CHARACTERIZATION OF THE COMPONENTS OF RATE-REDUCING RESISTANCE IN VICIA FABA TO UROMYCES VICIAE-FABAE

by

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A thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

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FOREWARD

The format adopted for the presentation of this thesis conforms to 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.

Two manuscripts, each consisting of the following sections: introduction, materials and methods, results and discussion, were prepared to adhere to the guidelines of the Canadian Journal of Plant Pathology, to which these manuscripts will be submitted for publication. A general introduction precedes, and a general discussion follows the manuscripts. The thesis finishes with a bibliography and a set of appendices.

GENERAL ABSTRACT

Mass-selected and bulk faba bean populations were evaluated at three developmental stages for the following components of rate-reducing resistance, to Uromyces viciae-fabae, in both field and growth cabinet studies: fleck number (FKN), uredinia number (UDN), infection type (IT), range of infection types (ITR), latent period (LP and LP_{50}), and LPSM, a standardized disease index combining latent period and uredinial density data. In addition, population performance in the field was compared using the following indicators: mean and final rust severity (RS and FRS, respectively), individual weekly assessments of rust severity (RS1 - RS4), apparent infection rate (AIR), and area under the disease progress curve (AUDPC). Significant differences (p-value <0.01) among the populations were found for all resistance components and population indicators. There was some variation in the expression of these characters among individual faba bean populations, but the division between the mass-selected and bulk populations was distinct. The mass-selected populations had fewer flecks and uredinia, a smaller infection type, a narrower range of infection types, and a longer latent period, in addition to reduced rust development in the field as determined by the performance indicators. The developmental stage of the faba bean plants, at the time of inoculation, significantly affected all of the components in the growth cabinet experiments and most in the field studies, suggesting that selection for rate-reducing resistance calls for the use of plants at the same developmental stage. Comparisons between components evaluated in the field and those evaluated in growth cabinets indicated

that the components UDN, latent period, and the index LPSM corresponded best with population performance in the field. These components could effectively be used in growth cabinets to screen faba beans, for rate-reducing resistance. On the other hand, the components FKN and IT did not correlate well with the field results.

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GENERAL INTRODUCTION

Disease resistance can be characterized in one of two ways, depending upon the type of host reaction elicited by the pathogen. The host can respond to invasion either by restricting the establishment of a parasitic relationship, or by restricting the colonization and growth of the pathogen following successful infection (Nelson, 1975).

Terms used to describe these two types of resistance are numerous because authors have attempted to describe and categorize resistance genetically, mechanistically, as well as epidemiologically (Robinson, 1969; Browning et al., 1977). Resistance to the establishment of a viable host-parasite relationship is often referred to as hypersensitive, race-specific, vertical, major-gene, or as qualitative resistance. On the other hand, terminology used to describe resistance to colonization and growth of the pathogen subsequent to infection includes the terms non-hypersensitive, race-non-specific, horizontal, minor-gene, quantitative, and rate-reducing, among others (Nelson, 1973; Robinson, 1976).

Race-specific resistance (synonymous with vertical resistance) is characterized genetically by the expression of a differential interaction between host genotypes and pathogen genotypes. It is effective against one or a few races of a pathogen, but ineffective against others. Epidemiologically, it functions by reducing the initial amount of inoculum that is available for disease development; thus it delays

the start of the epidemic (Van der Plank, 1968). Race-specific resistance usually behaves as a single gene trait in which resistance is dominant, and susceptibility recessive. This type of resistance has dominated conventional breeding programmes due to its ease of recognition in seedlings, simple inheritance patterns, and lack of variability in response to environmental fluctuations. However, race-specific resistance is subject to collapse when new physiologic races of a pathogen arise. Often the pathogen requires only a single genetic change to overcome a gene for resistance; consequently there are many examples of the ephemerality of this form of resistance (Van der Plank, 1978).

Host plants may also possess several resistance mechanisms which become functional once infection sites are established. These mechanisms tend to restrict the extent of colonization of host tissues, as well as the extent to which pathogens are capable of producing inoculum for subsequent infection. Resistances of this type reduce the amount of disease that develops by reducing the amount of disease that occurs within an infection cycle, as well as the rate of disease development from one infection cycle to another (Browning et al., 1977; Nelson, 1978). These resistances are known as race-non-specific (synonymous with horizontal resistance) and they are characterized by a lack of differential interactions with pathogen genotypes. They, often, but not always, result from the combined action of several genes, and it is their polygenic nature which accounts for their greater durability.

Race-non-specific resistance can be expressed in a variety of ways and a number of mechanisms have been proposed which might singly, or in combination, act in reducing the rate of epidemic development

(Parlevliet, 1979). Van der Plank (1963) described the following four manifestations of race-non-specific resistance: (1) reduced infection frequency, (2) reduced spore production, (3) increased latent period, and (4) reduced infectious period. Parlevliet (1979) has since suggested the addition of a fifth component to this list on the basis that differences in colony and lesion size have been noted in many host-pathogen systems. The latter component, however, may be monogenically inherited and as such is not by itself indicative of a more durable resistance (Parlevliet, 1979; Rashid, 1983).

