INHERITANCE OF SPECIFIC RESISTANCE TO RUST (*UROMYCES VICIAE-FABAE*) IN FABA BEAN (*VICIA FABA*) AND EVALUATION OF SLOW-RUSTING RESISTANCE

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Khalid Youssef Rashid

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FOREWORD

The format adopted for writing this thesis follows the manuscript style and has been approved by the Council of the Faculty of Graduate Studies and the Department of Plant Science at the University of Manitoba. Three manuscripts, including materials, methods and results, are prepared to comply with the requirements of the Canadian Journal of Plant Pathology in which these are intended to be published. A general abstract and a general introduction precedes the manuscripts, a general discussion follows, and the thesis terminates with bibliography and appendices.

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GENERAL ABSTRACT

Rashid, Khalid Youssef. Ph.D., The University of Manitoba, February, 1983. Inheritance of Specific Resistance to Rust (Uromyces viciae-fabae) in Faba Bean (Vicia faba) and Evaluation of Slow-Rusting Resistance. Major Professor; Dr. C.C. Bernier.

Open-pollinated accessions of faba bean (Vicia faba L.) representing a wide range of germplasm from various regions of the world were evaluated for their reaction to two single-pustule isolates (SP3 and SP51) of Uromyces viciae-fabae (Pers.) Schroet. from Manitoba. After three cycles of testing, selection and selfing, 117 lines homozygous for resistance (infection type 0-2) to either one or both rust isolates were identified and grouped into nine classes.

Inheritance of resistance to the rust isolates SP3 and SP51 was investigated in 10 faba bean inbred lines and four open-pollinated field selections. Analyses of the F_1 and F_2 data from 27 reciprocal crosses showed the presence of eight genes for resistance. Three genes provide resistance to SP3 and are designated Fr1 in Ack-A, 2N43 and 2N43-A; Fr5 in ILB938-8 and Fr8 in ILB159-1, ILB159-4 and Diana-2. Two genes, Fr6 in ILB938-8 and Fr9 in ILB159-4 condition resistance to SP51. Three additional genes, Fr2 in Erf-2 and 2N5, Fr4 in Erf-2 and Fr7 in ILB938-8, ILB479-7 and ILB159-1, provide resistance to both isolates. Susceptibility in the accession 2N40-5 to SP3 was shown to be dominant or epistatic to the resistance in some moderately resistant accessions. Field selections were shown to have additional non-identified genes for resistance.

Evaluation of 253 open-pollinated faba bean accessions for their

ability to retard rust development was carried out in small adjacent field plots using a mixture of rust isolates in 1978-1979 and the isolates SP3 and SP51 in 1980-1981. The area under the disease progress curve (AUDPC), final disease severity and percentage infected plants were used as criteria for evaluation. Mass (MS) and single-plant (SP) selection were used for selection within accessions. Eight slow-rusting selections with low AUDPC values [2N6 (MS), 2N29 (SP), 2N43 (MS and SP), 2N122 (SP), ILB938 (MS), ILB(332X133)A (MS) and ILB(332X133)B (MS)] and four moderate-rusting selections with intermediate AUDPC values [2N291 (MS), 2N319 (SP), ILB697 (MS) and ILB866 (MS)] were identified over 3-4 years of testing. Other accessions tested were found to be either fast rusters or inconsistent from one year to another. Rust spread and development was also evaluated in isolated test plots using two selections with low AUDPC values and one fast ruster. Slow rusting selections had lower AUDPC values and the fast-rusting selection had higher AUDPC values in isolated plots than in small adjacent plots.

GENERAL INTRODUCTION

The rust, Uromyces viciae-fabae (Pers.) Schroet., is common on various leguminous species of the genera Vicia, Lens, Pisum and Lathyrus. Rust causes severe losses in faba bean (Vicia faba L.) throughout the Middle East and North Africa (Bekhit et al. 1970, Hawtin and Stewart 1979, Mohamed 1981). Estimates of yield losses range from 5-20% (Mansour et al. 1968) to 23-30% (Papoyan 1970) and 17-45% (Williams 1978). In Canada, the rust has been reported from Manitoba and Saskatchewan on this crop since its introduction into Western Canada but has not presented a serious problem in commercial fields (Bernier 1975, McKenzie and Morrall 1975). Conner (1981) showed that in Manitoba, primary inoculum may come from native vetches of the genera Vicia and Lathyrus and confirmed the potential threat of the pathogen to faba bean.

Pathogenic variability in U. viciae-fabae has been reported on faba bean and peas (Gaumann 1934, Kispatic 1949). Conner and Bernier (1982c), using faba bean inbred lines, were able to identify seven races of the pathogen. An additional four races were also identified with the use of pea cultivars. Conner (1981) found that U. viciae-fabae had a wide host range with little relationship to the formae speciales described by Gaumann (1934).

The heterogeneity of faba bean cultivars and accessions for agronomic traits is also observed in their response to rust (Kispatic 1944, 1949, Ibrahim and Nassib 1979, Conner and Bernier 1982c). This was attributed to the partially out-crossing nature of the crop (Holden and Bond 1960, Poulsen 1975, Hawtin and Omar 1981b).

The failure of Hiratsuka (1934) to find resistance to rust in faba bean cultivars may be due to the fact that specific resistance was masked by pathogen variability and host heterogeneity. Moderately resistant cultivars were identified by Kispatic (1949) using single-spore isolates of the rust, by Papoyan (1970) and Mohamed (1981) using field collections of urediospores, but resistance genes were not identified. Specific resistance in faba bean inbred lines to two single-pustule rust isolates SP3 and SP51 from Manitoba was recently found by Conner (1981) to be governed by three different genes.

Race specific resistance has been found to be short-lived (Johnson 1961, Stakman 1964, Hooker 1967, Caldwell 1968). Modern cultivars with specific resistance often break down and become highly susceptible (Day 1974, Robinson 1980). In an attempt to find more durable and stable resistance to faba bean rust, Conner and Bernier (1982b) evaluated open-pollinated accessions of faba bean for their ability to retard rust development under field conditions. Three accessions with consistently low AUDPC values were identified as slow-rusting and six other accessions had AUDPC values that shifted from low to intermediate during the 3 years of testing.

The objectives of these studies were: 1) to evaluate a large number of open-pollinated faba bean accessions from various regions of the world for specific resistance to rust, 2) to investigate the genetics of specific resistance in selected inbred lines in order to find new sources of resistance, and 3) to evaluate open-pollinated faba bean accessions and selections in small adjacent field plots for their ability to retard rust development. Mass and single plant selections were used in an attempt to improve the uniformity of the accessions.

LITERATURE REVIEW

1. The Host Crop (Vicia faba)

1.1 Center of Origin and World Distribution

Carbonized remains of faba beans appeared in several Bronze Age sites of the Eastern Mediterranean region. Such remains were also common in Central Europe during the late Bronze Age and in Western Europe during the Neolithic Age (Zohary and Hopf 1973). Cubero (1973, 1974) believed that the cultivation of faba bean species began in the Near East following the Neolithic culture, but this does not mean that the species was not known in the Mediterranean region by then. Cubero (1974) supposed that the faba beans spread from the Near East into the Old World along four main routes: a European route through Anatolia and Greece, a North African route to Spain through the Nile Delta, a Nile River route through the Nile Valley to Sudan and Ethiopia and an Asian route through Mesopotamia to India and the Far East. Bond (1979) reported that faba beans have been cultivated in England for more than 2,000 years. In North America, faba beans were first introduced during the early 17th century (Evans and Slinkard 1975). It is also believed that the species reached China around 100 years B.C. (Tao 1981) and Japan around the year 700 A.D. (Kogure 1979).

In addition to the Near East as a center of origin of the species, other regions such as Ethiopia and Afghanistan are considered as secondary centers of diversity (Bond 1976). With regards to variability,

Witcombe (1981) did not recognize any one region as the only center of diversity of the species and indicated that germplasm materials collected from different parts of the world are equally important.

1.2 Progenitors of Faba Beans

The wild progenitors of the faba beans are not known. Zohary and Hopf (1973) assumed that Vicia narbonensis L., a Mediterranean wild species, is the progenitor of the present Vicia faba L. Another species, Vicia galilea Plitm. et Zoh., was also believed to be an ancestor of V. faba L. because morphologically these two species are similar. Abdalla and Gunzel (1979), using protein electrophoretic patterns, found that V. narbonensis has a protein pattern distinct from V. faba. The protein patterns in the subspecies of V. faba are essentially similar, indicating that they likely evolved from the same ancestors. The work of Ladizinsky (1975) supports these findings and shows that the albumin profile of seed protein from the species V. faba, V. galilea, V. narbonensis and V. hyaeniscyamus Mont. have little in common.

Attempts to cross V. faba with V. galilea, V. narbonensis and V. hyaeniscyamus have failed (Abdalla and Gunzel 1979, Haq 1979, Witcombe 1981). Chooi (1971) showed that V. narbonensis has half the DNA/cell when compared with V. faba. Vicia narbonensis was believed by many workers to be an ancestor of V. faba, although the two species have different chromosome numbers, different karyotypes and fail to hybridize. Hawtin and Stewart (1979) reviewed the development of V. faba and concluded that the similarity between chromosomes of V. faba and those of V. narbonensis and V. serratifolia Jacq. suggests that these two species are as closely related to V. faba as V. galilea.

1.3 Present Status of Faba Beans

The cultivation of faba beans extends from 9-40° N latitude and from near sea level to over 2,000 m altitude (Kay 1979) and it has recently extended to 53° N latitude (Clarke 1980). The crop ranks as the fourth most important pulse crop in the world after dry beans, dry peas and chickpeas (Hawtin and Stewart 1979). Two-thirds of the world production is in China while the Middle East, North Africa and Europe collectively produce around 30%. Faba bean production is gaining ground in new regions like Canada and Japan. In the Middle East and North Africa, one-third of the region's production is in the Nile Valley (Hawtin 1977) with Turkey, Morocco and Iran as the other major producers (Hawtin and Stewart 1979).

In Canada, faba beans have been planted as a vegetable since the 19th century utilizing the large-seeded types (Evans *et al*. 1972). The interest in small-seeded faba beans as a crop began in the 70's (Evans and Slinkard 1975, Furgal and Evans 1981), especially in the provinces of Manitoba, Saskatchewan and Alberta. Several European cultivars, as well as other faba bean collections, were introduced into the breeding program at the University of Manitoba. The major objectives of this program have been to develop better adapted varieties to the local conditions. The future of faba bean is promising and the first local variety, Aladin, was licensed in 1980. Crop yields comparable to those of cereal crops have been achieved in Western Canada and so the potential of faba beans as a break crop is quite high (Evans and Slinkard 1975). Similar reports and prospects for the crop were reported from England (Chapman and Peat 1978).

Collections of *V. faba* germplasm from different parts of the world

are held in several research institutes and centers. The largest collection is held at the International Center for Agricultural Research in the Dry Areas (ICARDA) and contains 2,000 entries as well as 2,500 inbred lines (Hawtin and Omar 1980a, Witcombe 1981).

In the last few decades research efforts have been concentrated on faba bean for its importance in the world agriculture and food supplies as a high protein and a high nitrogen fixing crop (Griffith and Lawes 1978, Clarke 1980). Most of the current research is conducted in Europe (England, France, Germany and Spain), in the Middle East (ICARDA, Egypt and Sudan) and in Canada in North America. Very little is known regarding research on faba beans in Russia and China.

1.4 Nature of the Crop

Vicia faba has been generally subdivided into three subspecies: major, equina and minor based mainly on seed size (Muratova 1931, Hanelt 1972, Evans and Slinkard 1975). The use of a fourth subspecies, paucijuga, is also common in literature (Cubero 1973, 1974). The faba bean is basically a self-pollinated crop with high variability in cross-pollination ranging from 5-70% (Holden and Bond 1960, Poulsen 1975, Hawtin and Omar 1980b). The extent of cross-pollination depends on many factors, some of which are related to the genetics and physiology of the crop. The only fertilization barrier in the species is due to incompatibility factors (Holden and Bond 1960). Having a typical papilionaceous flower, the faba beans are associated with the necessity for tripping which may help to rupture the stigma papillae and enhance the differential growth of foreign pollen (Rowlands 1958, 1961). An observed decline in self-incompatibility in inbred lines was related to a decline in heterozygosity (Drayner 1956, Hawtin 1981). Rowlands (1958)

explained the decline in terms of homozygous deleterious genes which can accumulate in out-breeding systems. The failure of young pods to survive and mature is attributed to competition between the large number of pods (Kambal et al. 1976). It is also interesting to note that decapitation seems to reduce the vegetative growth and improve the pod setting (Chapman and Peat 1978, Toynbee-Clarke 1979, Gehriger and Keller 1980). Similar observations of better pod-setting in decapitated plants were made by the author in several experiments in the greenhouse at the University of Manitoba (unpublished results).

The high rate of cross-fertilization is the major reason for the high degree of non-uniformity in either open-pollinated or synthetic cultivars (Evans and Slinkard 1975, Hawtin 1981). The degree of out-crossing is also affected by factors other than the crop itself such as the population and activity of bees and the distances between test plots or cultivars (Gottschalk 1978, Hawtin and Omar 1980a). Autofertility was shown to be high in Mediterranean cultivars compared to European cultivars (Hawtin 1977, 1981, Saxena 1981) and in the subspecies paucijuga collections from India, Africa and the Mediterranean region (Evans and Slinkard 1975). The close association between inbreeding and reduction in autofertility and hence reduction in yield is due to the loss of heterosis (Drayner 1959, Toynbee-Clarke 1971, Poulsen 1977). Hawtin (1981) reported that all faba beans show inbreeding depression when compared to their best crossbred offsprings but yield levels of inbred lines equal to those of open-pollinated populations have been identified.

1.5 Breeding Methods

In spite of the interspecific hybridization barrier in V. faba and

the closed genetic system of the species (Chapman and Peat 1978), the most significant feature of the recent work is an understanding of the extent of its genetic variation. The variation present in the species is the result of natural as well as man-made selection under different environmental conditions throughout the long history of the faba beans (Witcombe 1981). This variation is well expressed in the various characteristics of the species such as protein content which ranges between 20-40% (Chapman and Peat 1978, Griffiths and Lawes 1978) and yield which ranges from 1.6-3.2 T/ha in England (Bond 1979), from 2.5-3.5 T/ha in Canada (Evans and Slinkard 1975, Furgal and Evans 1980) and from 3.0-7.5 T/ha in China (Tao 1981).

The basic requirements of any genetic improvement is the hybridization process which allows for gene recombination and releases new or improved gene combinations. Coupled with continuous selection, this is capable of exploiting the genetic variability in the crop (Hawtin 1981).

Mass selection is still the most widely used breeding method in faba bean improvement especially in upgrading local populations following hybridization (Hawtin 1981, Nassib and Khalil 1981). The advantages of mass selection in improving uniformity and other characters of high heritability are recognized by Hawtin (1981) and its application has led to high improvement of yield and stability among local populations of faba beans in Egypt (Nassib and Khalil 1981).

Recurrent selection is another effective way of improving populations especially in out-crossing crops (Rachie and Gardner 1975). This method is currently used by ICARDA (Hawtin 1981) and in Egypt (Nassib et al. 1979). The advantages of this method lie in the production of improved open-pollinated cultivars as well as providing a genetic pool

for further selection and improvement.

Pure line selection has been employed (Nassib et al. 1979) but has not lead to any effective improvement in faba beans. This method would be more effective in autofertile lines of Mediterranean origin or in the subspecies paucijuga (Toynbee-Clarke 1971, Poulsen 1977). Inbreeding may help to identify some recessive genes which are masked in heterozygous conditions (Hawtin 1981) and also help to improve simply inherited qualitative traits. Inbred lines are homozygous and their narrow genetic base may result in high disease vulnerability. Bond (1979) found that inbred lines are highly influenced by environment and that their yield fluctuates greatly.

A single-seed descent procedure proposed by Brim (1966) is also useful for selection in advanced populations without limiting genetic variability.

The system used at ICARDA aims to develop relatively homozygous subpopulations with desired specific characteristics by using mass-selection in F_2 generation. The desired characters could be transferred to the mainstream populations when sufficient advancement is achieved in those subpopulations (Hawtin 1981, Nassib and Khalil 1981). In a similar manner, Witcombe (1981) suggested the use of trait specific gene pool approach.

1.6 Major Diseases of Faba Beans

Faba beans are subject to a number of diseases wherever they are cultivated in the world. The most serious diseases threatening the crop are found in the Middle East and North African countries (Hawtin and Stewart 1979, Hussein 1981, Mohamed 1981). Reports from Europe (Bond 1979, Bond and Jellis 1980, Berthelem 1980, Bos 1981, Salt 1981) showed that diseases of faba beans are less common than in the Middle East and

may not be as destructive. In Canada, the major diseases reported in the Middle East have been observed (McKenzie and Morrall 1973, Gourley and Delbridge 1973, Bernier 1975, Howard 1981) but were not considered to be of any immediate threat to the crop. However, several diseases including rust, Ascochyta blight and bean yellow mosaic virus were considered to be potentially destructive (Bernier 1975).

Chocolate spot caused by Botrytis fabae Sard. and to a lesser extent by B. cinerea Pers. is present in all areas where faba beans are planted, especially in the Mediterranean basin (Hawtin 1981, Hanounik and Hawtin 1981, Mohamed 1981). In Europe, this disease has been reported to be of major importance in England (Bond 1979) and France (Berthelem 1980). In Canada, chocolate spot was first reported by Gourley and Delbridge (1973) in Nova Scotia and in Saskatchewan by McKenzie and Morrall (1973). In Manitoba, it was first reported by Platford et al. (1974) and its incidence has been insignificant since then. Chocolate spot is the most prevalent disease of faba beans in Alberta (Sumar et al. 1981).

The Ascochyta leaf blight and pod spot caused by Ascochyta fabae Speg. is a destructive disease of faba beans and the most widely distributed in the world (Bernier 1975, Hawtin and Stewart 1979). In Canada, the disease has been reported by Bernier (1975) and Lachance and Choquette (1974).

The rust caused by Uromyces viciae-fabae Pers. Schroet. is another important and common disease of faba beans in the Middle East, North Africa and Europe (Hawtin and Stewart 1979, Mohamed 1981). The rust was reported from Manitoba (Bernier 1975) and Saskatchewan (McKenzie and Morrall 1975). As previously mentioned, the potential of this disease

as a threat to faba bean production in Manitoba should not be underestimated.

Powdery mildew on faba beans is caused by Erysiphe polygoni D.C. and Leveillula taurica (Lev.) Arnaud. in the Middle East (Hawtin and Stewart 1979) and by Mycrosphaera penicillata (Wall. ex. Fr.) Lév. var ludens (Salm.) Cooke (Kharbanda and Bernier 1977, Sumar et al. 1981) in all the western provinces in Canada (Howard 1981).

Other minor foliar diseases caused by fungi such as Alternaria spp., Cercospora spp., Cladosporium spp., Peronospora viciae (Berk.) Casp. have been reported from different areas of faba bean production (McKenzie and Morrall 1975, Hawtin and Stewart 1979, Mohamed 1981). Recently, a bacterial blight was reported by Reddy and Hawtin (1980) and was suspected to be caused by a Xanthomonas spp.

A number of virus diseases are very common on faba beans including broadbean mosaic virus (BBMV), bean yellow mosaic virus (BYMV), bean wilt virus (BWV) and pea mosaic virus (PMV) (Bernier 1975, Hawtin and Stewart 1979, Bos 1981). Bos (1981) reported the presence of 16 different viruses on the field-grown faba beans. In Canada, BYMV has been reported by Bernier (1975) and by Frowd and Bernier (1977).

Root rot and stem rot caused by a number of pathogens such as Fusarium spp., Rhizoctonia spp., Sclerotinia spp., Pythium spp. and Cylindrocarpon spp. are sometimes of major threat to the crop (Bernier 1975, Hawtin and Stewart 1979, Salt 1981). In Canada, Rhizoctonia solani Kuehn., Sclerotinia sclerotiorum (Lib.) de Bary and Fusarium oxysporum Schlecht. have been reported from Manitoba, Saskatchewan and Alberta (Bernier 1975, McKenzie and Morrall 1975, Sumar et al. 1981). Recently a serious seedling blight caused by Aphanomyces euteiches

Drechs. has been reported in Manitoba (Lamari 1982).

1.7 Prospects for the Future

Hawtin and Stewart (1979) considered V. faba as an incompletely domesticated species and they anticipated a tremendous need for improvement before it reaches the level of productivity of the other important food crops of the world. Hawtin (1977) summarized the major problems of faba beans affecting yield stability such as autofertility, flower drop, pod drop and poor agronomic characteristics. Other problems include Rhizobium association, weed competition and disease and pest resistance in addition to some problems limiting the utilization of the crop such as phenols, tannin contents and favism. The future of the crop lies in finding solutions to such problems (Evans and Slinkard 1975, Hawtin 1977, Bond 1979).

