dominant (Kelly et al, 1996). Most of these genes have been identified in common bean cultivars belonging to the first uniform set of bean rust differential cultivars proposed in 1983 in Puerto Rico. Please see Tables 2.

Nine of the rust resistance genes have been named and mapped on various linkage groups (LG) of the consensus linkage map of *Phaseolus vulgaris* (Kelly et al., 2003; Miklas et al., 2006). These rust resistance genes (with their location on the linkage map in parenthesis) are: *Ur-3* (Pv 11), *Ur-4* (Pv 01), *Ur-5* (Pv 04), *Ur-6* (Pv 11), *Ur-7* (Pv 11), *Ur-9* (Pv 01), *Ur-11* (Pv 11), *Ur-12* (Pv 07), and *Ur-13* (Pv 08). Four other rust resistance genes have not been named. These include BAC 6 (Ur-BAC 6), Ouro Negro (Ur-Ouro Negro), and two from the Middle American bean Dorado (Ur-Dorado-108, Ur-Dorado-53) (Miklas et al., 2002). These four genes have been tagged with RAPD or SCAR markers and placed on the common bean genetic linkage map. Other rust resistance genes are Ur-US-3 (Ur-8, tentative name), and Ur-Resisto (Ur-10, tentative name).

As expected, some of the rust resistance genes are from beans of the Andean gene pool (*Ur-4*, *Ur-6*, *Ur-9*, and *Ur-12*), while others genes are from beans from the Middle America gene pool (*Ur-3*, *Ur-5*, *Ur-7*, *Ur-11*, etc.). The Andean rust resistance genes are susceptible to most Andean races of the rust pathogen. For instance, the *Ur-4* gene present in snap bean Early Gallatin is susceptible to all know Andean races maintained at Beltsville. Similarly, the Andean *Ur-6* gene is also susceptible to almost all the same Andean races. However these genes provide resistance to many of the Middle American races of this pathogen. The Middle American rust resistance genes tend to be very effective against most or all Andean races of rust pathogen.

All rust resistance genes differ in their resistance spectrum. For example, the *Ur-3*, *Ur-4*, *Ur-*5, *Ur-6*, and *Ur-11* genes control 44, 30, 70, 22, and 89 of 90 races maintained at Beltsville, respectively (Stavely, 2000). Using this information it is apparent that Middle American genes - in general - have a broader spectrum of resistance (Pastor-Corrales, 2006). . The Andean rust resistance genes *Ur-4* and *Ur-6* are resistant to 30 and 22 of 100 races, respectively. On the other hand, Middle American *Ur-3, Ur-5,* and *Ur-11* genes are resistant to 44, 70, and 99, respectively, of the same 100 races maintained at Beltsville.

The *Ur-11* gene has the broadest spectrum of resistance and it is resistant to all known but one race of the rust pathogen from Honduras (race 108). It is considered the most effective rust gene. However, combining Andean and Middle American rust resistance genes results in very effective gene combinations. For instance, the Middle American *Ur-11* gene is only susceptible to race 108 but the Andean *Ur-4* gene is resistant to race 108; thus, combining these two complementary genes results in resistance to all 100 races of the rust pathogen maintained at Beltsville.

The usefulness of host resistance under field conditions may be limited by high the virulence diversity of the bean rust pathogen. The large number of races of this pathogen is a major factor contributing to rendering dry or snap bean varieties that are rust resistance in one location or year, susceptible in another. This is particularly the case when bean varieties have single genes for rust resistance.

Some genes, for instance the now defeated *Ur-3* (Groth and Shrum, 1977; Stavely et al. 1999; Gross & Venette 2002), and certain gene combinations, such as *Ur-3* + *Ur-11* (Pastor-Corrales, 2003), have proved more durable than others (Pastor-Corrales, 2002). The Andean genes *Ur-4, -6, -8, -9* have proved useful in localized regions of the Americas and the resistance in PI 260418 (probably resulting from three genes) has given broad resistance to Beltsville races (Pastor-Corrales, 2005). However, it is generally accepted that a combination of MA and Andean genes is necessary for durable resistance. In Africa, RR genes of MA origin, and in particular *Ur-*