In the rust of faba beans (Vicia faba L.), caused by Uromyces viciae-fabae (Pers.) Schroet., race-specific resistance has traditionally been employed in conventional breeding programmes (Papoyan, 1970; Mohamed, 1981). However, U. viciae-fabae, which is widespread on faba beans in the Middle East, North Africa, and on spring-sown crops in Europe (Mansour et al., 1968; Mohamed, 1981; Lapwood et al., 1984), has recently been shown to exist as numerous races (Conner and Bernier, 1982b; Singh and Sokhi, 1980). In Manitoba, it is thought that native species of Vicia and Lathyrus could be important sources of initial inoculum for these races (Conner and Bernier, 1982a,b). As a result, faba bean cultivars with specific single gene resistance to Uromyces viciae-fabae would be expected to give only short-lived control. Consequently, faba beans have recently been evaluated for more durable types of resistance such as the polygenically inherited rate-reducing resistance. At the University of Manitoba, Conner and Bernier (1982d) evaluated open-pollinated faba beans for their ability to retard development of rust. In field trials, they recognized three accessions which had consistently low area under the disease progress curve (AUDPC)

values, as well as six others which had AUDPC scores that varied from low to intermediate during three years of testing without selection. Shortly thereafter, Rashid (1983) recognized eight other faba bean selections as slow-rusters, and an additional four as moderate-rusters. These were characterized on the basis of AUDPC and final rust severity scores over three to four years of testing using mass selection techniques in which selections with high scores as well as those with undesirable reaction types (highly resistant or highly susceptible) were eliminated prior to harvest.

The objectives of this study were to evaluate the slow- and moderate-rusting faba bean selections for the components of rate-reducing resistance to determine if they could be used to differentiate among the populations. In order to investigate the variation in expression of the rust components, the faba beans were evaluated at three developmental stages, in both field and controlled environment studies, using two prevalent races of Uromyces viciae-fabae.

LITERATURE REVIEW

2.1 VICIA FABA L. (THE HOST CROP)

Faba beans (Vicia faba L.), the world's fourth most important pulse crop after dry beans, dry peas, and chickpeas (Hawtin and Stewart, 1979), have a potential as a 'medium protein and energy crop' (Hebblethwaite, 1983). As a member of the Order Leguminosae, Family Papilionaceae, faba beans have the capability to fix atmospheric nitrogen, thereby enhancing their use as a break for cereals (Slinkard and Buchan, 1980). In addition to its use as a source of vegetable protein for human consumption, the crop may also be used as a replacement for soybean meal in animal feeds (Canada, 1975), and as a 'high nitrogen green manure' (Robinson, 1968).

Despite these benefits, world-wide production of faba beans has remained relatively constant over the past decade with present production levels being approximately 4.2 metric tonnes. The crop is grown on 3.2 million hectares annually, in over 50 countries. China is the principal producer, with 55% of the total 1985 world production, whereas the next major producer, Ethiopia, contributed only 12%. Countries with faba bean yields in excess of 50 metric tonnes include Egypt, Italy,

France, Morocco, East Germany, Spain, and Turkey (FAO, 1985). Recently, production of the crop on a commercial scale has commenced in Canada, the United States, Australia, and New Zealand (Hebblethwaite, 1983).

Records indicate that Vicia faba is one of the oldest cultivated plants, with the earliest found remains dating back to 2000 B.C. (Kramer, 1956). The species is commonly divided into two subspecies, paucijuga and eu-fabae, according to a classification scheme proposed by Muratova (1931). Within the eu-fabae, three varieties based upon seed size and shape are recognized: the large-seeded var. major Herz., the intermediate-seeded var. equina Pers., and the small-seeded var. minor Beck. A significant quantity of the major type is harvested green for use as a vegetable whereas the equina and minor types are usually harvested dry (Hawtin and Hebblethwaite, 1983).

It is thought that Vicia faba probably originated in West (Cubero, 1974) or Central Asia (Ladizinsky, 1975a) and that the related species, V. narbonensis L. (Zohary and Hopf, 1973), is a possible progenitor. However, due to a lack of archaeological evidence neither the place of origin of V. faba nor the progenitor is known with certainty. Two species morphologically similar to Vicia faba, V. galilaea Plitm. et Zoh. and V. hyaeniscyamus Mout., have also been suggested as possible progenitors; however, as with V. narbonensis, dissimilarities in karyotype (Abdalla and Gunzel, 1979) and in albumin profiles of seed protein, as well as failure to hybridize, indicate a lack of affinity between the three wild species and Vicia faba (Ladizinsky, 1975b).