2. The Pathogen: Uromyces viciae-fabae

2.1 The Importance of Faba Bean Rust

Uromyces viciae-fabae (Pers.) Schroet. is widespread, occurring on various leguminous species in different areas of the world (Grove 1913, Wilson and Henderson 1966). This rust is common on cultivated pulse crops such as faba beans, peas and lentils and its host range extends to a large number of other Vicia, Pisum, Lathyrus and Lens species (Cummins 1934, Anon· 1960, Wilson and Henderson 1966, Conners 1967, Kapooria and Sinha 1966, 1971).

Uromyces viciae-fabae is very common throughout the Middle East and North Africa and is a serious threat to the faba bean crop in certain countries (Hawtin and Stewart 1979). The rust is considered one of the most destructive diseases of faba beans in Egypt. It prevails in the

northern region of the Nile Delta where conditions of relatively low temperature and high relative humidity favour its spread. The losses from this disease range between 5-20% depending on the time of infection and severity of the disease (El-Helaly 1939, Mansour *et al*. 1968, Bekhit *et al*. 1970, Mohamed 1981). Still higher losses of 23% of green yield and 30% of grain yield were reported by Papoyan (1970) from the Armenian state in the U.S.S.R. In Australia, Williams (1978) studied the effect of rust severity on the growth and yield of faba beans. He found that yield loss ranges between 10-45% depending on cultivars used and the level of rust severity. This loss appeared to be due to a shortage in assimilates during the pod filling stage.

In India, *U. viciae-fabae* is an important pathogen on lentils and peas. On lentils, it is very common in the northern part of India where aeciospore infection prevails at the temperature range 17-20° C leading to the formation of secondary aecia while at a temperature of 25° C and above the uredia and urediospores are formed (Prasada and Verma 1948). The role of secondary aecia requires further confirmation. In field peas, the aecia and aeciospores are very common and the disease causes stem deformations as well as complete death of the plant (Kapooria and Sinha 1966, 1971, Gupta 1974).

In Canada, the rust is present on faba beans in Manitoba and Saskatchewan (Bernier 1975, McKenzie and Morrall 1975). It has also been reported on different species of *Lathyrus*, *Vicia* and *Pisum* (Conners 1967). Recently the importance of this rust and its wide host range has been confirmed by Conner (1981) and different isolates have been collected from *V. faba*, *V. americana* Muhl., *Lathyrus* species and *Pisum sativum* L. for host range and pathogenic variability studies. All

isolates were capable of infecting lentils. It has been also found that part of the natural inoculum on faba beans came from the vetches in Manitoba and this could build up to become a serious problem on faba beans, lentils and peas (Conner 1981).

2.2 Taxonomy

Faba bean rust is an old, well-known pathogen reported by Persoon under the name Uredo fabae in 1794 and later on under the name Uredo viciae-fabae in 1801. It was then reported by de Bary in 1863 under the name Uromyces fabae (Cunningham 1931). The name Uromyces fabae (Pers.) de Bary remained in use for a long time (Cummins 1934). This rust has been since described by a number of mycologists and plant pathologists using different binomial names (Wilson and Henderson 1966, Boerema and Verhoeven 1979). Boerema and Verhoeven (1979) put forward a strong argument for the name Uromyces fabae (Grev.) de Bary ex. Fuckel. based on the fact that the first description of the telia and teliospores was done by P. Karsten in 1879 under the name Uromyces viciae-fabae after the description of Puccinia fabae Greville in 1822. To them this took priority in naming the fungus.

Wilson and Henderson (1966) and Laundon (1968), on the other hand, agreed to the name Uromyces viciae-fabae (Pers.) Schroet. based on certain facts such as the findings of some telia in Persoon's original collection of Uredo viciae-fabae by Jørstad in 1958 (Boerema and Verhoeven 1979) and the fact that Persoon did indeed describe the telia but not the teliospores. Thus, Persoon's naming takes priority in describing the perfect stage of the fungus (paragraph 3 of the present Act 59 of the International Code of Botanical Nomenclature) and is the legitimate basionym for the telial state.

Laundon and Waterston (1965), in the Commonwealth Mycological Institute description of pathogenic fungi and bacteria, agreed to Uromyces viciae-fabae (Pers.) Schroet. as the valid legitimate name with other names as synonyms.

= Uredo viciae-fabae Pers. (1801)

= Uromyces fabae (Pers.) de Bary (1863)

= Uromyces orobi (Pers.) Fuckel (1869)

= Uromyces viciae Fuckel (1869)

= Uromyces polymorphus Peck and Clint (1878)

= Uromyces yoshinagai P. Henn. (1901)

In spite of the legitimacy of the name U. viciae-fabae and its common use, the other names are still being used in literature (Kapooria 1971, Nene et al. 1975, McKenzie and Morrall 1975, Srivastava et al. 1980).

2.3 Biology and Life Cycle of Uromyces viciae-fabae

Uromyces viciae-fabae is a eu-autoecious, heterothalic rust. The five spore stages: pycniospores, aeciospores, urediospores, teliospores and basidiospores, are well known and described by various sources (Grove 1913, Cunningham 1931, Cummins 1934, Butler and Jones 1961, Laundon and Waterston 1965, Wilson and Henderson 1966, Kapooria 1971).

The pycnia are amphigenous in small groups growing among the aecia and are usually found on the upper side of the leaf. Fertilization of the pycnial flexuous hyphae with pycniospores from a different monosporidial pustule is necessary for the formation of aecia, which is typical of heterothalic rusts (Brown 1940, Prasada and Singh 1975). During the course of their studies, Prasada and Singh (1975) found some aborted pycnia on the lower surface of the leaves which is a common phenomenon in both homo- and heterothalic rusts (Brown 1940, Johnson and Green

1954). Aecia are also amphigenous or hypophyllous, seated on pale yellow spots which are scattered or in clusters of whitish cup-shaped structure. Aeciospores are spheroid and densely verrucose, yellow to hyaline in color and range from 14-26 μ in diameter (Laundon and Waterston 1965, Wilson and Henderson 1966). Pycnia are very rarely seen in nature, although they have been frequently encountered in research work (Brown 1940, Prasada and Singh 1975), while aecia are commonly found on Lathyrus and Vicia species (Buller 1950) but they are rare on V. faba. Aecia have been reported to occur in late autumn and early spring in England (Wilson and Henderson 1966) and this suggests that some teliospores are capable of readily germinating in the fall. Aecia and aeciospores cannot survive in severe winter of northern regions in Europe but probably will remain viable under the Mediterranean climate (Kispatic 1949) where aecial production could be repeated throughout the whole season. Prasada and Verma (1948) have shown that in Northern India, cool temperatures (17-20° C) favour the recycling of aecial stage on lentils to a level where it becomes as destructive as the uredial stage.

Uredia are amphigenous, scattered or clustered pustules exposed by the ruptured host epidermis. Urediospores are obovoid or ellipsoidal with a finely echinulated thin wall which is light golden brown in color. Their size ranges from 20-30 x 18-26 μ and they have three to four pores in their walls (Wilson and Henderson 1966). Uredia are very common, especially on Vicia faba and sometimes they are associated with aecia early in the season and with telia at the end of the season (Brown 1940, Prasada and Verma 1948, Prasada and Singh 1975). Urediospores are the most destructive stage of the fungus since they can recycle during the growing season and cause severe epidemics. Kispatic (1949) reported

one to nine uredial generations per season in Yugoslavia.

Telia are similar to uredia except for their blackish dark-brown color and they are commonly associated with uredia in which both urediospores and teliospores are produced in the same pustules. Teliospores are subglobois, ellipsoid with a round or truncated apex and a thick dark-brown wall having one apical pore. They measure 25-38 x 18-28 μ and are pedicelate with long pedicels up to 100 μ long (Laundon and Waterston 1965, Wilson and Henderson 1966). Teliospores are the survival state of the fungus under adverse conditions of both low and high temperature (Kispatic 1949, Prasada and Singh 1975, Prasada and Verma 1948).

There is little known about the germination behavior of the teliospores. Studies by Prasada and Verma (1948) showed that the teliospores do not require a resting period and can germinate readily under suitable conditions of 12-22^{o} C. These results were supported by Kispatic (1949) in Yugoslavia and by Willson and Henderson (1966) in England. Studies by Kapooria (1971) showed that attempts to germinate fresh teliospores collected before November in North India often failed while successful germination was always obtained when spores were collected after November. This indicates that teliospores developed under temperature in North India did not germinate while those developed under colder temperatures towards the end of the season can germinate readily.

2.3.1 The short-cycling phenomenon. Uromyces viciae-fabae is a long-cycled (macrocyclic) rust capable of producing all its spore stages on one and the same host plant of various Lathyrus, Pisum, Lens and Vicia species (Buller 1950). The rust tends to shorten its life cycle by producing aecia and uredia on the same mycelial colony. Brown (1940) studied the

behavior of the rust and confirmed that the association of urediospores and aeciospores in the same pustules is very high and that short cycling may cause the complete omission of the aecial stage. This phenomenon supports the theory that through the course of evolution the short-cycled rusts have been derived from the long-cycled rusts (Buller 1950).

2.4 Pathogen Variability and Host Range

The variation in the species Uromyces viciae-fabae and the lack of information on the subspecies, varieties or isolates used in research work in different parts of the world makes it difficult to standardize the host range of the fungus. The earliest work on the specialization of U. viciae-fabae was done by Plowright in 1889 and cited by Wilson and Henderson (1966). More recent studies have been carried out by Hiratsuka (1933) and Gaumann (1934). Gaumann (1934) summarized the work done up to his time and recognized six formae speciales.

(i) f. sp. viciae-fabae de Bary on Pisum sativum and Vicia faba.

(ii) f. sp. pisi-sativi Hiratsuka on P. sativum.

(iii) f. sp. craccae Fisher on V. cracca, P. sativum and weakly on V. hirsuta.

(iv) f. sp. viciae-sepium Gaumann on V. sepium and V. faba.

(v) f. sp. viciae-nipponicae Hiratsuka on V. nipponica.

(vi) f. sp. viciae-unijugai Hiratsuka on V. unijuga.

Another species, Uromyces orobi (Pers.) Lev., was regarded as a distinct species by Gaumann (1934) where he recognized three formae speciales: (i) f. sp. orobi Jordi, (ii) f. sp. Lathyri-vermi Jordi and (iii) f. sp. Lathyri-maritimi Hiratsuka. Recently, the U. orobi has been transferred to U. viciae-fabae by Jørstad and is classified as var. orobi under the U. viciae-fabae (Wilson and Henderson 1966). It

differs from var. viciae-fabae only in its average thickness of urediospore walls. Gaumann's work (1934) shows that the specificity of each subspecies or formae speciales of U. viciae-fabae is limited to two or three host species at the maximum while the isolates used by Kispatic (1949) showed a wider host range including six Vicia spp. in addition to V. faba and Pisum sativum. The isolates used by Kapooria and Sinha (1966) showed some differences in host range which includes six Vicia spp. in addition to V. faba, of which only two are in common with Kispatic's host range. Further studies by Kapooria and Sinha (1971), using different collections of rust due to the loss of their 1966 collection, showed a completely different host range including two Lathyrus spp. and three Pisum spp. besides Pisum sativum which is the only common host with Kispatic's host range. Obviously, every rust isolate or collection is giving a different host range which could be partially due to the variation in the rust population and partially to the heterogeneity in the host species cultivars used in the studies.

As early as 1913, Grove reported on the host range of U. fabae de Bary to include Vicia spp., Lathyrus spp. and Pisum spp. Similarly, Cunningham (1931) reported U. fabae on Vicia faba, Lathyrus, Pisum and other Vicia spp. in New Zealand.

In North America, U. viciae-fabae has been reported to infect 21 Lathyrus spp., eight Vicia spp. including V. faba and Pisum sativum (Cummins 1934, Anonymous 1960). In Canada, U. viciae-fabae has been reported to infect six Lathyrus spp., six Vicia spp. including Vicia faba and Pisum sativum in different regions from coast to coast (Conners 1967). In recent studies on the pathogenic variability and the host range of the U. viciae-fabae, Conner (1981) demonstrated a considerable

degree of variability within populations of the pathogen. He used isolates from Vicia faba, V. americana, Pisum sativum and different Lathyrus spp. and found that there are at least two distinct groups of isolates of the fungus from V. faba. The isolates from V. americana fit closely to some V. faba isolates while the isolates from Lathyrus seem to be different. The Pisum isolates from Manitoba and Quebec differ in their host range. All the isolates used by Conner (1981), except one, were capable of infecting faba beans, while all except one, were capable of infecting lentils (Lens culinaris). This study confirmed the presence of host specificity among the isolates of the fungus and showed a wider host range with little relationship to the formae speciales described by Gaumann (1934).

Reports of U. viciae-fabae on lentils are very common. Prasada and Verma (1948) reported severe outbreaks of rust on lentils (Lens esculenta) in India where the pathogen is known to infect lentils, field peas, sweet peas and faba beans. Reports by Nene et al. (1975), Gupta (1974), and Narsinghani et al. (1980) claimed that the U. fabae de Bary is one of the major diseases on peas in North Eastern India. Faba bean is a common host of U. viciae-fabae in the Middle East and North Africa (Kaiser et al. 1967, Djerbi et al. 1978, Hawtin and Stewart 1979, Mohamed 1981). Lentil is a common host for U. viciae-fabae in Ethiopia (Mengistu 1978) and Syria (Hanounik 1978). In Europe, faba beans have been reported to be the common host of U. viciae-fabae (Gaumann 1934, Kispatic 1944, 1949, Papoyan 1970, Berthelem 1980).

2.5 Host Resistance

Kispatic (1944) was the first to use the infection type reaction of 0, ;, 1, II, III, IV and IV^{+} to quantify the interaction of faba bean

cultivars to the rust. The results of his work showed variability in uredial size and number as well as in the formation of secondary rings of uredia around the primary uredia. Two different groups of isolates were recognized; one of which being very aggressive on faba bean cultivars. Considerable variation in resistance was reported between, as well as within, faba bean cultivars confirming the heterogeniety of the cultivars. Using single-spore isolates, Kispatic (1949) was able to detect moderately resistant faba bean cultivars and differentiated nine races of U. viciae-fabae based on their reaction on different pea cultivars. Varietal resistance to U. viciae-fabae was also investigated in Armenia among 19 different varieties of faba bean to local isolates of the rust during the years 1961-1964 (Papoyon 1970). Ackerperle was one of the highly resistant varieties and Herz Freya was among the resistant varieties, while the local varieties were either moderately resistant or susceptible. In Japan, Hiratsuka (1934) failed to find resistant cultivars among faba beans. This may be due to the different collections of rust he used and the fact that specific resistance was masked by the pathogen variability and the host heterogeniety. Varietal resistance in faba beans in Egypt was studied using a local rust collection on detached leaf tests, seedling tests and field experiments (Mohamed 1981). Uniform resistance was detected in some varieties in different tests. Some cultivars showed more resistance when inoculated at 75 days, compared to 50 days of plant age while others showed the opposite reaction. This may be comparable to the phenomenon of adult plant resistance reported in cereals (Depauw and Buchanon 1975, Sunderwith and Roelfs 1980). A comprehensive study on the inheritance of resistance to faba bean rust in inbred lines revealed the presence of three different

dominant genes (Conner 1981). Two of these genes conditioned resistance to isolate SS3 while one conditioned resistance to isolate SP51. In addition, some inbred lines were found to have other resistance genes in heterozygous condition.

Studies on rust resistance in peas were carried out using 49 different genotypes of diverse origin in India employing the Stakman and Levine (1922) system of evaluation and selection (Narsinghani et al. 1980). A few resistant and moderately resistant lines were found but the majority of the lines tested were susceptible with some showing heterogeneous reactions. Similar results were reported by Sohi et al. (1974) using 35 lines of peas. Another large scale field screening for resistance in pea germplasm has been carried out in Bangalore, India (Pal et al. 1980). Of 269 entries from 23 species of Pisum, only three were resistant to local rust collections.

Lentil resistance to U. fabae de Bary was also studied in Utter Pradish, India using 129 lines and varieties (Nene et al. 1975). Several lines were immune, while others were resistant and could be used in breeding for resistance. Some of the resistant lines found by Nene et al. (1975) were also resistant to the wilt organism Fusarium oxysporum Schl. f. sp. lentis Vasud. and Sriniv. under field conditions. Field resistance in 1183 lentil lines to U. fabae (Pers.) de Bary was investigated by Agrawal et al. (1976) in India where the disease was reported to be very severe on lentils. Only 22 lines were reported free from rust, while 149 lines had trace infections. The importance of lentil resistance to U. viciae-fabae was also shown by Singh and Sokhi (1980) in their work on pathogenic variability of this rust. Their results showed that neither peas nor sweet peas have any differential reaction

to any of the seven rust isolates from Punjab, while the lentils did. Thus, 11 lentil lines were used as host differentials for race identification in Punjab. Lentils were also shown to be infected by all except one of the rust isolates used by Conner (1981).

3. The Concepts of Disease Resistance in Plants

3.1 Types and Terminology

Day (1974) described host plant resistance in functional and genetic terms referring to highly specific and non-specific types of resistance in comparison with Vanderplank's (1963) functional terms vertical and horizontal resistance. In genetic terms, Day (1974) described resistance as oligogenic or major gene resistance determined by one or few genes whose individual effects are easily observed, polygenic resistance determined by many genes of individually small effects and cytoplasmic resistance under the control of cytoplasmic factors and not the nucleic genome. Browning et al. (1977) looked at Vanderplank's vertical and horizontal resistance as genetically defined and epidemiologically projected. They proposed the use of "discriminatory resistance" which distinguish among different pathogen genotypes and "dilatory resistance" to delay pathogenicity in epidemiological terms.

Nelson (1973) defined resistance as an inherent ability of the host plant to prevent or resist the establishment of a successful parasitic relationship either by restricting the infection site and the infection process or by resisting the colonization and subsequent growth of the pathogen following a successful infection process. This first type of resistance is known as specific resistance and usually associated with differential interactions among the genotypes of the host and those of

the pathogen. The nature and performance of this type of host resistance is expressed as a reaction to specific races of the pathogen. In response to the resistant reaction, the specific races may acquire virulence to enable them to overcome the specific genes for resistance (Nelson 1973, Day 1974, Browning et al. 1977). This kind of resistance is referred to as race-specific, vertical, major gene, monogenic, oligogenic, hypersensitive and non-uniform resistance (Vanderplank 1963, Robinson 1969, Day 1974, Browning et al. 1977, Parlevliet and Zadoks 1977, Nelson 1978).

The second type of host plant resistance (Nelson 1973) which resists colonization and subsequent growth of the pathogen is capable of reducing the infection rate and hence is called rate-reducing resistance (Nelson 1978). This type of resistance is associated with non-differential interaction among the host and the pathogen genotypes (Vanderplank 1963, 1968, Nelson 1978). It confers an enduring and stable reaction by the host to all pathotypes or races of a pathogen. Time has been recognized as a prime factor in the epidemiological approach of studying disease resistance which involves the rate of development of an epidemic (Stevens 1960, Zadoks 1972, Vanderplank 1975). The terminology used to describe the epidemiological concept of resistance is quite variable and includes general resistance, field resistance, partial resistance, slow-rusting, race non-specific, uniform, horizontal and minor-gene resistance (Vanderplank 1963, 1968, Nelson 1973, Day 1974, Browning et al. 1977, Horsfall et al. 1977, Parlevliet and Zadoks 1977). Vanderplank's (1963) concept of horizontal resistance implies a race non-specific resistance which acts against all biotypes of a pathogen and is controlled by a polygenic system. The confusion arose from the fact that Vanderplank defined horizontal resistance in genetic terms and took the epidemiological

approach to explain the hypothesis (Ellingboe 1981). In contrast to the horizontal resistance, the slow-rusting resistance does not imply effectiveness against all races of a pathogen (Wilcoxson 1981), nor does it imply anything about the genetics of the resistance or whether it is polygenic or oligogenic in nature.

Ellingboe, in a recent review (1981) on the host-pathogen genetic concepts, suggested that horizontal resistance is an artifact of experimental conditions and is a resistance that has not yet been shown to be vertical or specific and concluded that almost all the naturally occurring genetic variability seems to follow the gene-for-gene pattern. Working on the slow-mildewing of wheat, Ellingboe (1981) found that upon careful analysis the slow-mildewing which is typical of the original description of horizontal resistance or race non-specific is a simply inherited trait that is race-specific. Martin and Ellingboe (1976) found that the major gene; Pm4, conferring high resistance or immunity to powdery mildew in wheat, reacted by reducing the infection efficiency when tested to two strains of Erysiphe graminis f. sp. tritici and by lengthening the generation time when tested to a third strain. The Pm4 major gene showed a horizontal resistance performance when tested with the appropriate strains in a precise analytical experiment.