3+, Ur-5 and *Ur-11*, have proved the most useful, although African races have been identified which overcome each of these. *Ur-11+* (as in the source PI 181996) and the combination *Ur-3* + *Ur-11* (bred at USDA, Beltsville) have not yet been defeated. Other good sources have been the CIAT line 'A 286' (registered as 'Mkuzi' in South Africa and as 'Kambidzi' in Malawi), 'Ouro Negro', 'CNC' and 'Mexico 54'. The MA gene *Ur-13*, present in most large seeded South African cultivars, has proved useful but now needs protection by another suitable MA source. No Andean source has yet been identified as resistant in Africa. The resistance in the Andean accession 'PI 260418' is moderately resistant to moderately susceptible to Southern African races and moderately susceptible in the field. It is also inclined to sporulate profusely (Liebenberg & Pretorius, 2010). It is moderately resistant to the Tanzanian race Ua-TZ11 which overcomes *Ur-11.*

Several dry and snap bean varieties released as rust resistant have later lost their resistance to the appearance of a new race of the rust pathogen. The most recent reported case of the appearance of new races of the rust pathogen occurred in Michigan in 2007 and in North Dakota in 2008 (Markell et al., 2009; Wright et al., 2008, and 2009; Pastor-Corrales et al., 2010). These similar but not identical races of the rust pathogen from Michigan and North Dakota were found on many previously rust resistant dry bean cultivars carrying the Ur-3 rust resistance gene that were naturally infected under field conditions.

Many of these rust resistance genes have been used with success in resistance breeding programs (Table 5).

Table 5. Some examples of cultivars bred for resistance to bean rust in different market seed classes.

Line/Cultivar	Seed color / type	Resistance genes	Reference
Kodiak	2M / Pinto	*Ur-3*	Kelly et al. (1999)
Merlot	7 / Red Mexican	*Ur-3*	Hosfield et al. (2004)
Teebus-RR1	1 / Navy	*Ur-3+*	Liebenberg et al, (2010)
Teebus-RCR 2	1 / Navy	*Ur-5 (+ CBB resistance)*	Liebenberg et al. (2010)
BelDade-RGMR-4-6	1 / Snap	*Ur-3+, Ur-4*	Stavely et al. (1997)
BelMiDak-RMR-10-12	1 / Navy	*Ur-4,Ur-11*	Pastor-Corrales (2003)
BelDakMi-RMR-19-23	2M / Pinto	*Ur-3,Ur-4, Ur-6,Ur-11*	Pastor-Corrales (2003)
BelMiNeb-RMR-9-13	1 / Great Northern	*Ur-3,Ur-6,Ur-11*	Pastor-Corrales (2003)
Rosada Nativa	5/ Pink	*Ur-5*	Beaver et. al. (1999)
PC-50	6M / Red mottled	*Ur-9, Ur-12*	Saladin et al. (2000)
Sederberg; Tygerberg	5/ Cranberry	*Ur-11; Ur-13*	Liebenberg et al, 2010
Ouro Negro	9 / Black	*Ur*-Ouro-Negro	Corrêa et al., 2000

At the ARS-USDA Beltsvile Agricultural research Center snap and dry bean, cultivars have developed and released that combine two, three and four rust resistance genes, using a process known as gene pyramiding. Most of these released navy, great northern, and pinto bean germplasm lines express broad rust resistance to all known races of the bean rust pathogen in the greenhouse as well as under field conditions in many parts of the world. These release lines include, BelMiDak-RMR-18, and BelMiNeb-RMR-9, -10, -11, -12, and -13 with four genes for rust resistance and two genes for resistance to the bean common mosaic and bean common mosaic necrosis potyviruses (Pastor et al, 2007). Several sources of adult plant resistance (APR) have been identified (summarized in Liebenberg & Pretorius, 2010) and at least one (single dominant) gene for APR (*Ur-12*) has been identified (Jung et al. 1998). True horizontal resistance to common bean rust remains to be proven and utilized. Molecular markers (summarized in Liebenberg & Pretorius, 2010) are available for most known resistance genes (Mienie et al., 2005; Miklas et al. 1993; Haley et al.1993, 1994; Johnson et al. 1995; Park et al. 2004, 2008), and some have been used with success in marker assisted selection (MAS) (Corrêa et al. 2000; Alzate-Marin et al. 2001; Kelly et al. 1994, 2003; Ragagnin et al. 2003; de Queiroz et al. 2004; Faleiro et al. 2004).

The interested reader is referred to two more comprehensive reviews, namely Sousa (2008) and Liebenberg & Pretorius (2010).

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Fig. 6. Large pustules (uredinia) surrounded by a chlorotic halo, (Photograph provided by Talo Pastor-Corrales)

Fig. 7. Different types of pustules (Uredinia) can be present on the same leaf under field conditions (left); Fig. 8. Telia contain dark, robust overwintering teliospores (right)

Photograph provided by M. M. Liebenberg (left); Howard Schwartz (right)