Domestication of faba beans occurred during the late Neolithic period and the crop is believed to have spread into Spain, Portugal, and

Eastern Europe during this time (Zohary and Hopf, 1973). By 3000 B.C., V. faba had spread throughout the Mediterranean region, south along the Nile Valley, and northwards into Europe where finds dating back to the Bronze Age have been uncovered (Hawtin and Stewart, 1979). In addition, it is assumed that faba beans were cultivated as far south as Ethiopia and as far east as Afganistan and that these two areas represent secondary centers of diversity (Lawes et al., 1983). Although uncertain, it is believed that this crop has been grown for some time in the Himalayan region of India and that it was introduced with the silk trade into China c.100 B.C. (Tao, 1981), and subsequently into Japan around 700 A.D. (Kogure, 1979). Remains more than 2,000 years old have been uncovered in the United Kingdom indicating that faba bean cultivation was widespread throughout this area (Bond, 1979). In the New World, faba beans were introduced into Central and South America by the Spaniards and Portuguese during the 16th century (Bond, 1976) and into eastern North America as a vegetable crop during the early 1600's (Hawtin and Hebblethwaite, 1983).

Field-scale cultivation in Canada began in 1972 when European cultivars were introduced as a potential protein crop during a period of high soybean meal prices (Furgal and Evans, 1980). These varieties were not well adapted to the drier Canadian conditions and it was in 1981 that Aladin, the first locally-bred cultivar, was licensed. This is a higher-yielding cultivar with greater yield stability and with protein content similar to the introduced cultivars (McVetty et al., 1981). Also in that year, a second Canadian cultivar, Outlook, was released for use in the irrigated areas of Saskatchewan and Alberta where it consistently out-yielded Aladin (Rowland et al., 1982). Recently, Pegasus,

the third Canadian bred small-seeded cultivar was released. Pegasus is 5% and 7% higher yielding than Outlook and Aladin, respectively (McVetty et al., 1985).

Faba bean yields in this country are comparable to those of cereals (Evans and Slinkard, 1975; Furgal and Evans, 1980), and at an average of 2,000 kg/ha (Platford et al., 1981), considerably higher than the 1983 world average of 1229 kg/ha (FAO, 1985). The area sown to faba beans in Canada is projected to be 40,000 ha by 1990(Slinkard and Buchan, 1980). The crop is confined primarily to Alberta and Saskatchewan where it is mainly grown under irrigation, and to the province of Manitoba where it is almost exclusively rain-fed. To facilitate handling with conventional cereal equipment, only major and equina varieties are grown, and these primarily for livestock feed, and since 1977, for export as human food. In Alberta, the crop is grown for silage, and in recent years between 2,000 and 5,000 ha have been allocated for this purpose (Slinkard and Buchan, 1980).

2.1.1 Cross-Fertilization in Vicia Faba

Vicia faba has a breeding behavior that lies somewhere between totally self-pollinating and obligately cross-pollinating. The mean amount of cross-fertilization in this crop is approximately 35% although values ranging from 4-84% have been reported (Bond and Poulsen, 1983). In Manitoba, the amount of cross-pollination has ranged from 8.5-58.8% (McVetty and Nugent-Rigby, 1984). According to Hawtin (1982), this

intermediate breeding mechanism couples some of the advantages of full autogamy such as independence of pollen vectors with some of the benefits of full allogamy including the exploitation of heterosis and the maintenance of heterogeneity within populations. However variability in the amount of cross-fertilization is responsible for the high degree of non-uniformity in open-pollinated populations and synthetics (DeVries, 1978) and this has led to difficulties in improving yield stability as well as in breeding for other traits (Gates et al., 1983). Consequently, considerable emphasis has been placed on the development of autogamous beans (Lawes, 1973) despite problems with reduced levels of autofertility and the loss of heterosis in inbred lines (Hawtin, 1982) although these may be restored upon hybridization (Poulsen, 1975).

Many factors other than plant genotype influence the level of cross-fertilization in faba beans. Bond and Poulsen (1983) in their discussion of the results obtained by a number of researchers (Picard, 1960; Kambal, 1969; El-Sherbeeny, 1970; Cubero, 1976; Hawtin and Omar, 1980; Porceddu et al., 1980) have concluded that while geographical location may play a role, the results are inconclusive. Nevertheless one would expect a trend towards increasing levels of outcrossing with higher latitudes due to an increased number of long-tongued bumble bees (Bombus spp.) in cooler regions. The size of fields and the location of plants within fields may also be important. Bond and Pope (1974) reported that more crossing occurs in small than in large fields and that a higher proportion of cross-breds result from field centers than from borders. On the other hand, Derenne (1966) noted 52% crossing on border plants and only 35% for plants further within a field. Hawtin and Omar (1980) observed similiar results. Bond and Poulsen (1983) suggest that in

fields up to 12 ha there is probably little difference in outcrossing except in the extreme border plants to which bees may have greater access. Plant density may affect the degree of crossing, but reports in the literature are inconsistent (Holden and Bond, 1960; Homola, 1973). Porceddu et al., (1980) noted higher levels of outcrossing on flowers at the lowest five nodes. This observation is in agreement with other reports (Hanna and Lawes, 1967; Poulsen, 1975) and is consistent with the reported tendency towards higher levels of auto- fertility on the upper nodes (Bond and Poulsen, 1983). It is suggested that this differentiation between the upper and lower nodes to ensures seed production during periods of variable pollen vectors (Poulsen, 1975). Also, higher percentages of outcrossing, in general, have been associated with the small-seeded variety minor (Holden and Bond, 1960; Filippetti and De Pace, 1982) although there are conflicting reports in the literature (Bond, 1976).