3.2 Genetics of Race-Specific Resistance

Race-specific resistance has been, until recently, the major genetic approach for plant disease control in breeding programs (Nelson 1973). It is described by Nelson to have the following characteristics: (i) resists the establishment of a successful infection site, (ii) is expressed in the form of hypersensitive reaction, (iii) has an all or nothing type reaction, (iv) is differentially reactive to different races,

(v) is dramatically expressed and simply inherited, (vi) is inactive and undetectible in the absence of matching virulent genes in the pathogen and (vii) is generally unstable.

Vanderplank (1963, 1968) referred to vertical resistance (race-specific) as a discontinuous variation in resistance with a qualitative expression which is monogenically or oligogenically controlled. The fact that vertical or race-specific resistance is a reflection of the gene-for-gene system (Day 1974, Parlevliet and Zadoks 1977) does not mean that only major genes are involved in such reactions because they are easily identified, but also minor genes with small additive effects may react in the same way with minor genes in the pathogen (Nelson 1973, 1978, Parlevliet and Zadoks 1977). Nelson (1978) goes further in his explanation about the function of major and minor genes to say that there is no such differentiation and that genes function in race-specific (vertical) manner when they are alone and as race non-specific (horizontal) when they are together. Evidence for this is present in maize with resistance to the northern leaf blight, Helminthosporium turcicum Pass. where the effect of resistance genes was additive (Hooker 1973). Further evidence is also provided in Solanum demissum Lindl. resistance to Phytophthora infestans (Mont.) de Bary (Niederhauser 1961). Although Solanum demissum showed field resistance to late blight, genes expressing vertical or race-specific resistance were continuously extracted from the species. Thus, it is believed that the race-specific genes extracted from S. demissum were collectively responsible for its field or horizontal resistance (Nelson 1978). Some race-specific genes for resistance maintain measurable residual effect in restricting disease increase and severity after being overcome by virulent races and this supports the

hypothesis that horizontal or non-specific resistance is controlled by the same genes controlling race-specific or vertical resistance (Martin and Ellingboe 1976, Ellingboe 1981, Nass et al. 1981).

The complementary genetic system developed by host-parasite interaction during their evolution was fully explored in the flax rust, Melampsora lini (Pers.) Lev. (Flor 1955, 1956). This has been demonstrated in an increasing number of host-parasite systems especially in cereal rusts as well as many other host-parasite systems (Day 1974). Triticum - Puccinia graminis tritici (Green 1966), Avena - Puccinia graminis avenae (Martens et al. 1970) and Triticum - Puccinia recondita (Samborski and Dyck 1968) are three typical illustrations of the gene-for-gene system. An important feature of these systems is that the hosts are all economically important crops and the resistance is controlled by race-specific genes. Day (1974) refers to this as an "unnatural" situation because resistance in natural plant populations is a combination of both specific and non-specific types, whereas most breeding programs have attempted to isolate race-specific genes from their natural hosts (Johnson 1961) and thus render them vulnerable to attack due to pathogen variability (e.g. a mutation at one locus). Thus, the gene-for-gene concept becomes an artifact of breeding for resistance (Day 1974).

The mode of inheritance of this type of resistance is commonly controlled by completely dominant genes to most of the cereal rusts (Hooker 1967). In the flax rust system, it has been demonstrated that dominant genes have been the sole basis for resistance to Melampsora lini (Flor 1971, Hoes and Kenaschuk 1980, Lawrence et al. 1981). In wheat stem rust, all cultivars released in Canada since 1950 are characterized by race-specific resistance but they may possess more than one

resistance gene (Green and Campbell 1979). Some of these wheat cultivars have complex genetic resistance involving genes for hypersensitive reaction as well as low receptivity (Mortensen and Green 1978). Resistance in 13 wheat cultivars to Puccinia graminis tritici was shown to be controlled by single dominant genes which segregate independently (Gough et al. 1980). In corn, resistance to Puccinia polysora Underw., the southern corn rust, was determined to be a dominant character (Futrell et al. 1975).

Resistance controlled by recessive genes in the host is known in several host-parasite systems. Thatcher and Marquis wheat resistance to race 9 of P. recondita was determined to be a single recessive gene (Bartos et al. 1969). Glenlea wheat also has one recessive gene controlling resistance to four races of P. graminis tritici (Ndondi 1978). Chotti lerma resistance to race 122 of P. graminis tritici was also found to be controlled by two recessive genes (Sawhney et al. 1978). Platford (1976) found that resistance to Claviceps purpurea (Fr.) Tul. is controlled by two recessive genes in Kenya Farmer wheat while resistance in Carleton wheat is governed by two dominant genes.

Resistance in corn was shown to be dominant when tested with culture 901 of Puccinia sorghi Shw., while it was a recessive trait when tested with culture 933 of the same fungus (Saxena and Hooker 1974). In this case, it may be the same gene reacting differently to the two different cultures of rust or two closely linked alleles.

Dyck and Samborski (1968) reported on the effect of different backgrounds on resistant genes and the reaction of the two alleles $Lr2^2$ and $Lr2^4$ in wheat to P. recondita. The reaction of these two alleles changed from dominance to intermediate and recessive when crossed to different

susceptible cultivars. Similarly, McDaniel (1973) found a background effect on the expression of the gene PC45 from Avena sterilis to two races of the crown rust of oat, P. coronata avenae Eriks. Riley (1973) found that resistance to Claviceps purpurea in Triticum timopheevi Shank. to be a dominant trait when crossed with tetraploid wheat and recessive when crossed with hexaploid wheat. Complementary gene effect may be the case of resistance in some oat cultivars to the crown rust P. coronata avenae (Simons 1966) and to stem rust of wheat P. graminis tritici as reported by Knott and Anderson (1956).

3.3 Slow Rusting

Slow rusting was first reported by Farrer in 1898 (Hooker 1967) as a measure of host resistance and was noted to be an inherited trait. It has been described as a reduced rate of epidemic development (Nelson 1973, MacKenzie 1976) and is characterized by delaying, inhibiting and, ultimately, reducing fungus sporulation and multiplication (Statler et al. 1977), yet the host plants are infected with susceptible infection type (Parlevliet 1979a). Parlevliet (1979a) referred to this kind of resistance as partial, which retards disease development through its effects on disease epidemiology. In genetic terms, slow-rusting could be a single gene trait such as in the resistance of the wheat cultivar Hopps to P. graminis tritici which is controlled by one single gene Sr_2 (Sunderwith and Roelfs 1980). In other cases, a few to many genes could be involved in the slow-rusting resistance such as the resistances in wheat to P. recondita tritici that was shown to be under the control of four to 14 genes (Gavinlertvatana and Wilcoxson 1978). Cultivars may carry genes that condition both specific types of resistance as well as slow-rusting and this was demonstrated by Parlevliet and Kuiper (1977) in some barley

cultivars against P. hordei.

Slow-rusting resistance has become more useful in plant breeding for disease resistance due to its durable nature and wide genetic base (Nelson 1978, Parlevliet 1979b, Wilcoxson 1981). Slow rusting has been reported and documented in crown rust of oat (Luke et al. 1975, Luke et al. 1981), barley leaf rust (Parlevliet and Van Ommeren 1975, Johnson and Wilcoxson 1979), wheat stem rust (Skovmand et al. 1978, Martins et al. 1979, Ayers et al. 1981), wheat leaf rust (Shaner et al. 1978, Kuhn et al. 1978, Shaner and Finney 1980), corn rusts (Lewellen et al. 1967, Hooker 1969), rice blast (Villareal et al. 1981) and powdery mildew in wheat (Shaner 1973).

3.3.1 Components of slow-rusting. Slow-rusting involves different mechanisms or components operating after the parasite infects the host. Parlevliet (1979a) categorized the components into resistance to infection, resistance to colonization and resistance to sporulation. These are accepted in general epidemiological terms, but they are usually subdivided into more significant components (Berger 1977, Parlevliet 1979a, Wilcoxson 1981) which can be easily studied and quantitatively measured (Martins et al. 1979).

Infection frequency (receptivity) is one of the main factors contributing to slow-rusting in wheat to P. graminis tritici and was reported to vary in effectiveness against different races (Mortensen and Green 1978). High and low receptivity in some wheat cultivars was reported to be controlled by one dominant gene in Idaed 59, one recessive gene in Lee and two recessive genes in Thatcher (Rowell and McVay 1979). With barley leaf rust, Parlevliet and Kuiper (1977) found that some partially resistant barley cultivars produced fewer uredia than susceptible ones

and when this was coupled with a longer latent period, lower infection frequencies resulted (Parlevliet 1977b, Parlevliet and Zadoks 1977). Luke et al. (1981) reported a 60-65 fold reduction in receptivity in the field as compared to growth chambers with slow-rusters to oat crown rust, whereas there were no significant differences with fast rusters. Low receptivity was also reported to be a prime factor responsible for slow-mildewing of wheat (Shaner 1973).

Latent period was found to be the most important and reliable component of partial resistance to barley leaf rust with a high correlation between the two traits (Parlevliet and Van Ommeren 1975, Neervoort and Parlevliet 1978). Similarly, high correlations between area under disease progress curve (AUDPC) and latent period were reported by Johnson and Wilcoxson (1978). Shaner and Finney (1980) found that the latent period was longer in slow-rusting compared to fast-rusting wheat cultivars and concluded that latent period is the component of resistance measured with the least error. Latent period could be the most stable selection criterion on a large scale in greenhouse screening (Parlevliet 1977b). Latent period was estimated to be controlled by three to six genes in the barley cultivars Sultan, Volla, Julia and Vada, with these genes acting in an additive manner (Parlevliet 1978). Another important factor of latent period in partial resistance is its effect on the onset of the next cycle of spore production as well as the growth rate of the parasite in the host plant (Neervoort and Parlevliet 1978).

Lesion size reflects the growth rate of the parasite in the host. Resistant corn cultivars reacted by producing smaller lesion types in response to Helminthosporium spp. than susceptible cultivars (Johnson and Taylor 1976). Krull et al. (1965) also reported that oat cultivars resistant to

P. graminis tritici bore small uredia compared to susceptible ones. Ohm and Shaner (1976) found that smaller uredia, especially on the younger leaves, characterized the resistance of two wheat cultivars to P. graminis tritici. Lesion size was also found to be an important component of slow-blasting of rice with large differences in lesion size between resistant and susceptible cultivars. Another type of host resistance to lesion size is related to a reduction in the rate of lesion growth.

The effect of host resistance on sporulation is dependent on, and related to, other components including infection frequency, latent period, lesion size and infectious period (Parlevliet 1979a). Mortensen and Green (1978) found that low spore production per pustule is an important factor in the resistance of the wheat cultivar Exchange. Neervoort and Parlevliet (1978) equated total spore production to the interaction between infection frequency, lesion size and infectious period, and found that barley cultivars vary greatly (ratio 1:7) in their capacity of spore production of P. hordei per unit area. Similarly, Villareal et al. (1981) found clear differences between resistant and susceptible rice cultivars to three isolates of Pyricularia oryzae and their spore production. Slow-mildewing on wheat was also attributed to both low receptivity and low spore production under low inoculum potential suggesting that low spore production seems to be limiting the disease development (Shaner 1973).

Resistance based on shortening the infectious period (the time that infectious propagules are produced on diseased host tissue) was demonstrated by Neervoort and Parlevliet (1978) and variation from 5-3 weeks of infectious period was reported between resistant and susceptible cultivars of barley to leaf rust. Sztejnberg and Wahl (1976) studied the patterns of spore production in Avena sterilis infected with P.

graminis avenae and found that besides the differences in total spore production between resistant and susceptible lines, there were also differences in the patterns and rates of spore production and this may have affected the total spore production.

Another component of slow-rusting is characterized by the high infection threshold (a minimum concentration of pathogen propagules necessary for infection) requirement (Berger 1977). Such varieties would have a slow rate of disease infection and few subsequent infections. Luke et al. (1972) associated this phenomenon with "late rusting" where concentrations of arriving fluxes of spores determine the incidence and severity of oat crown rust. The "late rusting" resistance seems to have a different mechanism than slow-rusting because such cultivars can be very susceptible later on during the season under the influence of heavy inoculum potential.

3.3.2 Stability of slow-rusting. For any kind of resistance to be long lasting, it has to be effective against many, if not all, variants of the pathogen and should remain effective over a long period of time under a wide range of geographical areas (Caldwell 1968). A recent review of the genetics of slow-rusting by Wilcoxson (1981) focused the attention on the stability of this trait. He reported that slow-rusting in the oat cultivar Red Rustproof to P. coronata f. sp. avenae has been stable for more than 100 years (Luke et al. 1972) and in the wheat cultivars, Thatcher and Lee, the slow-rusting character to P. graminis tritici, has also been stable for 55 and 30 years, respectively. Similarly, the winter wheat variety, Knox, has been shown to be a slow ruster with P. graminis tritici for more than 25 years (Ohm and Shaner 1976).

In other diseases, the slow development of potato late blight was

shown to maintain its stability (Caldwell 1968). Also, the slow-rusting of corn with Puccinia sorghi and P. polysora has been shown to be very stable for a long time (Robinson 1976 in Wilcoxson 1981).

It is generally believed that slow-rusting is a quantitative trait under polygenic control (Wilcoxson 1981). This was clearly shown in the wheat cultivars Thatcher, Lee, Marquis, Prelude and Barat to wheat stem rust (Ayers et al. 1981, Skovmand et al. 1978), in barley leaf rust (Johnson and Wilcoxson 1979), in wheat leaf rust (Gavinlertvatana and Wilcoxson 1978) and in oat crown rust (Luke et al. 1975).

On the other hand, some reports refer to slow-rusting character as race-specific. Browder (1973) found that the slow-rusting of "Bulgarie 88" wheat to leaf rust was a race-specific trait and could be overcome easily by certain strains of P. recondita. This agrees with the findings of Johnson and Taylor (1976) that slowing down the epidemic is not a long lasting type of resistance. The interaction between specific races and slow-rusting cultivars characterized by long latent period and reduced spore production was demonstrated by Parlevliet (1978) and Mortensen and Green (1978). Parlevliet (1978) suggested that the gene-for-gene system could be also functioning in slow-rusting host-parasite interactions. An interaction between race-specific resistance genes and genes controlling slow-rusting to wheat stem rust was demonstrated by Skovmand et al. (1978). They found that slow-rusting resistance is not controlled by race-specific genes and that additive gene action was predominent in the genetic control of slow-rusting. Ayers et al. (1981) used the AUDPC as a measure of slow-rusting and found no association between that and the number of resistance genes in the host. In some cases, the increased numbers of resistance genes in the host caused an increase in AUDPC

measurement. These findings by Ayers et al. (1981) do not agree with Nelson's (1978) approach for pyramiding genes for a "rate-reducing" resistance.

Transgressive segregation was demonstrated in each cross between slow and fast rusting wheat cultivars to P. graminis tritici (Skovmand et al. 1978) leaf rust of barley (Johnson and Wilcoxson 1979) and in winter wheat leaf rust (Gavinlertvatana and Wilcoxson 1976). The presence of transgressive segregation was also demonstrated in crosses between 10 cultivars of wheat resistant to stripe rust, P. striiformis West., where many F_4-F_6 plant progenies were more resistant than the parental cultivars (Lewellen et al. 1967, Krupinsky and Sharp 1979).

The heritability of slow-rusting in cereal crops has been studied by different researchers and was estimated to range between 46-92% (Luke et al. 1975, Gavinlertvatana and Wilcoxson 1978, Skovmand et al. 1978). Wilcoxson (1981) pointed out that the interest in slow-rusting has increased greatly in the last 10 years due mainly to its stability. Similarly, Luke et al. (1975) suggested breeding for slow leaf-rusting resistant wheat cultivars and anticipated that slow-rusting should play a more important role in protecting crops from disease epidemics in the future.

3.3.3 Measurement and selection for slow-rusting. Assessment of slow-rusting resistance is done by monitoring and studying the development of disease severity during the growing season. Data accumulated from the series of disease evaluations can be summarized by calculating the infection rate

$$r = \frac{2.3}{t_2-t_1} \log 10 \frac{x_2(1-x_1)}{x_1(1-x_2)}$$ as proposed by Vanderplank (1963),

or by calculating the area under the disease progress curve AUDPC = $\sum_{i=1}^{K} 1/2(S_i+S_{i+1})$ (Wilcoxson et al. 1975).

Although Statler et al. (1977) found that the infection rate measurements gave significant differences among wheat varieties infected with P. recondita tritici, the infection rate was reported to be less convenient than the AUDPC and not as reliable in evaluating wheat cultivars and their ability to retard the development of P. graminis tritici (Wilcoxson et al. 1975). Vanderplank (1963) suggested that r-values are more accurate when estimated at the early phase of disease development. Shaner and Finney (1977), working with slow-mildewing on wheat found that early in the season the infection rate was strongly influenced by minor differences in disease severity and the stage of crop development while the AUDPC was only slightly affected and thus it was considered to be more reliable for slow-mildewing assessment. Wilcoxson et al. (1975) found that the AUDPC is a more reliable and convenient method than the r-value and that the differences among wheat cultivars infected with P. graminis tritici were distinct and consistent from one trial to another. The AUDPC is thus the most common method used for evaluating slow-rusting and comparing disease development (Wilcoxson et al. 1975, Shaner and Finney 1977, Johnson and Wilcoxson 1978, Skovmand et al. 1978).

Screening in small adjacent plots is commonly used to evaluate slow-rusting between different cultivars. Vanderplank (1963) pointed out that testing in adjacent plots tends to underestimate the partial resistance (horizontal resistance). Parlevliet and Van Ommeren (1975) studied partial resistance among 16 barley cultivars to P. hordei in

(i) adjacent single-row plots, (ii) 1-m square plots separated by 2-m of slow rusting barley, (iii) small 3x4-m isolated plots, as well as the latent period at the seedling and adult plant stages. Their results from single-row adjacent plots and the 1-m separated plots were essentially the same (correlation coefficient = 0.95). Similarly, the correlation coefficient between adjacent and isolated plots was very high (r = 0.95 and 0.96). The latent period of the adult plant stage was also highly correlated with partial resistance (r = 0.94), with a lower correlation between latent period of seedling stage and partial resistance (r = 0.57). These results indicate that selection for partial resistance (slow-rusting) is fairly easy and can be done either in small adjacent plots in the field or by selecting for longer latent period in adult plants in the greenhouse.

Parlevliet et al. (1980) evaluated the partial resistance of 40 Western European barley cultivars to P. hordei and reported significant correlations for latent period between adjacent and isolated plots but the correlations were not as high as those reported by Parlevliet and Van Ommeren (1975). Data from small adjacent plots were believed to underevaluate the partial resistance due to the inter-plot interference which was relatively small. Parlevliet et al. (1980) suggested that selection at the seedling stage is most effective when based on latent period and least effective when based on infection frequency while the most effective selection is done in small adjacent plots in the field.

Johnson and Wilcoxson (1978, 1979) showed a high and significant correlation between AUDPC and the latent period in wheat stem rust as well as highly effective selection for barley leaf rust resistance based on the latent period. They suggested that selection for slow-rusting

could be practised in the field using the AUDPC and in the greenhouse using the latent period which is more effective and reliable than using the infection frequency. Wahl et al. (1980) reported on slow-rusting resistance to wheat stem rust in the greenhouse and concluded that selection for latent period and uredial size would be a very promising criterion for slow-rusting resistance.

4. Breeding Strategies for Disease Resistance

4.1 Monogenic Lines

The use of race-specific genes for resistance has been and continues to be an effective way of protecting many crops from disease epidemics provided they are handled carefully (Day 1974). Although monogenic resistance has been in use in Canadian wheat cultivars released since the early 50's, the cultivars with enduring resistance were reported to have many genes for resistance in different combinations (Green and Campbell 1979). This employs the use of pure line cultivars carrying specific genes for resistance against the most prevailing races of the pathogen. The advantage of using race-specific resistance is that it is readily transferred and yields rapid results. Since race-specific genes are simply inherited they can be bred into different varieties using the simple conventional breeding methods. The stability of monogenic resistance is unpredictable and may break down under any minor changes (a mutation for virulence or aggressiveness, sexual or somatic hybridization) in the pathogen populations (Nelson 1973, 1978, Day 1974). Using monogenic resistance requires tremendous survey effort to monitor the race-population in the agro-ecosystem and continuous search for race-specific resistance genes to counteract any shift in the pathogen population. It also necessitates fast incorporation of the new resistance genes into the cultivars and immediate release to farmers to replace the "defeated"

monogenic resistance. On the other hand, the employment of new resistance genes may disrupt the balance between host and pathogen by exerting high selection pressure on the pathogen for acquiring virulence genes (Johnson 1961, Ellingboe 1981). The use of monogenic resistant cultivars means a high level of crop uniformity and sometimes a narrow genetic base. This increases the vulnerability of the crop and often leads to serious disease epidemics (Horsfall et al. 1972) and was referred to by Day (1974) as a "technological hazard".