The considerable variation in levels of cross-pollination in faba beans and the consequent heterogeneity in progeny has led to difficulties in the development of a satisfactory breeding strategy. Breeding methods traditionally employed in the improvement of faba beans include modifications of either mass selection, recurrent selection or pure line selection (Hawtin, 1982). Perhaps the most success has been achieved by the use of mass selection. This technique has been particularly useful in the improvement of crop uniformity and has also been of benefit with characters of high heritability such as those associated with yield (Hawtin, 1982). Recurrent selection has also been useful, particularly with quantitatively inherited characters such as yield and disease resistance (Hawtin, 1978; Bernier and Conner, 1983). This technique is

in current use at the International Center for Agricultural Research in the Dry Areas (ICARDA), and in Egypt where it is used to improve populations for release as open-pollinated cultivars, or to provide a source of genetic variability through recombination for further improvements of the crop by other methods. In the past, it has been used successfully in the development of faba bean cultivars in England (Bond, 1979). Pure-line selection, on the other hand, has not led to much improvement in faba beans although this technique may be of some value with simply inherited traits (Nassib et al., 1978).

2.2 UROMYCES VICIAE-FABAE (PERS.)SCHROET. (THE PATHOGEN)

2.2.1 The Prevalence and Distribution of Uromyces viciae-fabae

Rust, caused by Uromyces viciae-fabae (Pers.)Schroet., is one of the more important foliar diseases of faba beans, possibly second in importance only to chocolate spot. U. viciae-fabae is world-wide in distribution. It causes a disease which is common in most faba bean growing areas yet it rarely results in significant yield reductions (Hiratsuka, 1933; Gaunt, 1983).

Rust of faba beans can be severe in the Middle East and North Africa. In Egypt, El Helaly (1939) reported that rust is the most destructive fungal disease of faba beans. It is prevalent in the northern areas, where disease severity can range up to 100% (Mohamed, 1981), although losses of 5 to 20% are more typical (Mansour et al., 1968). This

disease was first observed in Egypt, in 1925, and it is now of annual occurrence there, being most destructive on faba beans grown under irrigation or where rainfall is high (El Helaly, 1939; Mohamed, 1981). U. viciae-fabae has also been reported from Tunisia and Morocco where it is most severe along the wetter coastal regions (Blaeser-Diekmann, 1982). In Ethiopia, Iran, and Palestine, rust is considered to be responsible for significant reductions in faba bean yields, often in conjunction with chocolate spot (Palti, 1945; Kaiser et al., 1967; Mengistu, 1978). In Syria, Hanounik (1979) reported that faba bean rust was widespread, being present in 93% of the fields surveyed. He noted that rust was particularly severe late in the season, when it often resulted in extensive defoliation of the plants. Recently, this disease has been observed in the Sudan (for the first time since the early 1940's), in one of the largest faba bean growing areas within the country (Hussein, 1979). In Europe, Berthelem (1980) reported that U. viciae-fabae is more serious on spring-sown than on winter-sown faba beans because the fungus requires higher temperatures and lower humidities for superior growth. The author also noted that infection resulted in smaller and more shrivelled grain and that later-sown cultivars were most susceptible. In Scotland, Harrison (1984) reported that spring-sown faba beans were the most vulnerable, especially in drier weather, but that yield losses were still minor since the disease was most severe late in the season after many of the pods had already been set.

Reports of yield reductions attributable to rust infection are prevalent in the literature. Rademacher (1934) reported heavy losses in late-sown faba bean crops in Germany; and similarly, serious losses have been found to occur in Palestine (Reichert and Palti, 1946), Yugoslavia

(Kispatic, 1949), and more recently from Iran (Kaiser et al., 1967). Williams (1978), in Tasmania, observed a linear relationship between yield loss and rust severity at the pod filling stage. When rust was most severe, yields were reduced by as much as 45%. The yield losses were due almost entirely to a reduction in the weight of seeds per pod, an observation similar to that of El Helaly (1939).

In North America, faba bean rust has been recently reported from both Saskatchewan and Manitoba. In Manitoba, Bernier (1975) noted that rust occurred in trace amounts in 1973, but became more severe in 1974, especially on late-sown crops. He suggested that this disease may become serious, especially if infection should occur early in the growing season. In 1973, Mckenzie and Morrall observed rust in an irrigated field of faba beans and on two lines in an experimental plot at the University of Saskatchewan. The authors contend that the university isolate represents a new biotype of the fungus since these lines when grown previously remained infection-free. The authors consider rust to be a potential problem for faba bean production in Western Canada.

U. viciae-fabae has been found to be very damaging on lentils (Prasada and Verma, 1948; Gupta, 1974; Nene et al., 1975) and recently Richardson (1979) indicated that this pathogen can be seed-borne on this host. In the northern areas of India, U. viciae-fabae has also been shown to be economically important on peas (Sohi et al., 1974; Singh and Sokhi, 1980); however, some resistant material has been identified (Narsinghani et al., 1980).

2.2.2 Taxonomy of Uromyces viciae-fabae

The accepted name for faba bean rust is Uromyces viciae-fabae (Pers.)Schroet. (Laundon, 1968). Names synonymous with U. viciae-fabae include Uredo viciae-fabae Pers., Uromyces fabae (Pers.)De Bary, Uromyces orobi (Pers.)Fuckel, Uromyces viciae Fuckel, Uromyces polymorphus Peck & Clint., and Uromyces yoshingai P. Henn (Laundon and Waterston, 1965).

The legitimacy of the name Uromyces viciae-fabae is contingent upon the assumption that the original characterization of this rust by Persoon, in 1801, included a description of the telial state. Boerema and Verhoeven (1979) and Deighton (1960) contend that Persoon failed to describe the telia and therefore, based upon his description of the uredo only, Uredo viciae-fabae Pers. cannot be the legitimate basionym for the telial state. Boerema and Verhoeven (1979) state that the binomial Uromyces fabae based on Puccinia fabae Grev. has priority.

On the other hand, Jörstad (in Cummins, 1978) found telia in Persoon's collection of Uredo viciae-fabae, and Cummins (1978) and Laundon (1968) contend that Persoon did indeed refer to these in his original description. The authors point out that Persoon's reference to dark coloured sori suggests the presence of either telia or sori containing teliospores and that as a result the name Uredo viciae-fabae Pers. is an appropriate basionym for the perfect state and that the combination, Uromyces viciae-fabae (Pers.)Scroet., is the valid name for this species.

Although the name Uromyces viciae-fabae has gained wide acceptance in the literature (Cummins, 1962, 1978; Laundon and Waterston, 1965; Wilson

and Henderson, 1966; Cummins and Hiratsuka, 1983), names such as Uromyces fabae continue to be used (Kapooria, 1971; McKenzie and Morrall, 1975; Narsinghani et al., 1980; Pal et al., 1980; Hanounik and Maliha, 1985).

2.2.3 Biology and Life-Cycle of Uromyces viciae-fabae

Infection of faba beans with Uromyces viciae-fabae is usually restricted to the upper and lower leaf surfaces of the plants. However, when conditions are favourable for the pathogen, infection may spread to include stems and pods (Kaiser et al., 1967), and occasionally, partial or complete defoliation of plants may occur (Gaunt, 1983). Symptoms of this disease include the development of distinctive rust-coloured eruptions or pustules which at times may be surrounded by chlorotic halos. Late in the growing season, the pustules darken in colour due to the production of overwintering propagules (Martens et al., 1984).

Uromyces viciae-fabae is an autoecious macrocyclic rust known to infect many wild and cultivated members of the genera Lathyrus, Pisum, Vicia, Lens, and Orobus. The life-cycle of this fungus is complex, involving five different spore states, all of which may be produced on a single host. There are numerous descriptions of the five successive spore stages (basidiospores, pycniospores, aeciospores, urediniospores, teliospores) and those referring specifically to faba bean rust include Cummins (1978), Hiratsuka (1933), and Laundon and Waterston (1965).

Typically, it is the urediniospore state which is responsible for the damage attributable to this disease. However, in the lentil growing areas of India, aeciospores rather than urediniospores are the predomi-

nant source of inoculum, and when repeated production of aeciospores occurs, urediniospores are short-lived, being produced only very late in the season, and then followed rapidly by the production of teliospores (Prasada and Verma, 1948).

The teliospores, formed usually late in the season, are dark brown to black, single-celled, thick-walled, stalked spores which facilitate the survival of the fungus during periods of adverse environmental conditions. These spores germinate readily without a dormancy requirement when temperatures are suitable (12 to 22°C), and humidity is high (Prasada and Verma, 1948; Kispatic, 1949; Gupta 1974). Kispatic (1949) noted that teliospores on faba bean petioles germinated 10 to 15 days earlier than those on stems. This observation, in conjunction with the lack of a dormancy requirement, is important, particularly with autumn-sown faba beans (Kispatic, 1949).

Basidiospores are produced on germination of the teliospores and give rise to pycnia on upper and lower leaf surfaces. The pycnial stage occurs only infrequently in field-grown faba beans, but it is often observed in the laboratory (Gupta, 1974; Prasada and Singh, 1975). Studies on the sexual behavior of this rust have shown it to be heterothallic. Aecia develop most commonly on the underside of leaflets, but only when pycniospores from a pycnium of a particular mating type come into contact with a pycnium of opposite mating type (Brown, 1940; Prasada and Singh, 1975). Aeciospores are usually produced early in the season just prior to the formation of urediniospores. However, repeating aeciospores are known to occur, and secondary aecia are often visible eight to ten days after the appearance of the initial aecia; the former can be distinguished from the latter by the absence of pycnia

(Wilson and Henderson, 1966). Kispatic (1949) observed six to nine generations of aeciospores per season in Yugoslavia and he suggested that more generations per season were likely to occur in other faba bean growing areas. In northern India, as previously mentioned, rust spread from plant to plant occurs primarily by means of aeciospores; these may be produced in such great numbers that severe damage to the lentil crop ensues (Prasada and Verma, 1948). However, the authors noted that aeciospores were unable to retain their viability from one season to the next. This observation was also supported by Kispatic (1949) who added that aeciospores could possibly survive year-round in Mediterranean climates. Wilson and Henderson (1966) have suggested that the intermittent occurrence of rust on faba beans in February in south-western England may be due to the survival of aeciospores on seedling plants.