4.2 Multilines

The multiline concept has been introduced to incorporate greater variability and diversity into the self-pollinated crops by using isogenic or near-isogenic lines carrying different race-specific resistant genes (Nelson 1973, Day 1974, Parlevliet 1979b). Browning and Frey (1969) found that since the multiline cultivars carry different genes for specific resistance, they act by reducing the initial inoculum and subsequently lower the rate of disease progress. Similarly, Nelson (1973) believed that multilines exhibit both vertical as well as horizontal resistance by reducing the initial inoculum available for successful infections and curb the subsequent increase in disease severity. A multiline cultivar usually utilizes several resistant genes (7-12 genes according to Nelson 1973, Day 1974) and may confer more stable and durable resistance over a wide area by acting as a buffer for any new virulence races. Nelson (1973) believed that it is unlikely that a race would acquire all the necessary virulence genes to overcome all the resistance genes in a multiline cultivar, but it still could acquire some of the necessary virulence genes and end up with the occurrence of some disease. In this case, new lines with different specific

resistance genes could always be added to the multiline or substituted for the ones with highly susceptible background (Nelson 1973, Parlevliet 1979b).

Another point of view expressed by Hooker (1967) is that extensive use of multiline cultivars will result in heterogeneous rust populations with biotypes collectively virulent on all components of the multiline cultivars. Little work has been done in this area but Parlevliet (1979b) believes that stabilizing selection has little or no importance in preventing the development of complex races. Careful selection of components of the multilines based on levels of stabilizing selection associated with each virulence gene in the pathogen may be capable of maintaining the effectiveness of the multiline (Groth 1976). The durability of multilines is related to the number of component lines, the level of stabilizing selection, the efficiency in monitoring the pathogen variability and the replacement of some components when needed (Parlevliet 1979b).

Multilines are believed to have another mechanism for disease control through induced resistance. Johnson and Allen (1975) worked with induced resistance on host and non-host pathogens and pointed out that multilines with a mixture of both susceptible and resistant lines could provide a suitable environment for induced resistance which would probably contribute to the resistant mechanism of the multilines.

The advantage of multilines lies in the diversity of resistance genes used. However, they are practically uniform in all other aspects and this makes them very vulnerable to other pathogens (Day 1974). Therefore, a compromise has to be reached between demands for uniformity and the advantages of diversity.

4.3 Gene-Pyramiding

The failure of race-specific (vertical) genes for resistance in monogenic lines to counteract the shift in wheat stem rust, oat crown and stem rust and potato late blight focused the attention on producing multigenic lines. This involves the formation of double, triple or multigenic barrier by incorporating several race-specific genes into a single genetic background. The effectiveness of multigenic lines is associated with the difficulty in acquiring two, three or more simultaneous changes for virulence in a new race of the pathogen (Nelson 1973, Parlevliet 1979b).

Careful selection of these gene combinations in different cultivars is very essential especially in a confined geographical area, in order to avoid any stepwise change in virulence and subsequently a complete destruction of the multigenic cultivars (Knott 1972, Parlevliet 1979b). Nelson (1978) pointed out the modifying effect of major and minor genes and their role in conditioning horizontal resistance. He also reviewed the additive effect of resistance genes and suggested that genes act vertically when they are separate and horizontally when they are together in one background. The accumulation of several vertical genes for resistance to wheat stripe rust showed an additive effect and this was expected to be a long-lasting effect (Sharp 1972). Parlevliet (1976) showed that the greater the number of specific genes for resistance to P. hordei in barley cultivars the longer is the latent period.

4.4 Gene Deployment

Some parasites persist in large geographical areas and move within its epidemiological subunits between seasons along with crop development and prevailing winds such as the Puccinia pathway in Central North

America. It has been suggested that the use of different resistance genes in different regions along the geographic range of the pathogen movement may interfere with the yearly epidemic development and the formation of complex races (Nelson 1973, Parlevliet 1979b). However, Nelson (1973) pointed out that geographical gene deployment carries a risk of severe disease loss in one region where pathogen races have acquired the matching virulence genes while in the meantime protecting the other regions.

A high degree of co-operation is essential for the success of the gene deployment to ensure that many different genes are deployed in each region without duplication since a few genes may be inadequate and any duplication of genes may enable the pathogen to bridge the gap between regions (Day 1974).

RESULTS OF RESEARCH

1. Evaluation of Resistance in *Vicia faba* to Two Isolates of Rust *Uromyces viciae-fabae* from Manitoba

ABSTRACT

Faba bean (*Vicia faba* L.) accessions from various regions of the world were evaluated to single-pustule isolates SP3 and SP51 of the rust, *Uromyces viciae-fabae* (Pers.) Schroet. in the greenhouse. Accessions with at least one resistant plant (infection type 0-2) were common and a few accessions with several resistant plants were also observed.

After three cycles of testing and selfing, 117 homozygous lines were grouped into nine classes on the basis of their reactions to the two rust isolates. Eleven lines showed a high level of resistance (infection type 0-;) to both rust isolates and eight lines showed a high level of resistance to SP51 but were moderately resistant (infection type 1-2) to SP3. Additional useful combinations of resistance included lines with moderate resistance to SP51 and high to moderate resistance to SP3 and lines with a high level of resistance to SP3 and moderate resistance to SP51. The resistant accessions were from various regions of the world.

INTRODUCTION

The rust fungus, Uromyces viciae-fabae (Pers.) Schroet,, is a major disease of faba beans (Vicia faba L.) in the Middle East and North Africa where epidemics causing yield losses of up to 20% often occur (Bekhit et al. 1970; Mohamed 1981). The rust has also been reported in both Manitoba and Saskatchewan on this crop since its introduction into Western Canada in 1970 (Bernier 1975; McKenzie and Morrall 1975).

The three subspecies of V. faba, major, equina and minor, are characterized by a high degree of cross-pollination (Poulsen 1975) which may reach 70% (Holden and Bond 1960). The heterogeniety of the crop is reflected in the lack of uniformity in the reaction of cultivars to both rust (Kispatic 1944, 1949; Conner 1981) and to chocolate spot, Botrytis fabae Sard. (Jennifer and Whittington 1979). The failure to find resistance to rust in previous attempts has been attributed to a lack of cultivar uniformity (Kispatic 1944, 1949) or to the absence of resistance (Hiratsuka 1933, 1934). Recently, Conner (1981), in Manitoba, tested 17 cultivars and accessions of faba bean to two single-pustule isolates (SP3 and SP51) of rust with distinct virulence patterns. After three generations of selfing, three lines were uniformly resistant to isolate SP3 and one line to both isolates SP3 and SP51.

The purpose of this study was to evaluate faba bean accessions from various regions of the world to rust isolates from Manitoba with a view to finding additional sources of resistance and to determine the distribution of resistance in germplasm collections. Accessions with resistance to individual isolates were repeatedly tested and selfed to provide homozygous inbred lines for genetic studies.

MATERIALS AND METHODS

Seventy-six faba bean accessions from various regions of the world provided by the International Center for Agricultural Research in the Dry Areas (ICARDA) were evaluated in addition to the susceptible line, 2N40 (PI222128) and four cultivars (Ackerperle, Diana, Erfordia and Herz Freya) presently grown in Western Canada. Eight seeds of each accession or cultivar were planted in two 15-cm clay pots using a 2:1:1' (v/v) mixture of soil, sand and peat. The two youngest fully developed leaves of the seedlings were inoculated with a suspension of uredospores in a light oil (Soltrol 170, Philips Petroleum Co. Special Products Div., Borger TX 79007) with a fine nylon brush. After drying, the seedlings were incubated at 100% relative humidity for 24 hr and then moved into the growthroom at a photoperiod of 16 hr and a night and day temperature of 15-20^{o} C. The seedlings were scored for infection type (Table 1) after 11-12 days and selected plants were saved for selfing and seed increase.

In the first two cycles of testing, a mixture of rust isolates was used as inoculum while in the third cycle two single-pustule isolates (SP3 and SP51) with distinct virulence patterns (Conner 1981) were used. Plants were first inoculated with the less virulent isolate (SP3) and scored for infection type after 11 days. The infected leaves were removed and the plants were then inoculated with isolate SP51 and were treated as outlined for isolate SP3.

Uredospores were increased on 2-week-old plants of the susceptible line PI222128, with standard procedures to prevent contamination (Green

TABLE 1. Infection types of Uromyces viciae-fabae on Vicia faba and Pisum sativum.

Infection type	Cultivar reaction	Reaction class
0	No sign of infection	Immune
;	Necrotic flecks	Hypersensitive
1	Uredia minute, barely sporulating	Very resistant
2	Uredia small (about .5 mm in diameter)	Resistant
3	Uredia large (about 1.0 mm in diameter)	Susceptible
4	Uredia very large (> 1.0 mm in diameter)	Very susceptible

Modified from Conner (1981).

1981; Appendix 1). The inoculated plants were covered with polyvinyl tubes, incubated at 100% relative humidity for 24 hr and then moved to the greenhouse where the tubes were connected to a source of filtered air to prevent cross-contamination of isolates and the build up of moisture under the tubes. Uredospores were collected two to three times with a cyclone spore collector (Browder 1971) and stored at 5^{o} C for 2-3 months.

RESULTS AND DISCUSSION

All the accessions and cultivars tested expressed considerable variability in their reaction to rust when inoculated with a mixture of isolates. However, accessions with at least one resistant plant (infection type 0-2) were common and a few accessions had several plants with resistant to highly resistant reactions. The variability can be attributed to the heterozygosity of the accessions as well as to the use of a mixture of rust isolates. Progenies from 239 selfed single plant selections with resistance were subjected to a second cycle of testing and reselection. The level of heterogeniety within the selections was reduced considerably in the second cycle of selfing and 199 single resistant plants (infection type 0-2) were selected for a third cycle of testing to single-pustule isolates SP3 and SP51. One hundred and seventeen selections from the third selfing (S_3), homozygous for infection type to either one or both rust isolates (Appendix 2) were grouped into nine classes based on their reaction to the rust isolates (Table 2).

Resistance to isolate SP51 was less common than to isolate SP3: 63 S_3 lines showed resistance to SP51 in comparison to 100 lines with resistance to SP3 (Appendix 2). These results support Conner's (1981) findings that isolate SP51 is more virulent than isolate SP3.

Eleven S_3 lines possessed a high level of resistance (0-;) to both isolates (Class 1 Table 2) and eight lines possessed a high level of resistance (0-;) to isolate SP51 and a moderate level of resistance (1-2) to isolate SP3 (Class 2 Table 2). In addition, five S_3 lines showed high to moderate resistance to SP51 but were susceptible to SP3

TABLE 2. Classification of S_3 faba bean inbred lines based on their reaction to isolates SP3 and SP51 of Uromyces viciae-fabae.

Class	Reaction to rust[1]		Accession number[2] and regions of origin[3]
	SP3	SP51	
1	HR	HR	2N311 (NA), 2N319 (EU), Ackerperle (EU), Erfordia (EU), ILB96 (CA), ILB403 (NA), ILB431 (NA), ILB479 (EA), ILB866 (EU), ILB919 (NA), ILB938 (SA)
2	MR	HR	2N192 (ME), 2N319 (EU), 2N255 (ME), 2N441 (NA), ILB315 (EU), ILB411 (EU), ILB479 (EA), ILB920 (NA)
3	S	HR	2N168 (CA), 2N319 (EU), ILB920 (NA)
4	S	MR	2N281 (CA), ILB Giza 3 (EA)
5	S	S	2N34 (EA), 2N122 (EU), 2N285 (EU), 2N319 (EU), Herz Freya (EU), ILB534 (EA)
6	MR	S	2N26 (EU), 2N34 (EA), 2N122 (EU), 2N285 (EU), 2N319 (EU)
7	HR	S	2N168 (CA), 2N175 (CA), 2N255 (ME), 2N285 (EU), 2N319 (EU), 2N431 (EA), 2N432 (EA), 2N435 (NA), ILB75 (EU), ILB335 (EU), ILB431 (NA), ILB490 (CA), ILB534 (EA), ILB864 (EU)
8	HR	MR	2N311 (NA), 2N319 (EU), 2N382 (ME), 2N435 (NA), Diana (EU), Erfordia (EU), Herz Freya (EU), ILB96 (CA), ILB226 (ME), ILB318 (EU), ILB335 (EU), ILB403 (NA), ILB431 (NA), ILB490 (CA), ILB919 (NA)
9	MR	MR	2N431 (EA), ILB335 (EU)

[1]Reaction to rust: HR = highly resistant with infection types 0-;
MR = moderately resistant with infection types 1-2
S = susceptible with infection types 3-4

[2]Letters preceding accession numbers refer to faba bean collections
2N = University of Manitoba collection
ILB = International Legume faba bean collection at ICARDA

[3]Letters between brackets refer to region of origin
EA = East Africa; NA = North Africa; CA = Central Asia;
ME = Middle East; EU = Europe; SA = South America

(Classes 3 and 4 Table 2).

Twenty-nine S_3 lines characterized as highly resistant (0-;) to isolate SP3 were either susceptible (3-4) or moderately resistant (1-2) to isolate SP51 (Classes 7 and 8 Table 2). Seven additional S_3 lines characterized as moderately resistant (1-2) to isolate SP3 were also either susceptible (3-4) or moderately resistant (1-2) to isolate SP51 (Classes 6 and 9). Susceptibility to both isolates SP3 and SP51 was expressed only in six S_3 lines (Class 5).

Resistance specific to rust isolates from Manitoba was present in accessions and cultivars originating from various regions of the world (Table 2), suggesting that the accessions had been exposed previously to rust isolates identical to SP3 and SP51 either in the various regions or in the center of origin of Vicia faba which is believed to be in the Near East (Cubero 1973).

Minor characters of the host reaction such as chlorotic and necrotic zones surrounding the rust pustules were observed occasionally and found to be influenced by environmental conditions rather than by host genotypes. Such characters were not useful in further characterization of the infection type.

Accessions such as 2N319 and ILB431 gave rise to several single plant selections homozygous for a range of resistant infection types to each rust isolate indicating that the accessions are heterogenous populations of several resistant genotypes. The range of resistant reactions (infection types 0-2) observed in this study was greater than that reported by Conner (1981) who found only infection types 0 or ;. The high and moderate sources of resistance identified in this study could be useful in developing faba bean cultivars with durable rust resistance based on

either gene pyramiding (Sharp 1972, Green 1981, Nelson 1978) or multi-lines (Browning and Frey 1969, Nelson 1973, Marshall 1977).

2. Inheritance of Specific Resistance in *Vicia faba* to Two Isolates of *Uromyces viciae-fabae* from Manitoba

ABSTRACT

Inheritance of resistance to two isolates SP3 and/or SP51 of rust (*Uromyces viciae-fabae* Pers. Schroet.) from Manitoba was investigated in 10 faba bean (*Vicia faba* L.) inbred lines and four field selections. A series of crosses involving these hosts was made and the F_1 and F_2 generations were studied.

Eight genes for resistance were identified in the various inbred lines and field selections. The genes Fr1 in the field selections Ack-A, 2N43 and 2N43-A; Fr5 in ILB938-8 and Fr8 in ILB159-1, ILB159-4 and Diana-2 provide resistance to SP3. Two additional genes Fr6 in ILB938-8 and Fr9 in ILB159-4 condition resistance to SP51. Three genes for resistance to both isolates were detected: Fr2 in Erf-2 and 2N5; Fr4 in Erf-2 and Fr7 in ILB938-8, ILB479-7 and ILB159-1. The results also showed that susceptibility to the rust isolate SP3 in susceptible parent 2N40-5 is dominant or epistatic to the resistance in some moderately resistant lines. Crosses between faba bean field selections such as 2N5, 2N43, 2N43-A and Ack-A revealed that these lines may have additional non-identified genes for resistance.

INTRODUCTION

Faba bean rust, Uromyces viciae-fabae (Pers.) Schroet. causes severe losses in many faba bean growing areas of the world (Williams 1978, Mohamed 1981). In Manitoba and Saskatchewan, the rust has been reported on this crop since its introduction into Western Canada in 1970 (Bernier 1975, McKenzie and Morrall 1975) and a pathotype of the rust virulent on the commercial cultivars was identified (Conner 1981). Faba bean cultivars do not react uniformly to individual rust isolates (Kispatic 1944, 1949, Ibrahim and Nassib 1979, Conner and Bernier 1982a) due to the partially out-crossing nature of the crop (Holden and Bond 1960, Poulsen 1975, Hawtin and Omar 1981b). Recently, three genes conferring immunity to certain rust isolates from Manitoba have been identified using inbred faba bean lines (Conner and Bernier 1982b).

This study was carried out to investigate the genetics of resistance in 10 faba bean inbred lines from various regions of the world to two isolates of Uromyces viciae-fabae from Manitoba. Attempts were also made to establish the relationship between the resistance genes in the inbred lines and four field selections.

MATERIALS AND METHODS

Ten faba bean inbred lines with uniform reaction to rust isolates SP3 and SP51 after three cycles of selfing (Thesis section 1), and four heterogeneous faba bean field selections with resistance were used in this study. The origin and infection type (IT) of the inbred lines and the field selections to the rust isolates are presented in Table 1. The reaction of the inbred lines to each rust isolate was confirmed in the field at two separate sites in 1980.

Plants were grown in 7.5-cm peat pots (20/flat) in a rust free greenhouse at 16-20^{o} C under a 16 hr photoperiod. After testing and scoring for infection types,the plants were transplanted into 15-cm clay pots using 2:1:1 (V/V) mixture of soil, sand and peat. Reciprocal crosses were made between each resistant inbred line and the susceptible lines Herz Freya (HF-7) and 2N40-5 (PI222128) as well as between resistant inbred lines. Reciprocal crosses were also made between the field selections and the resistant inbred line Erf-2 as well as between the field selections.

The seedlings of F_1 and F_2 populations were tested sequentially to the two rust isolates as described previously (Thesis section 1) using the less virulent isolate SP3 in the first inoculation, followed by isolate SP51. Parental lines were included in all tests to ensure that the rust isolates were free of contaminations. Each rust isolate was increased in isolation on the susceptible line 2N40 (PI222128) following the procedure described previously (Thesis section 1; Appendix 1). Plants were categorized as susceptible or resistant based on the infection type (Thesis section 1; Table 1). Results from the F_2 families of the same

cross were pooled only when the Chi-square test for homogeneity and the Chi-square test for independence (Contingency Chi-square) had shown them to behave the same (Cochran and Cox 1957). The Chi-square test for goodness of fit was used to analyze the data from all the F_2 progenies.

TABLE 1. Identity, origin and infection type of faba bean inbred lines and field selections to rust isolates SP3 and SP51.

Inbred line*	Origin	Infection Type	
		SP3	SP51
ILB938-8	Colombia	0	0
Erf-2	Germany	0	2
ILB479-7	Ethiopia	1	1
ILB159-1	Greece	; 1	2
ILB159-4	Greece	2	2
Diana-2	Germany	1	4
ILB335-6	Egypt	2	2
ILB534-2	Ethiopia	2	4
HF-7	Germany	4	4
2N40-5	Afghanistan	4	4
Field selections**			
2N5	England	0	0 3†
2N43	Afghanistan	0 1	0 3
2N43-A	Afghanistan	0 ;	0 3
Ack-A	Germany	0 ;	2 3

*Inbred lines were selfed 3 times (S_3) before crossing.

**Field selections were not selfed before crossing.

†Some plants have infection type 0 while others have infection type 3.

RESULTS

Resistance Genes in Inbred Lines

The final analysis of the data includes pooled results from crosses and their reciprocals since there were no differences between the F_1's in each and every cross.

The F_1 progenies from the crosses between the resistant line ILB938-8 (IT 0 to SP3 and SP51) and the susceptible lines HF-7 and 2N40-5 were all resistant (Table 2). The F_2 populations from these crosses segregated in a ratio of 15 resistant:1 susceptible to each of the rust isolates (Table 3), supporting the hypothesis that ILB938-8 carries two dominant genes for resistance to each rust isolate. The combined data for both isolates produced a good fit of 57:3:3:1 ratio of resistant:susceptible (Table 4), indicating that ILB938-8 has a total of three genes for resistance, one for each rust isolate and one common to both isolates.

Crosses involving line Erf-2 (IT 0 to SP3, IT 2 to SP51) and the susceptible lines HF-7 and 2N40-5 produced only resistant F_1 plants (Table 2). The F_2 populations from two families in each cross segregated in a ratio of 15 resistant:1 susceptible to each rust isolate, however, three and two families from each cross respectively, segregated in a 3 resistant:1 susceptible ratio (Table 3). The combined data from all the families in each cross best fit a 27 resistant:5 susceptible ratio (i.e. half the F_1 plants heterozygous at both loci and half homozygous recessive at one locus), supporting the hypothesis that Erf-2 has two dominant genes for resistance, only one of which is homozygous. The two

TABLE 2. Reaction to rust isolates SP3 and SP51 in F_1 populations from crosses between faba bean inbred lines and field selections.

Cross	SP3		SP51	
	Parent reactions	F_1 R:S	Parent reactions	F_1 R:S
ILB938-8 X HF-7	RXS	52:0	RXS	52:0
ILB938-8 X 2N40-5	RXS	52:0	RXS	52:0
Erf-2 X HF-7	RXS	40:0	RXS	40:0
Erf-2 X 2N40-5	RXS	54:0	RXS	54:0
ILB938-8 X Erf-2	RXR	70:0	RXR	70:0
ILB479-7 X HF-7	RXS	51:0	RXS	51:0
ILB159-1 X HF-7	RXS	62:0	RXS	62:0
ILB159-4 X HF-7	RXS	63:6	RXS	66:3
Diana-2 X HF-7	RXS	58:8	SXS	0:66
ILB335-6 X HF-7	RXS	4:61	RXS	2:63
ILB534-2 X HF-7	RXS	0:79	SXS	0:79
ILB479-7 X 2N40-5	RXS	0:24	RXS	24:0
ILB159-1 X 2N40-5	RXS	53:0	RXS	53:0
ILB159-4 X 2N40-5	RXS	0:34	RXS	34:0
Diana-2 X 2N40-5	RXS	0:41	SXS	0:41
ILB534-2 X 2N40-5	RXS	0:63	SXS	0:63
ILB538-8 X ILB479-7	RXR	59:0	RXR	59:0
ILB938-8 X ILB159-1	RXR	34:0	RXR	34:0
Erf-2 X ILB479-7	RXR	55:0	RXR	55:0
ILB479-7 X ILB159-1	RXR	96:0	RXR	96:0
ILB159-4 X Diana-2	RXR	98:0	RXS	98:0
ILB335-6 X ILB534-2	RXR	65:6	RXS	59:2
HF-7 X 2N40-5	SXS	0:46	SXS	0:46
2N5 X Erf-2	RXR	103:0	RXR	55:48
2N5 X 2N43	RXR	87:2	RXR	35:54
2N43 X Erf-2	RXR	91:0	RXR	84:7
2N43-A X Ack-A	RXR	58:0	RXR	58:0

TABLE 3. Segregation of reactions to rust isolates SP3 and SP51 in F_2 populations from crosses between faba bean inbred lines.

Parents	Isolate SP3					Isolate SP51				
	Parent reaction	No. of families	Observed R:S	Expected R:S	Chi-Square prob.	Parent reaction	No. of families	Observed R:S	Expected R:S	Chi-Square prob.
ILB938-8 X HF-7	RXS		272:17	15:1	.50-.30	RXS		269:20	15:1	.70-.50
ILB938-8 X 2N40-5	RXS		279:25	15:1	.20-.10	RXS		280:24	15:1	.30-.20
Erf-2 X HF-7	RXS	2	63:5	15:1	.90-.70	RXS	2	62:5	15:1	.90-.70
		3	107:34	3:1	.90-.70		3	104:37	3:1	.90-.70
Erf-2 X 2N40-5	RXS	2	79:8	15:1	.30-.20	RXS	2	79:8	15:1	.30-.20
		2	71:21	3:1	.70-.50		2	71:21	3:1	.70-.50
ILB938-8 X Erf-2	RXR		165:4	63:1	.50-.30	RXR		165:4	63:1	.50-.30
ILB479-7 X HF-7	RXS		134:42	3:1	.90-.70	RXS		139:37	3:1	.30-.20
ILB159-1 X HF-7	RXS		123:40	3:1	.90-.70	RXS		127:36	3:1	.90-.70
ILB159-4 X HF-7	RXS		233:92	3:1	.20-.10	RXS		231:95	3:1	.20-.10
Diana-2 X HF-7	RXS		135:54	3:1	.30-.20	SXS		21:168	0:1	
ILB335-6 X HF-7	RXS		59:200	3:13	.20-.10	RXS		59:200	3:13	.20-.10
ILB534-2 X HF-7	RXS		60:238	3:13	.70-.50	SXS		35:263	0:1	
ILB479-7 X 2N40-5	RXS		62:229	3:13	.30-.20	RXS		211:72	3:1	.90-.70
ILB159-1 X 2N40-5	RXS		136:65	3:1	.05-.01	RXS		140:61	3:1	.10-.05
ILB159-4 X 2N40-5	RXS		57:200	3:13	.20-.10	RXS		192:56	3:1	.95-.90
Diana-2 X 2N40-5	RXS		53:193	3:13	.30-.20	SXS		30:213	0:1	
ILB534-2 X 2N40-5	RXS		73:242	3:13	.10-.05	SXS		22:295	0:1	
ILB938-8 X ILB479-7	RXR		172:0	1:0		RXR		172:0	1:0	
ILB938-8 X ILB159-1	RXR		174:0	1:0		RXR		174:0	1:0	
Erf-2 X ILB479-7	RXR		183:5	63:1	.30-.20	RXR		181:7	63:1	.05-.01
ILB479-7 X ILB159-1	RXR	7	334:20	15:1	.70-.50	RXR	7	354:0	1:0	
		4	164:0	1:0			4	164:0	1:0	
ILB159-4 X Diana-2	RXR		400:0	1:0		RXS		287:113	3:1	.20-.10
ILB335-6 X ILB534-2	RXR		265:51	27:5	.90-.70	RXS		238:78	3:1	.90-.70
HF-7 X 2N40-5	SXS		1:180	0:1		SXS		4:177	0:1	

TABLE 4. Relation of resistance to rust isolates SP3 and SP51 in F_2 populations derived from crosses between resistant X susceptible faba bean inbred lines.

Cross	Number of plants not infected	Number of plants infected by SP3 only	Number of plants infected by SP51 only	Number of plants infected by both isolates	Expected ratio	Chi-Square prob.
ILB938-8 X HF-7	260	9	12	8	57:3:3:1	.30-.20
ILB938-8 X 2N40-5	265	15	14	10	57:3:3:1	.70-.50
Erf-2 X HF-7	164	2	5	37	27:0:0:5	.10-.05
Erf-2 X 2N40-5	148	2	2	27	27:0:0:5	.90-.70
ILB479-7 X HF-7	133	1	6	36	3:0:0:1	.90-.70
ILB159-1 X HF-7	121	6	2	34	3:0:0:1	.05-.01
ILB159-1 X 2N40-5	132	7	3	58	3:0:0:1	.30-.20
ILB159-4 X HF-7	188	46	43	49	10:2:2:2	.30-.20

genes in Erf-2 control resistance against both rust isolates since the combined data best fit the ratio 27:0:0:5 of resistant:susceptible (Table 4).

The cross ILB938-8 (IT 0 to SP3 and SP51) X Erf-2 (IT 0 to SP3 and IT 2 to SP51) produced only resistant F_1 plants and a good fit to the ratio 63 resistant:1 susceptible in the F_2 populations for each rust isolate indicating that the two inbred lines carry different genes for resistance.

The F_1 plants from the crosses between the inbred lines ILB479-7 (IT 1 to SP3 and SP51) and ILB159-1 (IT ;1 to SP3 and IT 2 to SP51) with the susceptible line HF-7 were all resistant (Table 2). The F_2 populations segregated in a ratio of 3 resistant:1 susceptible to each isolate (Table 3) suggesting the presence of a single dominant gene conditioning resistance to each isolate. The dominant nature of the resistance gene(s) in ILB159-1 was confirmed by the resistance of the F_1 plants where this line was crossed to the susceptible line 2N40-5 and by a good fit of the F_2 data to a ratio of 3 resistant:1 susceptible (Table 3). The combined data against both isolates in the three crosses best fit the ratio 3:0:0:1 of resistant:susceptible suggesting that the genes in ILB479-7 and ILB159-1 condition resistance to both rust isolates (Table 4).

The cross ILB159-4 (IT 2 to SP3 and SP51) X HF-7 (IT 4 to SP3 and SP51) produced a few susceptible plants in the F_1 progeny (Table 2), and a ratio of 3 resistant:1 susceptible in the F_2 populations to each rust isolate (Table 3). However, the combined data against both isolates best fit the proposed ratio of 10:2:2:2 of resistant:susceptible supporting the hypothesis that ILB159-4 has two dominant genes for resistance, one for each rust isolate (Table 4).

The cross Diana-2 (IT 1 to SP3, IT 4 to SP51) X HF-7 (IT 4 to SP3 and SP51) produced eight susceptible and 58 resistant F_1 plants (Table 2), indicating that Diana-2 is not homozygous. The F_2 segregating populations best fit the ratio of 3 resistant:1 susceptible suggesting the presence of a single dominant gene for resistance in Diana-2 to SP3 (Table 3).

The line ILB335-6 (IT 2 to SP3 and SP51) gave susceptible F_1 plants when crossed with the susceptible line HF-7 (Table 2). The F_2 populations segregated in a ratio of 3 resistant:13 susceptible to each rust isolate indicating that susceptibility in HF-7 is either dominant or epistatic to the resistance in ILB335-6 (Table 3). Similar results were obtained when ILB534-2 (IT 2 to SP3, IT 4 to SP51) was crossed with the susceptible lines HF-7 and 2N40-5 in which all the F_1 plants were susceptible and the F_2 populations segregated in a ratio of 3 resistant:13 susceptible, suggesting that susceptibility in both HF-7 and 2N40-5 is either dominant or epistatic to the resistance in ILB534-2 (Tables 2 and 3).

The F_1 progenies from crossing ILB479-7 (IT 1 to SP3 and SP51) and ILB159-4 (IT 2 to SP3 and SP51) with the susceptible line 2N40-5 (IT 4 to SP3 and SP51) were susceptible to SP3 and resistant to SP51 (Table 2). The F_2 populations from these crosses segregated in a ratio of 3 resistant: 13 susceptible to SP3, indicating that susceptibility in 2N40-5 is dominant or epistatic to the resistance in ILB479-7 and ILB159-4. However, the good fit of the F_2 populations from both crosses into a ratio of 3 resistant: 1 susceptible to isolate SP51 confirms the dominant nature of resistance to this isolate in the two lines (Table 3). The dominant or epistatic nature of susceptibility in 2N40-5 to SP3 was also observed in the cross Diana-2 (IT 1 to SP3) X 2N40-5 (IT 4 to SP3 and SP51), where the F_1 progeny was susceptible and the F_2 data best fit a ratio of 3 resistant:13

susceptible (Table 3).

Crosses between the resistant lines ILB938-8 (IT 0 to SP3 and SP51) and ILB479-7 (IT 1 to SP3 and SP51) or ILB159-1 (IT ;1 to SP3 and IT 2 to SP51) produced only resistant plants in the F_1 and F_2 generations, indicating that the genes controlling resistance to both rust isolates in these lines are either identical, allelic or closely linked (Tables 2 and 3). However, the cross ILB479-7 (IT 1 to SP3 and SP51) X ILB159-1 (IT ;1 to SP3 and IT 2 to SP51) produced a 15 resistant:1 susceptible ratio in seven F_2 families to SP3, suggesting that ILB159-1 has another gene(s) conditioning resistance to SP3 (Table 3). The F_2 populations from the cross Erf-2 (IT 0 to SP3 and IT 2 to SP51) X ILB479-7 (IT 1 to SP3 and SP51) best fit the ratio 63 resistant:1 susceptible to each rust isolate (Table 3), indicating the presence of different genes for resistance in these two lines. The cross ILB159-4 (IT 2 to SP3 and SP51) X Diana-2 (IT 1 to SP3 and IT 4 to SP51) produced resistant plants in the F_1 and F_2 generations to SP3, suggesting that the genes controlling resistance to SP3 in both parents are identical, allelic or closely linked (Tables 2 and 3). The good fit of the F_2 populations into a ratio of 3 resistant: 1 susceptible to SP51 confirms the presence of a different gene for resistance to this isolate in ILB159-4 (Table 3). The segregation of the F_2 populations from the cross ILB335-6 (IT 2 to SP3 and SP51) X ILB534-2 (IT 2 to SP3 and IT 4 to SP51) into a ratio of 27 resistant:5 susceptible (i.e. half F_1 plants heterozygous at both loci and half homozygous recessive at one locus) to SP3 and into a ratio of 3 resistant:1 susceptible to SP51, suggesting the presence of different genes controlling resistance to SP3 in each line and that only one gene is homozygous (Table 3).

The F_1 and F_2 plants from the cross between the susceptible lines

HF-7 and 2N40-5 were susceptible to both isolates except for one and four F_2 plants which were found to be resistant to SP3 and SP51 respectively (Tables 2 and 3). It could be that these plants have escaped infection. Resistant plants were also observed when lines susceptible to SP51 such as ILB534-6 and Diana-2 were crossed to either HF-7 or 2N40-5 (Table 3). This resistance might be due to the presence of heterozygous genes for resistance in these lines as well as to escape from infection.

Resistance Genes in Field Selections

The crosses involving the field selections 2N5, 2N43, 2N43-A and Ack-A revealed the heterozygous nature of the genes for resistance in these selections. The crosses 2N5 (IT 0 to SP3 and IT 0-3 to SP51) and 2N43 (IT 0-1 to SP3 and IT 0-3 to SP51) to Erf-2 (IT 0 to SP3 and IT 2 to SP51) produced resistant F_1 plants to isolate SP3 and heterogeneous progenies to SP51, confirming the heterozygous nature of resistance to SP51 (Table 2). Susceptible plants were not observed in F_2 populations from the cross 2N5 X Erf-2 suggesting that these two parents carry the same gene(s) for resistance to SP3 and SP51 (Table 5). The grouping of F_2 families from the cross 2N43 (IT 0-1 to SP3 and IT 0-3 to SP51) best fit the ratios of 63:1, 15:1 and 3:1 resistant:susceptible plants to SP3 and SP51 suggests that the gene(s) conditioning resistance in these two parents are different (Table 5). The F_1 plants from the cross 2N5 (IT 0 to SP3 and IT 0-3 to SP51) X 2N43 (IT 0-1 to SP3 and IT 0-3 to SP51) were also resistant to SP3 and heterogeneous in their reaction to SP51, confirming the heterozygous nature of resistance to SP51 in the two parents (Table 2). However, four and three families in the F_2 populations from this cross segregated into a ratio of 15 resistant:1 susceptible and 3 resistant:1 susceptible respectively, to both rust isolates indicating

TABLE 5. Segregation of reactions to rust isolates SP3 and SP51 in F_2 populations from crosses between faba bean field selections.

Parents	Isolate SP3					Isolate SP51				
	Parent reaction	No. of families	Observed R:S	Expected R:S	Chi-Square prob.	Parent reaction	No. of families	Observed R:S	Expected R:S	Chi-Square prob.
2N5 X Erf-2	RXR		310:0	1:0		RXR		310:0	1:0	
2N5 X 2N43	RXR	4	193:13	15:1	.95	RXR	4	189:17	15:1	.30-.20
		3	27:12	3:1	.50-.30		3	25:14	3:1	.20-.10
2N43 X Erf-2	RXR	1	69:1	63:1	.95-.90	RXR	1	69:1	63:1	.95-.90
		3	152:13	15:1	.50-.30		3	152:13	15:1	.50-.30
		2	14:10	3:1	.10-.05		2	14:10	3:1	.10-.05
2N43-A X Ack-A	RXR		271:0	1:0		RXR		271:0	1:0	

that the gene(s) for resistance in these two parents are different (Table 5).

The cross between selections 2N43-A (IT 0; to SP3 and IT 0-3 to SP51) and Ack-A (IT 0; to SP3 and IT 2-3 to SP51) produced only resistant plants in F_1 and F_2 generations to both isolates (Tables 2 and 5), indicating that the gene(s) for resistance in the two parents are identical, allelic or closely linked. However, the gene conferring resistance in 2N5 and Erf-2 is different from the gene conferring resistance in 2N43, 2N43-A and Ack-A.

DISCUSSION

Crosses involving 10 faba bean inbred lines and four field selections revealed the presence of eight genes conditioning resistance to the rust isolates SP3 and SP51 (Table 6). The results of this study cannot be fully integrated with the recent findings of Conner (1981) who identified three genes for resistance to SP3 and SP51 in four faba bean inbred lines, because the studies were conducted concurrently and the resistant inbred lines were not inter-crossed. However, assuming that the genes in the inbred lines Ack-A and Erf-2 identified in this study are the same as genes Fr1 in Ack-11 and Fr2 in Erf-1-4 identified by Conner (1981), some of the genes can be tentatively identified (Table 6). The various selections originating from Ack and Erf need to be inter-crossed in order to establish the relationship of the genes involved.

The resistance genes designated as: Fr1 in Ack-A, 2N43 and 2N43-A; Fr2 in Erf-2 and 2N5; Fr5 in ILB938-8; Fr8 in ILB159-1, ILB159-4 and Diana-2 condition resistance to SP3. Furthermore, Fr2 was shown to condition moderate resistance (IT 2) to SP51. The genes designated as Fr6 in ILB938-8 and Fr9 in ILB159-4 condition resistance to SP51. Two additional resistance genes designated as Fr4 in Erf-2 and Fr7 in ILB938-8, ILB479-7 and ILB159-1 condition resistance to both isolates SP3 and SP51.

Further work is required in order to clarify the relationship between the resistance genes in the inbred lines ILB159-4, Diana-2, ILB335-6 and ILB534-2 or between these lines and ILB938-8, ILB159-1, ILB479-7 and Erf-2 because these lines were not inter-crossed in this study.

Inbred lines characterized by infection types 1 and 2 to isolate SP3

TABLE 6. Proposed genotypes of inbred lines and field selections of faba beans based on their reaction to rust isolates SP3 and SP51.

Parental lines	Proposed genotype
Inbred lines	
ILB938-8	fr2fr2fr4fr4Fr5Fr5Fr6Fr6Fr7Fr7
ILB479-7	fr2fr2fr4fr4fr5fr5fr6fr6Fr7Fr7
ILB159-1	fr2fr2fr4fr4fr5fr5fr6fr6Fr7Fr7Fr8fr8
Erf-2	Fr2Fr2Fr4fr4fr5fr5fr6fr6fr7fr7
ILB159-4	fr2fr2fr4fr4fr5fr5fr6fr6fr7fr7Fr8Fr8Fr9fr9
Diana-2	fr2fr2fr4fr4fr5fr5fr6fr6fr7fr7Fr8Fr8fr9fr9
Field selections	
2N5	Fr2Fr2
2N43	Fr1Fr1 , Rr
2N43-A	Fr1Fr1 , Rr
Ack-A	Fr1Fr1 , Rr

Fr1,Fr5 and Fr8 provide resistance to isolate SP3.

Fr6 and Fr9 provide resistance to isolate SP51.

Fr2, Fr4 and Fr7 provide resistance to both isolates SP3 and SP51.

such as ILB159-4, Diana-2 and ILB479-7 showed that resistance to SP3 is dominant when crossed to the susceptible parent HF-7 and recessive when crossed to the susceptible parent 2N40-5. Similar results were reported by Dyck and Samborski (1968) on the expression of the resistance genes $Lr_2 2$ and $Lr_2 4$ in wheat to Puccinia recondita Rob. ex Desm. f. sp. tritici and by McDaniel (1973) on the expression of resistance gene PC45 from Avena sterilis to crown rust Puccinia coronata avenae Eriks. The gene Fr7 was shown to condition infection types 0 in ILB938-8, 1 in ILB479-7 and 2 in ILB159-1, indicating that the expression of this gene is influenced by the genetic background of the inbred lines.

The high degree of heterogeniety in the field selections was reflected in the lack of uniformity in the F_1 progenies and in the poor fits of the F_2 segregating populations to the expected ratios in the crosses involving field selections (Tables 2 and 5). Nevertheless, resistance genes in heterozygous field selections could be identified by crossing them to inbred lines with known resistance genes. The task of identifying additional resistance genes in heterogeneous faba bean cultivars should be less difficult once a series of inbred lines with identified resistance genes is established.