Uredinospores in this rust can form on aecial mycelium. This short-cycling phenomenon was first reported by Brown (1940) and it results in the complete omission of the aecial stage. Uredinospores can reinfect the host to produce several generations of uredinia; consequently, they are referred to as 'repeating' spores (Littlefield, 1981). Under most climatic conditions, it is the uredinial phase which is reponsible for disease epidemics. Kispatic (1949) found that between six and nine urediniospore generations could occur during the growing season, in Zagreb, Yugoslavia. He indicated the possibility of even greater numbers of generations in Dalmatia, Yugoslavia.

Prasada and Verma (1948) observed that urediniospores lose their viability quickly with increases in temperatures above the optimum of 17 to 18^0 C. This result was in agreement with Hiratsuka (1934) who also reported that urediniospores of this rust were not very heat tolerant.

Kispatic (1949) and others (Hiratsuka, 1934; Prasada and Verma, 1948) have reported, however, that the uredomycelium is very resistant to heat and sunlight and that this probably is important for the continued development and survival of the rust in hot, dry conditions. This rust also has been reported to produce amphispores, a modified form of the urediniospore with thicker walls which enable it to survive extended periods at high temperatures (Wilson and Henderson, 1966; Mckenzie and Morrall, 1975). Gaunt (1983) notes that there is no shortage of inoculum of this fungus, but that in all likelihood the dominant form of survival probably varies with different locations.

2.2.4 Host Range of Uromyces viciae-fabae

Wilson and Henderson (1966) cited Plowright (1889) as having first investigated the host specialization of Uromyces viciae-fabae. Plowright failed to infect any Lathyrus or Vicia species other than V. faba. He was, however, successful in infecting P. sativum in addition to V. faba. Gaumann (1934), using the same race of U. viciae-fabae as Plowright, summarized the work done to date and established the following six formae speciales:

1. f. sp. viciae-fabae de Bary on P. sativum and V. faba
2. f. sp. pisi-sativi Hiratsuka on P. sativum
3. f. sp. craccae Fischer on V. cracca, P. sativum, and weakly on V. hirsuta
4. f. sp. viciae-sepium Gaumann on V. sepium and V. faba
5. f. sp. viciae-nipponicae Hiratsuka on V. nipponica
6. f. sp. viciae-unijugai Hiratsuka on V. unijuga.

In addition, he recognized U. orobi (Pers.)Lev. as a separate species comprised of three formae speciales. Subsequently, Jörstad (1958) moved U. orobi to the U. viciae-fabae as f. sp. orobi.

In 1949, Kispatic, working in Yugoslavia, reported a much wider host range for faba bean rust isolates than had previously been described by Gaumann (1934). Kispatic recognized nine races on the basis of rust reaction on nine Vicia species as well as on lentil and pea. He obtained no infection of lentils, and most pea varities were classified as relatively resistant. Although Kispatic did not use the same rust isolates as Gaumann, his work refuted Gaumann's claim that the specificity of the formae speciales of U. viciae-fabae was restricted to two or three host species. More recently, Kapooria and Sinha (1966) showed differences in host range when eight Vicia species as well as Lathyrus aphaca were tested. In addition to V. faba, only V. biennis and V. narbonensis were the same as Kispatic's hosts. Subsequently, using a different rust collection, Kapooria and Sinha (1971) reported conflicting results on L. aphaca. Their results indicated that rust isolates were capable of infecting species included in the host ranges of several formae speciales.

In North America, U. viciae-fabae has been reported on nine Vicia spp., 21 Lathyrus spp. and Pisum sativum (Anonymous, 1960; Conners, 1967). In Canada, it has been found to infect six Vicia spp., six Lathyrus spp., and Pisum sativum (Conners, 1967). Recently, cross-inoculation studies by Conner and Bernier (1982a) have demonstrated that U. viciae-fabae isolates from native and introduced host species of Vicia, Lathyrus, and Pisum have still wider host ranges than those indicated in previous studies. The authors observed that isolates from V.

faba could be categorized into two groups based on their ability to infect either V. americana or L. latifolius. Isolates in these groups were able to infect hosts included in the host ranges of several of the formae speciales described by Gaumann (1934). The Pisum isolates from Manitoba and Quebec differed in host range (Conner and Bernier, 1982a). This study verified the existence of host specificity among isolates of U. viciae-fabae and indicated that the wide host ranges showed little relationship to the formae speciales described by Gaumann (1934).