3. Selection for Slow-Rusting Resistance in Faba Bean (*Vicia faba*) to the Rust *Uromyces viciae-fabae*

ABSTRACT

Evaluation of 253 open-pollinated faba bean accessions of diverse origin for their ability to retard the development of rust *Uromyces viciae-fabae* (Pers.) Schroet. was carried out in small adjacent plots during the period 1978 to 1981. A mixture of rust isolates from Manitoba was used in the first 2 years and single-pustule isolates SP3 and SP51 were used in subsequent years. Significant differences at the 1% level were found between accessions for the area under the disease progress curve (AUDPC) and the final disease severity in the various trials. Mass (MS) and single plant (SP) selections were made within accessions for the slow-rusting character. Eight selections from six accessions: 2N6 (MS), 2N29 (SP), 2N43 (MS and SP), 2N122 (SP), ILB938 (MS), ILB(332X133)A (MS) and ILB(332X133)B (MS) had consistently low AUDPC values and were considered slow-rusting. Four additional selections: 2N291 (MS), 2N319 (SP), ILB697 (MS) and ILB866 (MS) had intermediate AUDPC values and were considered moderate-rusting. Other accessions tested were either fast rusting or showed inconsistent AUDPC values from one year to another. Rust spread and development were also evaluated in isolated test plots using one slow-rusting, one moderate-rusting and one fast-rusting selection. The results obtained confirmed the adequacy of using small adjacent plots for slow-rusting evaluation of a large number of accessions.

INTRODUCTION

In the last few decades race-specific resistance has often been found to be short-lived and this has led to a search for more durable resistance (Johnson 1979). Epidemiological evidence suggests that slow-rusting resistance could be very effective against rust diseases of cereals (Caldwell 1968, Clifford 1972, Wilcoxson et al. 1975).

Slow-rusting is determined by measuring the apparent infection rate (AIR) or comparing the area under the disease progress curve (AUDPC) in various cultivars (Wilcoxson 1981). The AUDPC was found to be a more sensitive and reliable criterion for evaluating slow-rusting and slow-mildewing than the apparent infection rate (Wilcoxson et al. 1975, Shaner and Finney 1977). The AUDPC was also highly correlated with different components of slow-rusting such as latent period and number of uredia per leaf area (Parlevliet and Van Ommeren 1975, Johnson and Wilcoxson 1978, Neervoort and Parlevliet 1978). It is believed that rapid progress could be achieved by using AUDPC for slow-rusting selection in the field (Johnson and Wilcoxson 1978). In spite of the fact that movement of inoculum between small adjacent plots is very high and slow-rusting may be underestimated (Parlevliet and Van Ommeren 1975, Wilcoxson et al. 1975, Shaner and Finney 1980), large differences were apparent among cultivars, suggesting the usefulness of small adjacent plots in evaluating a large number of cultivars for slow-rusting (Gavinlertvatana and Wilcoxson 1978, Johnson and Wilcoxson 1980, Parlevliet et al. 1980).

Slow-rusting in faba beans has been recently demonstrated by Conner

(1981) in small adjacent plots: three accessions had consistently low AUDPC values while six other accessions had AUDPC values that shifted from low to intermediate over 3 years of testing.

The purpose of this study was to develop a system for evaluating large number of open-pollinated faba bean accessions of diverse origin for their ability to retard rust development in small adjacent plots and to assess the progress that can be made through mass selection and single plant selection over several years. One slow-rusting, one moderate-rusting and one fast-rusting selection were also evaluated in isolated test plots.

MATERIALS AND METHODS

Evaluation for Slow-Rusting in Small Adjacent Plots

One hundred and twenty-seven faba bean accessions, 120 F_4 populations, the cultivars Ackerperle, Diana, Erfordia and Herz Freya and the rust susceptible accession 2N40 (PI222128) were evaluated in small adjacent plots for their ability to retard rust development at the campus farm of the University of Manitoba. In 1978, the entries were tested in two separate trials of 82 and 51 entries to facilitate the assessment of rust development. Entries in each trial were planted in single rows 2.5 m in length and .6 m apart (30-35 plants/row) in a randomized complete block design with three replications. The 120 F_4 populations from crosses made at ICARDA in 1975 were evaluated in single rows in a non-replicated trial.

In each trial, two rows of the rust susceptible accession 2N40 were planted at right angles along both sides of each plot to act as rust spreader rows. The spreader rows were inoculated 3-4 weeks after emergence by spraying uredospores suspended in water containing a few drops of Tween-20 (Polyoxyethylene sorbitan monolaurate) with a knapsack sprayer equipped with a fine nozzle. Inoculation was always done after sunset on cool evenings with a high relative humidity. When judged necessary, the spreader rows were sprayed with tap water or the entire plot was sprinkler-irrigated before inoculation to help maintain a high relative humidity. In the few cases when poor infection occurred as a result of inadequate leaf wetness, the spreader rows were inoculated again after 7-10 days.

In 1979, mass selections for slow- and moderate-rusting from the previous year were evaluated in two-row plots using a randomized complete block design with four replications. In 1980, 20 mass selections for slow-rusting were tested to single-pustule isolates SP3 and SP51 at two locations 2.5 km apart. A randomized complete block design with four replications was used at each location.

Three hundred single plant selections with low levels of rust were made in 1978 and evaluated in a non-replicated one-row plot in 1979 for their ability to retard rust development. Fifteen lines derived from single plant selections were tested in 1980 in a randomized complete block design with four replications to the rust isolate SP51 and in a non-replicated trial to SP3 due to limited seed supply.

Thirteen faba bean lines, derived from mass or single-plant selections, consistently showing slow- and moderate-rusting and one fast-rusting line were tested in 1981 to the rust isolate SP51 using a randomized complete block design with four replications.

Evaluation for Slow-Rusting in Isolated Test Plots

Two slow-rusting selections from the accessions 2N5 and 2N43 and one fast-rusting selection from the accession 2N240 were tested in isolated plots 6.25 m^2 and 3 m apart in 1980. A randomized complete block design was used with three replications. Each plot consisted of eight rows 2.5 m long and .3 m apart. Wheat was grown between the plots to reduce movement of inoculum. The two rust isolates SP3 and SP51 were used in separate fields 2.5 km apart. Plants infected with rust in the greenhouse were transplanted into the center of each plot 3 weeks after plot emergence and the spread of the rust in each plot was assessed at weekly intervals for 5 weeks. For analysis of the data, each plot was divided into four squares

measuring .3, .6, .9 and 1.2 m from the center of the plots. The values of percentage leaf area infected were averaged for each square and AUDPC values were calculated.

Rust Isolates Used and Assessment of Disease Reaction

A mixture of field isolates of Uromyces viciae-fabae (Pers.) Schroet. was used in 1978 and 1979. The single-pustule isolates SP3 and SP51 (Conner 1981) were used in 1980 while in 1981 only the more virulent isolate SP51 was used. The inoculum was increased in the greenhouse on plants of the susceptible accession 2N40 (PI222128) as described previously (Thesis Section 1, Appendix 1).

The build-up of rust on the faba bean accessions was assessed 2-3 weeks after inoculation of the spreader rows and at weekly intervals for 4-5 weeks. Assessment keys of 1, 5 and 10% leaf area covered by sporulating pustules were used to visually estimate the leaf area infected. The values of leaf area infected over time were summarized as AUDPC values (Conner 1981) using the formula $AUDPC = \sum_{i-1}^{K} 1/2 (S_i + S_{i+1})$ where S_i = the rust severity at week i and K is the number of successive observations (Wilcoxson et al. 1975). The percentage of non-infected plants and of plants with various reactions were estimated where accessions were heterogeneous in their reactions. Analyses of variance were carried out for AUDPC values and the final rust severity (Cochran and Cox 1957). The means of each accession were compared using Duncan's Multiple Range Test.

Twenty to 30% of the accessions with low and intermediate AUDPC values in each trial were selected for further testing (mass selections). Plants with undesirable reaction types (highly resistant or highly susceptible) were eliminated from heterogeneous accessions before harvesting

in an attempt to improve the uniformity of the accessions. To determine the feasibility of selecting for slow-rusting on the basis of the performance of single plants, plants with low rust severity were harvested individually in 1978 and their progenies further evaluated in 1979 and 1980.

RESULTS

Considerable variation was observed between individual faba bean accessions from ICARDA and the University of Manitoba and between the F_4 populations evaluated in 1978 for their ability to retard rust development (Figure 1). The AUDPC values ranged from high to relatively low levels of rust build up. Sixty-nine percent of the accessions had AUDPC values lower than six. Analyses of variances for AUDPC and final disease severity values showed significant differences between the various accessions at the 1% level (Appendices 1 and 2). However, the coefficients of variability for these values were high, ranging from 32 to 36 (Appendices 1 and 2).

Mass selections from accessions with low to moderate AUDPC values showed a narrower range of AUDPC values and a marked increase in the percentage of infected plants in 1979 than in the previous year (Tables 1-3). The AUDPC and final disease severity values were higher in 1979 than in 1978 due to more favorable weather conditions for rust development in 1979 (Appendix 14). Differences between selections were significant at the 1% level for values of AUDPC, final disease severity and percentage of infected plants (Appendices 3-5).

Mass selections from accessions with low AUDPC values reacted similarly to isolates SP3 and SP51 in 1980 with a trend to higher AUDPC values for isolate SP51 (Table 4). In general, the capacity of the selections tested in 1980 to retard rust development was consistent with their performance in previous years. However, some accessions such as ILB431, ILB864 and the cultivar Diana shifted from low AUDPC values to moderate or high values. Other cultivars such as Ackerperle, Erfordia and Herz

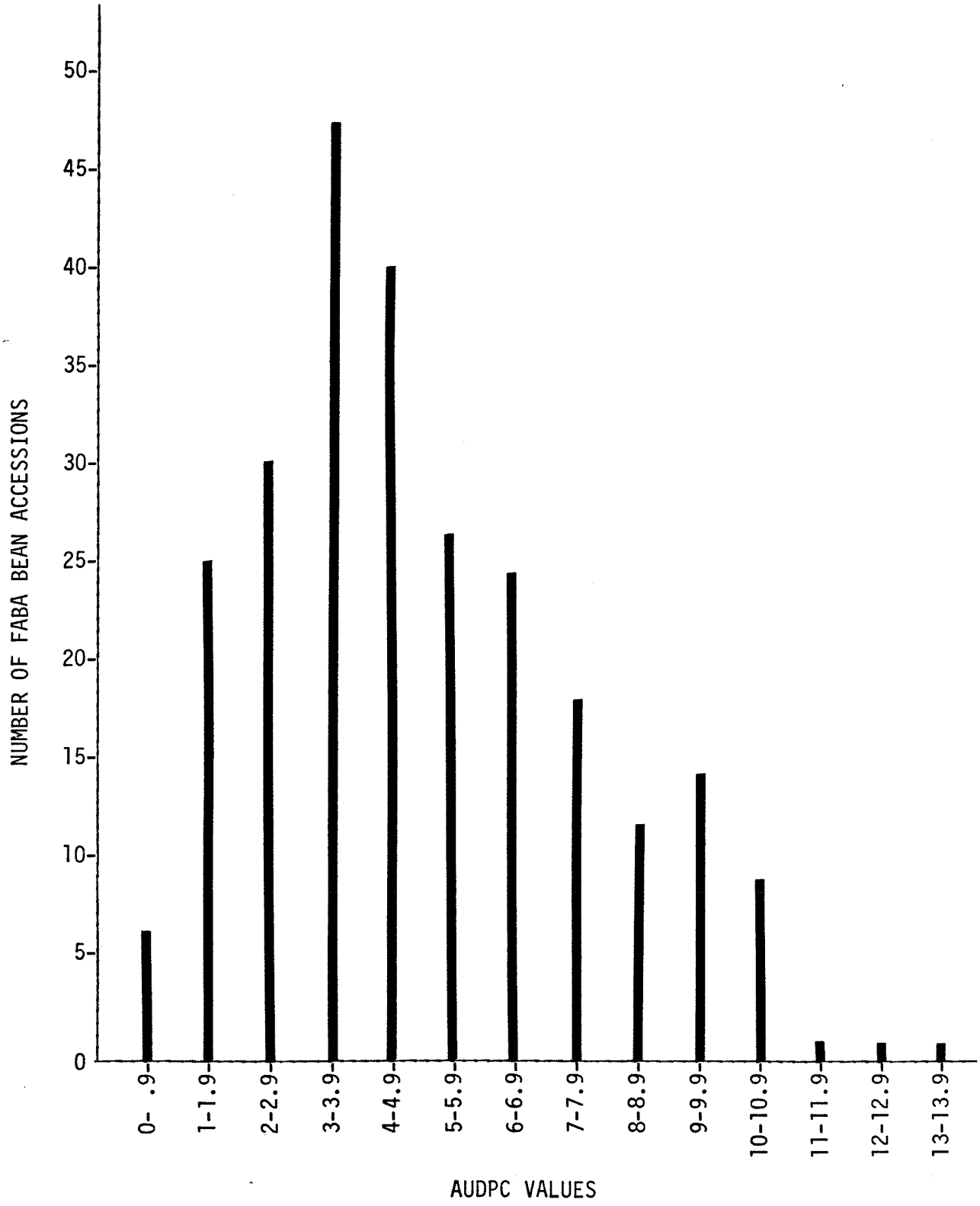

Figure 1. Distribution of area under the disease progress curve (AUDPC) in 253 faba bean accessions tested in 1978.

TABLE 1. Average values for area under the disease progress curve (AUDPC), final disease severity and percentage infected plants of 26 faba bean accessions from ICARDA tested in Manitoba in 1978 and 1979.

	1978			1979		
Accessions	AUDPC	Final disease severity	Percentage infected plants	AUDPC	Final disease severity	Percentage infected plants
2N40	15.83	9.00	100.00	20.00 a*	10.00 a*	100.00 a*
ILB938	2.66	2.00	98.00	5.38 b	2.62 bcde	100.00 a
ILB96	1.75	1.50	100.00	5.31 b	3.13 b	100.00 a
ILB142	3.42	2.50	95.00	5.06 bc	2.88 bc	100.00 a
ILB159	3.58	2.50	100.00	4.94 bc	2.75 bcd	100.00 a
ILB479	2.33	1.50	100.00	4.69 bc	2.50 bcde	100.00 a
ILB269	2.75	2.00	100.00	4.69 bc	2.50 bcde	100.00 a
ILB640	3.50	2.25	100.00	4.44 bcd	2.31 bcdef	100.00 a
ILB578	2.50	1.75	98.00	4.38 bcd	2.13 bcdef	100.00 a
ILB868	1.67	1.25	98.00	4.13 bcde	2.38 bcdef	100.00 a
ILB643	1.67	1.25	100.00	4.06 bcdef	2.06 bcdef	100.00 a
ILB159	2.08	1.50	95.00	4.04 bcdef	2.38 bcdef	100.00 a
ILB55	2.83	2.00	95.00	3.88 bcdef	2.36 bcdef	100.00 a
ILB815	2.33	2.00	100.00	3.81 bcdefg	2.25 bcdef	98.00 ab
ILB400	1.08	1.00	85.00	3.67 bcdefg	2.75 bcd	100.00 a
ILB920	4.08	3.50	95.00	3.06 cdefgh	1.38 defg	98.00 ab
ILB190	3.08	2.50	95.00	2.63 defghi	1.63 cdefg	97.50 b
ILB864	0.75	0.50	98.00	2.48 defghi	1.44 cdefg	95.00 bc
ILB697	1.33	1.00	95.00	2.35 efghi	1.25 efg	95.00 bc
ILB911	2.25	2.00	100.00	2.29 efghi	1.75 bcdefg	98.00 ab
ILB431	1.67	1.00	85.00	2.14 efghi	1.38 defg	95.00 bc
ILB61	1.33	0.75	98.00	2.10 fghi	1.63 cdefg	90.00 c
Diana	1.58	1.00	95.00	1.87 ghi	1.38 defg	95.00 bc
ILB938	1.33	1.00	85.00	1.37 hi	1.00 fg	90.00 c
ILB882	2.42	1.75	90.00	1.32 hi	1.00 fg	90.00 c
ILB866	0.75	0.50	75.00	0.92 i	0.50 g	90.00 c
C.V.				22.58	28.43	

*Duncan's Multiple Range Test, values followed by the same letter are not significantly different from each other at the 1% level.

TABLE 2. Average values for area under the disease progress curve (AUDPC), final disease severity and percentage infected plants of 25 F_4 faba bean populations from ICARDA tested in Manitoba in 1978 and 1979.

	1978			1979		
F_4 Population	AUDPC	Final disease severity	Percentage infected plants	AUDPC	Final disease severity	Percentage infected plants
2N40	15.83	9.00	100.00	20.00 a*	10.00 a*	100.00 a*
ILB(112X12)	4.00	2.50	100.00	5.50 b	3.00 b	100.00 a
ILB (53X10)	0.75	0.50	90.00	4.81 bc	2.31 bcd	100.00 a
ILB (53X10)	0.75	0.50	90.00	4.63 bcd	2.50 bc	100.00 a
ILB (199X133)	2.50	1.50	95.00	4.25 bcde	2.00 bcde	98.00 b
Giza2XILB133	2.50	1.50	90.00	4.00 bcde	2.00 bcde	98.00 b
ILB(425X284)	3.00	2.00	100.00	4.00 bcde	2.00 bcde	100.00 a
ILB(26X116)	2.50	2.00	95.00	4.00 bcde	2.50 bc	98.00 b
ILB(112X12)	1.00	0.50	90.00	3.75 cdef	2.38 bcd	100.00 a
ILB(62X12)	2.50	1.50	95.00	3.63 cdefg	2.13 bcde	98.00 a
Giza2XILB10	1.25	0.75	90.00	3.50 cdefgh	1.88 bcde	100.00 a
ILB(332X133)	4.00	2.50	95.00	3.44 cdefgh	2.13 bcde	98.00 b
Giza2XILB10	0.75	0.50	95.00	3.38 cdefgh	1.88 bcde	98.00 b
ILB(425X284)	2.50	2.00	95.00	3.00 defghi	2.00 bcde	98.00 b
ILB(199X133)	1.00	0.50	90.00	2.88 defghi	1.75 cdef	100.00 a
ILB(62X116)	1.00	0.50	80.00	2.75 efghij	1.25 defg	98.00 b
ILB(332X10)	1.50	0.75	95.00	2.50 efghij	1.25 defg	98.00 b
ILB(199X133)	1.50	1.00	90.00	2.50 efghij	1.50 cdefg	98.00 b
ILB(711X269)	3.00	2.00	90.00	2.19 fghij	1.69 cdef	95.00 bc
Giza2XILB31-B	1.00	0.50	90.00	2.06 fghij	1.25 defg	98.00 b
Giza2XILB133	2.50	1.50	90.00	1.88 ghij	1.00 efg	95.00 bc
ILB(332X31)	1.75	1.00	90.00	1.75 hij	0.63 fg	95.00 bc
Giza2XILB31-A	2.50	1.50	90.00	1.50 ij	1.00 efg	90.00 c
ILB(332X133)-B	1.00	0.50	90.00	1.25 ij	0.50 g	95.00 bc
ILB(332X133)-A	1.00	0.50	85.00	1.06 j	0.63 fg	90.00 c
C.V.				21.40	26.31	

*Duncan's Multiple Range Test, values followed by the same letter are not significantly different from each other at the 1% level.

TABLE 3. Average values for area under the disease progress curve (AUDPC), final disease severity and percentage infected plants of 10 faba bean accessions from the University of Manitoba tested in 1978 and 1979.

	1978			1979		
Accessions	AUDPC	Final disease severity	Percentage infected plants	AUDPC	Final disease severity	Percentage infected plants
2N40	15.83	9.00	100.00	20.00 a*	10.00 a*	100.00 a
2N240	3.33	2.25	100.00	6.44 b	3.75 b	100.00 a
2N134	3.67	2.25	95.00	5.88 bc	3.50 b	100.00 a
2N32	4.00	3.00	100.00	5.66 bc	3.00 bcd	100.00 a
2N41	2.42	1.50	90.00	5.19 bc	3.13 bc	100.00 a
2N291	3.58	2.00	95.00	4.75 cd	3.00 bcd	100.00 a
2N6	2.17	1.25	85.00	3.56 d	2.25 cde	100.00 a
2N29	3.42	2.00	90.00	3.50 d	2.00 de	100.00 a
2N43	2.17	1.25	90.00	1.94 e	1.25 ef	95.00 b
2N5	3.92	2.00	90.00	0.56 e	0.63 f	90.00 c
C.V.				13.04	15.41	

*Duncan's Multiple Range Test, values followed by the same letter are not significantly different from each other at the 1% level.