2.2.5 Pathogenic Variability in Uromyces viciae-fabae

Different physiologic forms within Uromyces viciae-fabae have been identified (Hiratsuka, 1933; Gaumann, 1934; Brown, 1940) and the variability in virulence of specific isolates has been confirmed (Kispatic, 1944, 1949; McKenzie and Morrall, 1975; Singh and Sokhi, 1980; Conner and Bernier, 1982b).

Kispatic (1944) tested 14 faba bean cultivars against single spore isolates from three locations. He found it difficult to differentiate races due to the lack of cultivar uniformity. However, in 1949, he established nine races on the basis of their reaction on a number of pea varieties.

In India, Singh and Sokhi (1980) identified six physiologic races from seven isolates of U. viciae-fabae based on differential reactions of 11 lentil hosts. The authors propose that six pathotypes from seven isolates indicates high variability within this pathogen. Recently, an additional race on sweet pea was identified (Sokhi, 1984).

In Canada, Conner and Bernier (1982b,c) were able to identify sources of resistance to specific isolates of U. viciae-fabae in faba beans. They used these to differentiate 17 rust isolates collected from species of Vicia, Lathyrus, and Pisum. Seven faba bean inbred lines allowed the identification of seven rust races, and the use of 12 lines and cultivars of pea in combination with the faba bean inbreds allowed the characterization of an additional four races. The authors suggest that their results indicate that a great deal of variability exists within populations of this pathogen, in Manitoba. Further studies within the province (Murithi, 1984) have idenified seven additional races with virulence patterns distinct from those races previously identified, thus supporting Conner and Bernier's contention of the variable nature of this pathogen.

2.3 THE CONCEPTS OF DISEASE RESISTANCE IN PLANTS

The Southern corn leaf blight epidemic in the United States of America, in 1970 (National Academy of Sciences, 1972) demonstrated unequivocally the vulnerability of the world's major crop plants. As a result the potential for catastrophic yield losses once again became an important concern to agriculturists. The basis for this concern lay in the hazards created by the genetic homogeneity of crop systems. Crop uniformity was such that more than 75 % of the U.S. corn crop was susceptible to a new race of Cochliobolus heterostrophus.

In order to protect crops from disease, man has relied most conspicuously on the use of either chemical or biological methods. The environmental hazards of chemicals as well as their lack of cost-effectiveness has made biological means of disease control increasingly attractive. The most widely used biological method has involved the development and deployment of disease resistant varieties.

2.3.1 Disease Resistance Terminology

Resistance to disease has been variously defined. Russell (1978) describes it in a very broad context as any inherited characteristic of a host plant which lessens the effects of parasitism. Similarly, Simmonds (1983) defines resistance as a state of less disease, with immunity or the lack of disease as the limiting case. Robinson (1969) has defined resistance in more specific terms as the ability of a host to hinder a pathogen or disease causing agent, and Day (1974) has expressed it genetically as an attribute of the host which enables it to resist pathogens that would otherwise grow on it. Nelson (1977) has described resistance as an active, dynamic response of a host to a parasite, therefore excluding from his definition such passive phenomena as immunity, klenducity, and disease escape.

Disease resistance can be characterized in one of two ways, depending upon the type of host reaction elicited by the pathogen. The host can respond to invasion by restricting the establishment of a parasitic relationship or by restricting the colonization and growth of the pathogen following successful infection. In the latter situation,

resistance tends to be effective against many races or biotypes of the pathogen whereas in the former case, it is often only effective against a few races or biotypes (Nelson, 1975).

Terms used to describe these two categories of resistance are numerous (Table 1). This multiplicity of terms has arisen, in part, from the attempts of various researchers to describe and categorize seemingly different forms of resistance. Unfortunately, many of the terms imply characteristics of the resistances other than their effectiveness or lack of effectiveness, and as a result, are not synonymous. For example, the mode of inheritance has been used to differentiate between three types of resistance: monogenic, oligogenic, and polygenic, in which resistance is governed by one, few, or a number of genes, respectively. Similarly, different terms have been used to describe resistance that is expressed at different growth stages of the host plant. Seedling resistance is most pronounced in very young plants, although as Russell (1978) has stated, it may exist in mature plants as well. On the other hand, mature or adult plant resistance is not usually expressed in seedlings (Parlevliet and Van Ommeren, 1975).

Van der Plank (1963, 1968) introduced the terms 'vertical' and 'horizontal' to describe the resistance reactions of potato (Solanum tuberosum L.) varieties infected with various pathogenic races of Phytophthora infestans (Mont.) deBary. He observed that two potato varieties (Maritta and Kennebec) responded differentially when infected with P. infestans. The vertical fluctuations in a diagram depicting the resistance of these varieties to 16 races of the late blight pathogen prompted him to propose the term vertical resistance (VR). Furthermore, when Van der Plank examined the performance of two other potato

TABLE 1. DISEASE RESISTANCE TERMINOLOGY.