TABLE 4. Average values of area under the disease progress curve (AUDPC), final disease severity and percentage infected plants of 20 faba bean mass selections tested in Manitoba to rust isolates SP51 and SP3 in 1980 with values for 1978 and 1979 for comparison.

Mass selection	1978			1979			1980					
							SP51			SP3		
	AUDPC	Final disease severity	Percentage infected plants	AUDPC	Final disease severity	Percentage infected plants	AUDPC	Final disease severity	Percentage infected plants	AUDPC	Final disease severity	Percentage infected plants
2N40	15.83	9.00	100.00	20.00	10.00	100.00	20.50 a*	10.00 a*	100.00	13.81 a*	8.63 a*	100.00
2N291	3.58	2.00	95.00	4.75	3.00	100.00	11.19 b	6.75 b	100.00	8.38 b	5.25 b	100.00
Diana	1.58	1.00	95.00	1.87	1.38	95.00	10.94 bc	6.25 bcd	100.00	7.25 bcd	5.00 bc	100.00
Giza2XILB31-A	2.50	1.50	90.00	1.50	1.00	90.00	10.31 bcd	6.63 bc	100.00	6.19 bcde	5.13 bc	100.00
ILB(711X269)	3.00	2.00	90.00	2.19	1.69	95.00	10.25 bcd	5.50 bcdef	100.00	7.81 bc	5.50 b	100.00
ILB190	3.08	2.50	95.00	2.63	1.63	97.50	9.75 bcde	5.50 bcdef	100.00	5.19 defghi	3.63 bcdef	97.50
2N29	3.42	2.00	90.00	3.50	2.00	100.00	9.63 bcde	6.00 bcde	100.00	6.94 bcde	4.38 bcde	95.00
2N5	3.92	2.00	90.00	0.56	0.63	85.00	8.63 bcdef	5.25 bcdef	100.00	4.00 fghi	3.25 cdef	97.50
ILB431	1.67	1.00	85.00	2.14	1.38	95.00	8.25 bcdef	4.75 cdef	100.00	6.25 bcdef	4.00 bcdef	100.00
ILB864	0.75	0.50	95.00	2.84	1.44	95.00	8.19 bcdef	4.38 def	97.50	4.69 efghi	3.63 bcdef	97.50
ILB882	2.42	1.75	90.00	1.32	1.00	90.00	8.00 cdef	5.13 bcdef	97.50	6.19 bcdefg	4.75 bcd	100.00
Giza2XILB31-B	1.00	0.50	95.00	2.06	1.25	100.00	7.88 cdef	5.00 bcdef	100.00	5.75 cdefgh	3.88 bcdef	100.00
Giza2XILB133	2.50	1.50	95.00	1.88	1.00	95.00	7.69 def	4.88 bcdef	97.50	7.13 bcde	4.75 bcd	100.00
ILB938	1.33	1.00	85.00	1.37	1.00	90.00	7.25 def	4.25 ef	96.00	3.13 i	2.13 f	85.00
2N43	2.17	1.25	90.00	1.94	1.25	95.00	7.13 def	4.50 def	100.00	3.81 fghi	2.50 ef	95.00
ILB(332X133)-A	1.00	0.50	90.00	1.06	0.63	90.00	6.88 ef	4.00 f	95.00	4.06 fghi	2.75 ef	95.00
2N6	2.17	1.25	85.00	3.56	2.25	100.00	6.63 ef	4.63 def	100.00	3.25 hi	2.25 f	85.00
ILB697	1.33	1.00	90.00	2.35	1.25	95.00	6.56 ef	4.00 f	97.50	3.69 ghi	3.00 def	97.50
ILB866	0.75	0.50	75.00	0.92	0.50	90.00	6.56 ef	3.88 f	97.50	5.25 defghi	4.25 bcde	100.00
ILB(332X133)-B	1.00	0.50	90.00	1.25	0.50	95.00	5.56 f	4.38 def	95.00	3.81 fghi	2.75 ef	85.00
C.V.							16.47	16.49		19.94	21.07	

*Duncan's Multiple Range Test, values followed by the same letter are not significantly different from each other at the 1% level.

Freya were very heterogeneous in their reactions in 1978, with a range of AUDPC values. These cultivars were not mass selected and only single plants were selected for further evaluation.

Faba bean lines derived from single plant selections showed a range and distribution of AUDPC values in 1979 (Figure 2) similar to that of the original accessions tested in 1978 (Figure 1). Eighty percent of the single plant selections had AUDPC values lower than six. Fifteen lines derived from single plant selections in 1979 had relatively lower values of AUDPC and final disease severity in 1980 to the rust isolate SP51 and even much lower values to the isolate SP3, than lines derived from mass selections (Tables 4 and 5). Analyses of variances for values of AUDPC, final disease severity and percentages of infected plants showed significant differences between the various mass selections and single plant selections at the 1% level (Appendices 6-8).

Mass selections (MS) and single plant selections (SP) evaluated in 1981 could be placed into three groups on the basis of AUDPC values: a slow-rusting group including the selections 2N6 (MS), 2N29 (SP), 2N43 (SP and MS), 2N122 (SP), ILB938 (MS), ILB(332X133)A (MS) and ILB(332X133)B (MS); a moderate-rusting group including the selections 2N291 (MS), 2N319 (SP), ILB697 (MS) and ILB866 (MS); and a third group represented by the fast ruster 2N40 (MS) (Table 6). These selections are characterized by susceptible infection types (IT 3 and 4) except for the selections 2N29 (SP), 2N43 (SP), 2N122 (SP) and ILB(332X133)B (MS) which showed low infection types (IT 2). The slow-rusting selections behaved consistently from 1978 through 1981, whereas some of the moderate rusters such as ILB697 and ILB866 shifted from slow-rusters in 1978-1980 to moderate rusters in 1981 (Tables 4-6). Differences between the various selections for

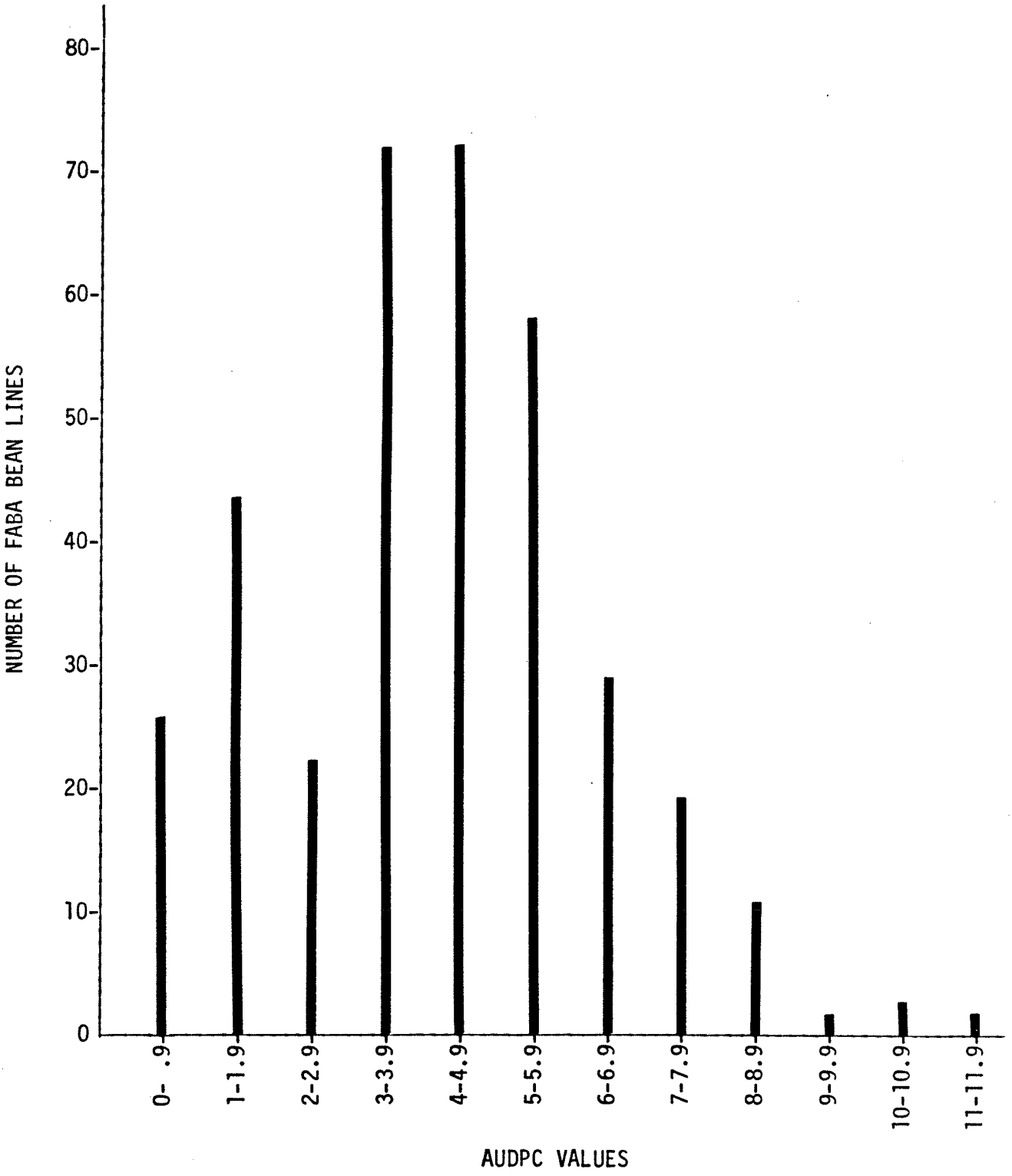

Figure 2. Distribution of area under the disease progress curve (AUDPC) in 360 faba bean lines from single plant selections tested in 1979.

TABLE 5. Average values for area under the disease progress curve (AUDPC), final disease severity and percentage infected plants of 15 faba bean lines from single plant selections tested in Manitoba to rust isolates SP51 and SP3 in 1980.

Single plant selections[1]	SP51			SP3[@]		
	AUDPC	Final disease severity	Percentage infected plants	AUDPC	Final disease severity	Percentage infected plants
2N40	18.00 a*	10.00 a*	100.00 a	10.50	6.00	100.00
2N5	9.69 b	6.38 b	100.00 a	2.25	1.50	90.00
2N240	9.50 bc	6.25 b	100.00 a	6.75	6.00	100.00
Herz Freya-A	8.44 bc	6.13 b	100.00 a	3.25	2.00	100.00
Herz Freya-B	8.19 bc	6.00 b	100.00 a	3.00	2.00	100.00
Herz Freya-C	7.31 bcd	4.75 bcde	100.00 a	2.25	2.00	95.00
2N119	7.06 cde	4.63 bcdef	100.00 a	2.50	1.50	95.00
Ackerperle	7.00 cde	4.83 bcde	100.00 a	3.50	2.50	90.00
2N22	7.00 cde	5.25 bc	100.00 a	1.00	1.00	100.00
Ackerperle-B	6.94 cde	5.38 bc	100.00 a	2.00	2.00	100.00
2N319	5.38 de	3.50 def	98.00 b	1.50	2.00	100.00
2N43	5.25 de	3.50 def	98.00 b	0.75	0.50	95.00
2N122	4.56 ef	3.88 cdef	100.00 a	1.75	1.50	95.00
2N6	4.50 ef	3.25 ef	95.00 c	1.25	1.50	90.00
2N29	2.69 f	2.88 f	98.00 b	0.25	0.50	80.00
C.V.	16.20	16.37				

[1]The 15 single plant selections were made in 1978 and tested in 1979. Results in Figure 2.

*Duncan's Multiple Range Test, values followed by the same letter are not significantly different from each other at the 1% level.

[@]Testing these selections to SP3 was carried out in a non-replicated trial due to limited seed supply.

TABLE 6. Average values for area under the disease progress curve (AUDPC) final disease severity and percentage infected plants for 13 faba bean slow-rusting selections tested to rust isolate SP51 in 1981.

Selections[a]	AUDPC	Final disease severity	Percentage infected plants
2N40 (MS)	25.25 a*	10.00 a*	100.00
2N291 (MS)	12.13 b	5.75 b	100.00
ILB697 (MS)	10.25 bc	4.00 c	100.00
ILB866 (MS)	9.00 cd	4.00 c	100.00
2N319 (SP)	7.00 de	3.50 cde	100.00
2N43 (MS)	6.50 def	3.75 cd	100.00
2N6 (MS)	5.88 dcf	3.00 cdef	98.00
2N122 (SP)	5.56 ef	2.25 ef	100.00
ILB938 (MS)	5.44 ef	2.38 def	100.00
2N29 (SP)	4.94 ef	2.50 ef	98.00
ILB(332X133)A (MS)	4.63 ef	2.13 ef	100.00
ILB(332X133)B (MS)	3.81 ef	1.75 f	98.00
2N43 (SP)	3.38 f	1.75 f	98.00
C.V.	18.98	19.38	

*Duncan's Multiple Range Test, values followed by the same letter are not significantly different from each other at the 1% level.

[a]MS = Mass Selections; SP = Lines from Single Plant Selections.

AUDPC and final disease severity values were significant at the 1% level (Appendix 9).

In the isolated test plots, development of rust isolates SP3 and SP51 was slower in the slow-rusting selection 2N43 than in the moderate-rusting selection 2N5. However, rust development in both selections was much slower than in the fast-rusting selection 2N240 (Table 7). Furthermore, AUDPC and final disease severity values for selections 2N43 and 2N5 were lower in the isolated test plots than in the small adjacent plots (Table 9). In contrast, the fast-rusting selection 2N240 showed a more rapid disease development as indicated by higher AUDPC and final disease severity values in the isolated test plots than in the small adjacent plots (Table 9). The AUDPC and final disease severity values were at their highest at the center and least in the outer square of each isolated test plot (Table 7). Higher values of AUDPC and final disease severity were obtained for isolate SP51 than for isolate SP3. However, the trend in disease development within the plots was almost similar for both isolates. Analyses of variances for AUDPC and final disease severity values showed significant differences between the three selections as well as between the four locations (squares within each plot) at the 1% level (Appendices 10 and 11).

The AUDPC values were highly correlated with the final disease severity values in all the trials conducted for this study from 1978 to 1981 (Table 8).

TABLE 7. Average values for area under the disease progress curve (AUDPC) and final disease severity for 3 faba bean selections tested in isolated test plots to rust isolates SP3 and SP51 at two locations in 1980.

Selections and locations	AUDPC		Final Disease Severity	
	SP3	SP51	SP3	SP51
2N5				
Square 1[@]	4.05 a*	10.67 a*	1.66 a*	4.50 a*
Square 2	2.45 b	8.95 b	1.41 a	3.83 ab
Square 3	1.58 c	6.80 bc	0.95 b	3.42 ab
Square 4	1.30 c	5.37 c	0.88 b	3.17 b
$\bar{X}$	2.35	7.95	1.23	3.73
2N43				
Square 1	3.58 a	8.17 a	1.83 a	2.83 a
Square 2	2.38 b	5.37 b	1.48 a	2.33 ab
Square 3	1.35 c	4.88 bc	0.85 b	2.66 ab
Square 4	1.32 c	4.35 c	0.83 b	2.50 b
$\bar{X}$	2.16	5.69	1.25	2.58
2N240				
Square 1	9.92 a	15.88 a	4.17 a	8.17 a
Square 2	8.85 b	14.70 b	4.50 a	8.17 a
Square 3	7.77 c	14.55 b	3.83 b	8.25 a
Square 4	6.75 c	12.38 c	3.50 b	7.83 b
$\bar{X}$	8.42	14.38	4.00	8.10
C.V.	9.89	11.27	8.05	10.86

[@]Each micro plot was divided into 4 squares of .30, .60, .90 and 1.20 m from the center of the plot. Square 1 is the closest and 4 the farthest from the source of inoculum at the center of each plot.

*Duncan's Multiple Range Test, values followed by the same letter in each line under each rust isolate are not significantly different at the 1% level.

TABLE 8. Correlation values between the area under the disease progress curve and final disease severity in the years 1978 to 1981 to faba bean rust in Manitoba.

Experimental trial	1978	1979	1980		1981
	Mixture*	Mixture	SP3	SP51	SP51
ICARDA accessions	0.92	0.98	--	--	--
ICARDA F_4	0.96	0.98	--	--	--
University of Manitoba accessions	0.97	0.99	--	--	--
Mass selections (MS)**	--	--	0.91	0.92	--
Single plant selections (SP)+	--	--	0.94	0.94	--
Mass and single plant selections++	--	--	--	--	0.97
Isolated test plots	--	--	0.98	0.95	--

*A mixture of rust isolates was used in 1978 and 1979 field trials. Single-pustule isolates SP3 and SP51 were used in 1980 in isolated locations while SP51 was the only isolate used in 1981.

**This trial consisted of mass selections made in 1979 from the ICARDA accessions, ICARDA F_4 populations and University of Manitoba accessions.

+This trial consisted of lines derived from single plant selections made in 1978 from the ICARDA accessions, F_4 populations and University of Manitoba accessions and evaluated in 1979.

++This trial consisted of selections made in 1980 from mass and single plant selections.

TABLE 9. Average values for area under the disease progress curve (AUDPC) and final disease severity for three faba bean selections evaluated in small adjacent plots and isolated test plots to Uromyces viciae-fabae in 1980.

	Adjacent Plots*				Isolated Test Plots+			
	SP3		SP51		SP3		SP51	
Accession	AUDPC	Final disease severity	AUDPC	Final disease severity	AUDPC	Final disease severity	AUDPC	Final disease severity
2N5	4.00	3.25	8.63	5.25	2.35	1.23	7.95	3.73
2N43	3.81	2.50	7.13	4.50	2.16	1.25	5.69	2.58
2N240	6.75	6.00	9.50	6.25	8.42	4.00	14.38	8.10

*Adjacent plots consisted of two rows of 2.5 m long and .6 m apart.

+Isolated test plots consisted of eight rows of 2.5 m long and .3 m apart (6.25 m^2). Plots were separated by 5 m strips of wheat.

DISCUSSION

Small adjacent plots were satisfactory for evaluating a large number of open-pollinated faba bean accessions and cultivars for their ability to retard rust development. Mass selections from accessions 2N6, 2N43, ILB938 and ILB9(332X133) and single plant selections from accessions 2N29, 2N43 and 2N122 had low AUDPC values over 3 to 4 years of testing, whereas other mass selections including 2N291, ILB697, ILB866 and Diana had low, intermediate or high AUDPC values (Tables 4 and 6). The variable response of some accessions might be due to varying levels of inter plot interference and/or environmental differences from one year to another. It would appear that accessions or their selections need to be evaluated over a minimum of 2 years to ensure that they are indeed slow-rusters.

The results from this study confirm a recent report by Conner (1981) on the ability of faba bean accessions to retard rust development. The distribution of the AUDPC values for the 253 accessions first tested in 1978 is skewed towards low AUDPC values (Figure 1) suggesting that many of the accessions had been naturally exposed to rust and that indirect selection for low levels of rust infection may have been practised.

Small adjacent plots underevaluate the differences in slow-rusting between cultivars due to interplot interference (Parlevliet and Van Ommeren 1975). In this study, rust development in the slow- and moderate-rusting selections 2N43 and 2N5 was also slower in isolated test plots than in small adjacent plots. However, in the isolated plots, the AUDPC values for 2N43 were again lower than for 2N5. The fast-rusting selection 2N240

had a more rapid rust development in isolated test plots than in small adjacent plots indicating that the less susceptible accessions have a buffering effect in small adjacent plots and reduce the amount of inoculum that reaches the highly susceptible accessions.

The coefficients of variation (CV) for the values of AUDPC and final disease severity were very high in 1978, ranging from 32 to 38 (Appendices 3 and 4). The reduction in the coefficient of variation values during the following years of testing to a range of 13 to 21 can be attributed to several factors including the increase in plot size, the reduced heterogeniety of the accessions as a result of mass selection for the slow-rusting character and to the use of a single rust isolate per test site rather than a mixture of isolates. However, plot size may be the most important factor since in 1980, the lowest coefficients of variation (8 to 11) were obtained from the large isolated test plots (Table 7).

Mass and single plant selection were both effective in reducing the number of plants with specific resistance. This is shown by the constant improvement in the percentage infected plants which reached 98 to 100% in all selections tested in 1981 (Table 6).

Low AUDPC values of some accessions may not be entirely due to the slow-rusting character. Mixtures of lines or cultivars in various proportions of susceptible and resistant components have been reported to be effective in reducing rust development (Browning and Frey 1969, Browning 1974). Wahl (1970) found that a frequency of 30% resistant genotypes in a diverse population of wild oat was adequate for protection against the most virulent strains of crown rust. In this study, the presence of 15 to 25% plants with specific resistance in the accessions 2N6, ILB431, ILB866 and ILB938 tested in 1978 and in the selections 2N6, ILB938 and ILB(332X133)B tested

to isolate SP3 in 1980 may have contributed to their rust retarding ability. On the other hand, the rust retarding ability of the selections evaluated in 1980 and 1981 would appear to be due entirely to the slow-rusting character and not to a mixture of resistant and susceptible genotypes since 98 to 100% of the plants in each selection were infected (Table 6).

Components responsible for slow-rusting in cereals like low receptivity, longer latent period, reduced sporulation and small pustules (Parlevliet 1975, Johnson and Wilcoxson 1978, Neervoort and Parlevliet 1978) may be responsible for the slow-rusting in faba beans. In some selections such as 2N29, 2N43, 2N122 and ILB(332X133)B, small pustule size (infection type 2) may be involved in retarding rust development. However, the identification of the component(s) responsible for slow-rusting in each selection requires further research.

The correlation between the AUDPC values and final rust severity values was not unexpected since final rust severity contributes in part to AUDPC values. Conner (1981) also found an association between these two values and suggested that final rust severity could be used as a criterion for selecting potential slow-rusters in preliminary tests. Final rust severity is less labor intense than recording rust development over time as required in order to obtain AUDPC values.

Eighty percent of the 360 lines derived from single plants selected for low rust severity values in this study had low to moderate AUDPC values in 1979 (Figure 2). Several lines from single plant selections were among the best slow rusters in subsequent years of testing (Tables 5 and 6). These findings suggest that it may be possible to select single plants within F_2 populations on the basis of final rust severity values. The rust retarding capacity of the F_3 and F_4 progenies could then be evaluated in

small adjacent plots and once sufficient seed is available, in large isolated plots.

Slow-rusting resistance is considered to be effective against all races of a pathogen and more stable than specific resistance (Van Der Plank 1968, Parlevliet and Van Ommeren 1975). Although the slow-rusting accessions and selections of faba bean identified in the present study were effective against two pathotypes of the rust from Manitoba, they should be evaluated in other areas to determine their effectiveness against a greater range of pathotypes.

GENERAL DISCUSSION

The evaluation of a large number of faba bean accessions for their resistance to the two rust isolates SP3 and SP51 showed that resistance to SP3 is more common than resistance to SP51, thus confirming Conner's (1981) findings that SP51 is more virulent than SP3. The different levels of resistance with infection types 0 to 2 in accessions from various regions of the world indicates that these accessions have been exposed in the past to similar biotypes of rust in their center(s) of origin.

The use of faba bean inbred lines selfed 3 to 4 times proved to be adequate to study the inheritance of rust resistance. The assumption that the two genes for resistance identified in this study in Ack-A and Erf-2 are the same as the genes Fr1 and Fr2 identified by Conner and Bernier (1982b) in the same accessions needs to be confirmed by inter-crossing the various selections. Of the six genes identified and designated Fr4 to Fr9, genes Fr4, Fr5, Fr6 and Fr7 were identified as distinct genes. However, inbred lines with genes Fr8 and Fr9 should be inter-crossed with inbreds carrying the identified distinct genes to establish whether Fr8 and Fr9 can be truly different or alleles.

The use of open-pollinated field selections 2N43, 2N43-A and Ack-A in crosses with inbred lines resistant to specific isolates showed that the field selections possessed additional genes for resistance. The establishment of a pool of inbred lines with identified resistance genes will facilitate the identification of additional resistance genes in open-pollinated field selections. However, further selection and selfing will be needed to allow the identification of the resistance genes involved.

The use of small adjacent field plots was shown to be adequate for evaluating large numbers of accessions for slow-rusting resistance. However, the high level of inoculum from fast-rusting accessions and spreader rows leads to underevaluation of moderate- and slow-rusting accessions. Rust development is more uniform and the rate limiting capability of the accessions is better expressed in isolated test plots than in small adjacent plots. Thus, after preliminary evaluation in small adjacent plots, slow- and moderate-rusting selections should be further tested in isolated plots in order to obtain a more realistic assessment of their ability to retard rust development.

Inbred lines and other homozygous selections identified in this study with specific resistance should be tested in other regions where rust is a problem to determine whether their resistance would remain effective. This would also serve to identify any more virulent pathotypes of the rust. Slow-rusting selections also should be tested in other regions to evaluate their effectiveness against a wider range of pathotypes.

Intravarietal diversity of cross-bred populations of corn have long been recognized to offer some protection against diseases (Hooker 1969, 1973, Browning and Frey 1969). In the present studies, intravarietal diversity was clearly shown in several faba bean accessions. Several single plants homozygous for one of the infection types ; to 2 to rust isolates SP3 and SP51, were selected from accessions such as 2N319, ILB335 and ILB431 (Manuscript 1). Accession 2N319 and the selections ILB159-1 and ILB159-4 which originated from 2N319, were found to possess three resistance genes Fr7, Fr8 and Fr9 to specific rust isolates (Manuscript 2). It seems possible that genes Fr7, Fr8 and Fr9 providing resistance with low infection types 1 and 2 in 2N319 may be responsible for moderate-rusting of this

accession or may have contributed to limiting rust development. Effectiveness of such genetically diverse accessions in restricting rust development in the field is expected to be much greater than that of cultivars with single specific genes for resistance and may be comparable to a multiline composite.

In considering breeding strategies for faba bean, it would appear desirable to maintain and improve the genetic diversity presently found in some of the germplasm. Reliance on specific resistance to rust would result in greater cultivar uniformity but reduce the genetic diversity. Durability could be improved by pyramiding 3 to 4 single genes into a given cultivar. A more logical approach to maintain genetic diversity in an open-pollinated crop such as faba bean is population improvement through recurrent selection. Improved populations could be generated by allowing several inbred lines with one or two resistance genes and agronomically adapted cultivars to inter-cross under screen cages using bees.

In faba bean, where quality requirements are not very stringent, multiline cultivars could also be produced within a few generations of back-crossing specific resistance genes into agronomically suitable lines. Multiline composites could be formed by mixing lines with specific resistance alone or in combination with slow-rusting lines.

Further research is required to identify the various components responsible for slow-rusting in faba bean. This information would facilitate selecting for slow-rusting resistance and simplify the task of the plant breeder.

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APPENDIX 1. Procedures for increasing rust isolates.

Rust uredospores were increased under strict sanitary measures to avoid any possibility of contamination with foreign spores. Plants of the susceptible faba bean PI222128 were inoculated in a plexiglass chamber equipped with a set of fine spray nozzles (Green 1981). The chamber was misted with water to remove spores from the air and wash the sides of the chamber between isolates. The inoculated plants were covered with polyvinyl tubes and incubated under 100% relative humidity for 24 hr. They were then moved into the greenhouse and the tubes connected to a source of filtered air to prevent cross-contamination and excessive build-up of moisture under the covers. Uredospores were collected using a cyclone spore collector (Browder 1971) and were stored at 5^{o} C for further use.

APPENDIX 2. The reaction and infection type of S_3 faba bean inbred lines to isolates SP3 and SP51 of Uromyces viciae-fabae.

Inbred lines	Rust Isolates: SP3 Reaction[1]	SP3 Infection type	SP51 Reaction	SP51 Infection type
2N 26-1-8	R	2	S	3 4
5-8	R	1 2	S	3 4
5-12	R*	1 2	S	3 4
2N 34-2-2	S	3	S	3 4
2-6	R	1 2	S	3 4
4-2	S	3	S	3 4
5-1	R	1 2	S	3 4
2N122-4-8	S	3 4	S	3 4
4-9	S	3 4	S*	3 4
5-2	S	3	S	3 4
2N168-5-3	S	3	R	1 2
8-1	R	0 ;	S	3 4
2N175-1-3	R	0	S	3 4
2N192-1-4	R*	1 2	R	; 1
2N225-3-10	R*	1 2	R	;
4-5	R	;	S	3 4
2N281-4-6	S*	3	R*	1^+
2N285-1-9	R	0	S	3 4
1-11	R	0	S	3 4
1-14	R	0	S	3 4
4-1	S	3 4	S	3 4
4-2	S	2 3	S	3 4
2N311-2-1	R	0	R	;
5-1	R	;	R	; 1
6-1	R	;	R	; 1^+
2N319-1-1	R	0	S	3 4
1-2	R	; 1	S*	3 4
1-5	R	0	S	3 4
1-7	R	;	S	3 4
2N319-1-8	R	; 1	R	; 1
1-14	R	; 1	S*	3 4
3-1	R	;	R	;
3-2	R	; 1	R*	1^+
3-6	R	; 1	S	3 4
4-1	R	0 2	R	;
4-2	R	1 2	R	;
6-4	R	1 2	R	;
6-5	R	;	R	;
6-7	S	3 4	S	3 4
6-8	S	3 4	R	1 2
7-1	R	;	R	1 2
7-2	R	1 2	S	3 4
7-4	R	0	S	3 4
7-5	R	; 1	S*	3 4
7-10	R	; 1	R	; 1
2N382-4-6	R	;	S*	3
2N431-3-5	R	; 1	R	1 2
4-8	R	;	S	2 3
2N432-5-3	R	0	S	3 4
2N435-2-5	R	;	R	; 1
2-6	R	0	R	; 1
5-1	R	0 ;	S	3 4
5-9	R	0 ;	S	3 4
5-11	R	; 2	S*	3 4
2N441-7-1	R	1 2	R	;
ILB75-7-6	R	;	S	2 3
7-9	R	;	S*	3 4
ILB96-1-2	R	;	R	; 1
7-2	R	; 1	R*	; 1

Inbred lines	Rust Isolates: SP3 Reaction	SP3 Infection type	SP51 Reaction	SP51 Infection type
ILB 96-7-3	R	;	R	;
7-4	R	0	R	;
ILB226-6-3	R	;	R	; 1^+
ILB315-5-1	R	; 1	R	0
ILB318-1-5	R	;	R	; 1^+
5-1	R	;	S*	3
5-4	R	;	R	2
ILB335-2-1	R	;	R	; 1^+
2-2	R	;	R	1 2
2-7	R	;	R	1 2
3-2	R	; 1^+	S	2 3
3-4	R	;	S*	2 3
7-5	S*	3	S	2 3
ILB403-5-1	R	0	R	1
5-2	R	0	R	0
ILB411-2-1	S	3	R	2
ILB431-2-7	R	;	R	;
3-1	R	;	S	3
3-5	R*	0 ;	S	3
5-3	R	;	R*	0 2
6-1	R	;	R*	1 2
ILB479-7-2	R	;	R	;
7-4	R*	; 1	R	;
ILB490-6-4	R	;	R	1 2
7-4	R	;	S	3
ILB534-6-3	R	0	S	3 4
6-5	R	0	S	3 4
6-7	S*	3 4	S	3 4
6-10	R	0	S	3 4
ILB864-4-3	R	0	S	3 4
8-2	R	0	S	3 4
ILB866-1-2	R	;	R	; 1
1-3	R	;	R	;
ILB919-4-4	R	;	R	1 2
4-6	R	0	R	;
8-3	R	;	R	; 1
ILB920-1-8	S*	3 4	R	;
1-9	R	1 2	R	;
ILB938-3-5	R	0	R	;
6-4	R	;	R	;
6-6	R	;	R	;
7-1	R	;	R	;
7-5	R	;	R	;
8-5	R	0	R	0
8-6	R	;	R	;
ILB Giza3-3-5	S	3 4	R	2
Ackerperle-1-3	R	0	R	;
3-7	R	;	R	; 1
Diana-2-3	R	;	S	3 4
2-4	R	;	R	1
6-7	R	0 ;	S	3 4
Erfordia-2-2	R	;	R	; 1^+
2-18	R	; 1	S*	3 4
Herz Freya-1-1	R	;	R	; 1
1-11	R	0 ;	R*	1 2
2-5	R	0 ;	S	3 4
7-2	S	3 4	S	3 4
7-7	R	0 ;	R	1 2

[1] Reaction to rust: R = Resistant; R* = Majority of plants are resistant;
S = Susceptible; S* = Majority of plants are susceptible.

APPENDIX 3. Analysis of variance for slow-rusting from 51 faba bean lines from University of Manitoba collection tested in Manitoba 1978.

Source	D.F.	Sum of squares	Mean square	F values
		AUDPC		
Replications	2	11.0351	5.5176	2.31
Lines	50	391.7067	7.8341	3.28**
Error	100	238.8315	2.3883	
Total	152	641.5734		
				C.V. = 31.76%
		Final Disease Severity		
Replications	2	4.4739	2.2369	2.45
Lines	50	167.3366	3.3467	3.66**
Error	100	91.3595	0.9136	
Total	152	263.1699		
				C.V. = 32.11%

**Significance at 1% level.

APPENDIX 4. Analysis of variance for slow-rusting from 82 faba bean lines from ICARDA tested in Manitoba 1978.

Source	D.F.	Sum of squares	Mean square	F values
		AUDPC		
Replications	2	56.0249	28.0125	7.78**
Lines	81	2380.7564	29.3920	8.16**
Error	162	583.5584	3.6022	
Total	245	3020.3397		
				C.V. = 38.25%
		Final Disease Severity		
Replications	2	9.7012	4.8506	3.30*
Lines	81	775.8913	9.5715	6.52**
Error	162	237.8654	1.4689	
Total	245	1023.4579		
				C.V. = 36.47%

*Significance at 5% level.

**Significance at 1% level.

APPENDIX 5. Analysis of variance for slow-rusting from 26 selected faba bean lines from ICARDA collection tested in Manitoba 1979.

Source	D.F.	Sum of squares	Mean square	F values
		AUDPC		
Replications	3	13.5496	4.5165	5.43**
Lines	25	1235.8874	49.4355	59.47**
Error	75	62.3482	0.8313	
Total	103	1311.7852		
				C.V. = 22.58%
		Final Disease Severity		
Replications	3	7.0787	2.3596	5.56**
Lines	25	293.3732	11.7349	27.67**
Error	75	31.8119	0.4241	
Total	103	332.2638		
				C.V. = 28.43%

**Significance at 1% level.

APPENDIX 6. Analysis of variance for slow-rusting from 25 faba bean lines of F_4 from ICARDA tested in Manitoba in 1979.

Source	D.F.	Sum of squares	Mean square	F values
		AUDPC		
Replications	3	2.1219	0.7073	1.09
Lines	24	1226.2350	51.0931	78.60**
Error	72	46.8000	0.6500	
Total	99	1275.1569		
				C.V. = 21.40%
		Final Disease Severity		
Replications	3	0.8075	0.2692	0.93
Lines	24	303.5163	12.6465	43.67**
Error	72	20.8488	0.2896	
Total	99	325.1725		
				C.V. = 26.31%

**Significance at 1% level.

APPENDIX 7. Analysis of variance for slow-rusting from 10 faba bean lines from University of Manitoba collection tested in 1979.

Source	D.F.	Sum of squares	Mean square	F values
		AUDPC		
Replications	3	0.2188	0.0729	0.13
Lines	9	1082.7250	120.3028	211.26**
Error	27	15.3750	0.5694	
Total	39	1098.3188		
				C.V. = 13.04%
		Final Disease Severity		
Replications	3	0.3500	0.1167	0.46
Lines	9	237.8750	26.4306	105.33**
Error	27	6.7750	0.2509	
Total	39	245.0000		
				C.V. = 15.41%

**Significance at 1% level.

APPENDIX 8. Analysis of variance for slow-rusting from 20 faba bean lines tested in Manitoba for the isolate SP51 in 1980.

Source	D.F.	Sum of squares	Mean square	F values
		AUDPC		
Replications	3	22.8438	7.6146	3.55*
Lines	19	762.2375	40.1177	18.72**
Error	57	122.1563	2.1431	
Total	79	907.2375		
				C.V. = 16.47%
		Final Disease Severity		
Replications	3	13.8344	4.6115	6.08**
Lines	19	149.3594	7.8610	10.37**
Error	57	43.2281	0.7584	
Total	79	206.4219		
				C.V. = 16.49%

*Significance at 5% level.

**Significance at 1% level.

APPENDIX 9. Analysis of variance for slow-rusting for 20 faba bean lines tested in Manitoba for isolate SP3 in 1980.

Source	D.F.	Sum of squares	Mean square	F values
		AUDPC		
Replications	3	24.5898	8.1966	6.07**
Lines	19	458.8711	24.1511	17.88**
Error	57	76.9883	1.3507	
Total	79	560.4492		
				C.V. = 19.94%
		Final Disease Severity		
Replications	3	1.4344	0.4781	0.65
Lines	19	170.0594	8.9505	12.18**
Error	57	41.8781	0.7347	
Total	79	213.3719		
				C.V. = 21.07%

**Significance at 1% level.

APPENDIX 10. Analysis of variance for slow-rusting from 15 faba bean selected lines tested to isolate SP51 in 1980.

Source	D.F.	Sum of squares	Mean square	F values
		AUDPC		
Replications	3	5.0583	1.6861	1.16
Lines	14	686.9208	49.0658	33.85**
Error	42	60.8792	1.4495	
Total	59	752.8583		
				C.V. = 16.20%
		Final Disease Severity		
Replications	3	0.4458	0.1486	0.21
Lines	14	177.2333	12.6595	18.11**
Error	42	29.3667	0.6992	
Total	59	207.0458		
				C.V. = 16.37%

**Significance at 1% level.

APPENDIX 11. Analysis of variance for slow-rusting from 13 faba bean lines tested to the isolate SP51 in 1981.

Source	D.F.	Sum of squares	Mean square	F values
		AUDPC		
Replications	3	5.1731	1.7244	0.75
Lines	12	1602.4183	133.5349	58.17**
Error	36	82.6394	2.2955	
Total	51	1690.2307		
				C.V. = 18.98%
		Final Disease Severity		
Replications	3	1.1346	0.3782	0.78
Lines	12	239.3942	19.9495	41.06**
Error	36	17.4904	0.4858	
Total	51	258.0192		
				C.V. = 19.38%

**Significance at 1% level.

APPENDIX 12. Analysis of variance for slow-rusting from isolated blocks of three faba bean lines tested to the isolate SP3 in 1980.

Source	D.F.	Sum of squares	Mean square	F values
		AUDPC		
Replications	2	6.1010	3.0505	1.06 NS
Lines	2	245.0418	147.5209	51.12**
Lines X Reps	4	11.5428	2.8857	16.17**
Locations	3	34.5097	13.1699	73.78**
Lines X Locations	6	1.3843	0.2307	1.29 NS
Error	18	3.2129	0.1785	
Total	35	356.7924		
				C.V. = 9.89%
		Final Disease Severity		
Replications	2	1.0485	0.5243	1.24 NS
Lines	2	60.9618	30.4809	71.90**
Lines X Reps	4	1.6957	0.4239	14.02**
Locations	3	4.5674	1.5225	50.36**
Lines X Locations	6	0.5565	0.0927	3.07*
Error	18	0.5442	0.0302	
Total	35	69.3741		
				C.V. = 8.05%

*Significance at 5% level.

**Significance at 1% level.

NS No significant differences.

APPENDIX 13. Analysis of variance for slow-rusting from isolated blocks of three faba bean lines tested to the isolate SP51 in 1980.

Source	D.F.	Sum of squares	Mean square	F values
		AUDPC		
Replications	2	15.4268	7.7134	2.91 NS
Lines	2	484.7476	242.3738	91.37**
Lines X Reps	4	10.6107	2.6527	2.39 NS
Locations	3	83.1039	27.7013	24.93**
Lines X Locations	6	9.5157	1.5859	1.43 NS
Error	18	20.0042	1.1113	
Total	35	623.4089		
				C.V. = 11.27%
		Final Disease Severity		
Replications	2	4.2118	2.1059	8.37*
Lines	2	203.7326	101.8663	404.66**
Lines X Reps	4	1.0069	0.2517	0.92 NS
Locations	3	2.0278	0.6759	2.48 NS
Lines X Locations	6	1.7535	0.2923	1.07 NS
Error	18	4.9063	0.2726	
Total	35	217.6389		
				C.V. = 10.86%

*Significance at 5% level.

**Significance at 1% level.

NS No significant differences.

APPENDIX 14. Precipitation for the years 1978, 1979, 1980 and 1981 at the University of Manitoba campus farm, Winnipeg.

	Total precipitation in mm.			
Period	1978	1979	1980	1981
June 1-15	8	10	00	40
June 16-30	20	53	39	51
July 1-15	44	7	4	21
July 15-31	39	7	18	14
Aug. 1-15	5	35	44	67
Aug. 15-31	50	61	50	35
Sept. 1-15	53	10	24	39
Total	219	183	179	267