1. RESISTANCE TO THE ESTABLISHMENT OF A PARASITIC RELATIONSHIP

hypersensitive	vertical
race-specific	monogenic
non-uniform	oligogenic
differential	major-gene
unstable	qualitative
discriminatory	

2. RESISTANCE TO COLONIZATION AND SUBSEQUENT GROWTH OF A PATHOGEN

field	horizontal
non-hypersensitive	multigenic/polygenic
race-non-specific	minor-gene
uniform	partial
generalized	quantitative
stable	rate-reducing
durable	incomplete
dilatory	slow-(rusting/mildewing...etc.)

varieties (Capella and Katahdin) he noted that they reacted similarly to all 16 races, although Capella was consistently more resistant than Katahdin. This type of host response, Van der Plank, termed horizontal resistance (HR). In 1975, Van der Plank expanded his definition of HR, stating that "Characteristically, horizontal resistance slows epidemics down (reduced r). Sporulation is less abundant, or fewer spores infect, or the time taken from infection to sporulation is increased, or these effects occur together. And the effects derive, I believe, from a genetic basis distinct from that of vertical resistance."

Van der Plank's (1963, 1968) categorization of resistance as either vertical or horizontal has generated much debate in the literature. His definitions implied that the lack of host-pathogen interactions conferred HR with an inherent stability not found with VR. In addition, he suggested that HR is quantitative in expression, polygenically inherited, and displays a non-reduced initial amount of inoculum (X_0), but a reduced apparent infection rate (r). As Parlevliet (1979) has pointed out, these characteristics may be associated, although not necessarily. Buddenhagen and DePonti (1983) contend that the inadequacy of Van der Plank's terminology relates to the fact that HR and VR were described not only in epidemiological and genetic terms but also in interaction and specificity terms. Others have voiced similar concerns (Browning et al., 1977; Parlevliet and Zadoks, 1977; Nelson, 1978; Russell, 1978; Ellingboe, 1981).

Perhaps the most controversial aspect of Van der Plank's definitions surrounds his assumption that HR is distinguished by a lack of host-cultivar interactions. Many examples in the literature refute this contention (Jeffrey et al., 1962; Caten, 1974; Clifford and Clothier,

1974; Habgood, 1976; Kuhn et al., 1978). For instance, Parlevliet (1978) has shown that the barley cultivars Vada, Berac, and Julia, when tested against four leaf - rust races show no interactions between cultivars and races; the cultivar Vada being consistently the most resistant. Vada, according to Parlevliet, represents HR as defined by Van der Plank. Resistance in this cultivar is inherited polygenically, appears to be stable, is quantitative in expression, and has a reduced apparent infection rate (Parlevliet and Van Ommeren, 1975; Parlevliet, 1976,1978). Parlevliet (1977) has, however, observed a small but significant interaction, when a fifth race is introduced, that indicates race-specific aspects in the partial resistance of cultivar Julia to race 18. More recently, Parlevliet and Van Ommeren (1985) have reported a similar race-specific effect for the cultivar Berac and the barley leaf rust race 22. Similarly, the Oryza sativa - Xanthomonas oryzae system, also seems to show small race-specific effects. The rice cultivars, when arranged according to their respective levels of resistance to the bacterial leaf blight pathogen, show small cultivar - isolate interactions. The cultivars Selem Gempel and Cicih Godangan show the same rating to isolate Xo-7323 but a very different response to Xo-7306. However, isolate Xo-7306 infects Cicih Godangan and the cultivar Ketan Bulu equally, but Xo-7323 does not (Yamamoto et al., 1977).

From the standpoint of disease epidemiology, VR functions by reducing the initial amount of inoculum that is available for disease development. Van der Plank (1968) states that for pathogens such as P. infestans and P. graminis, there is as a result, a delay in the start of the epidemic. The effect of VR on epidemic development can be demonstrated mathematically by the following equation:

$$Xo = Xov\ e^{r\Delta t}$$

where Xo is equal to the proportion of infected foliage in a field without VR; Xov equals the proportion of infected foliage in a field with VR; r equals the infection rate; Δt = the lag time required for disease to increase; and e, the base of the natural logarithms is equal to 2.718. According to Van der Plank (1968) manipulation of this equation reveals that the delay in the epidemic is proportional to the logarithm of the ratio Xo/Xov, although not particularly sensitive to it. This implies that at low rates of infection, the benefits of VR are large whereas the effects are very small at high rates of infection, unfortunately at a time when they are most needed.

Horizontal resistance can influence many aspects of the disease cycle. It does so not by reducing the amount of initial inoculum as observed with VR, but by retarding or slowing down the rate of epidemic development once it has been initiated. Nelson (1978) therefore proposed the term 'rate-reducing' to describe this type of resistance. In rate-reducing types of resistance, the apparent or logistic infection rate, r, measures the speed of the epidemic and is estimated as follows:

$$r = \frac{1}{t_2 - t_1} \log_e \frac{x_2(1-x_1)}{x_1(1-x_2)}$$

where x_1 and x_2 represent the amount of diseased tissue at sampling times 1 and 2, respectively (Zadoks and Schein, 1979; Van der Plank, 1963).

2.3.2 Genetics of Resistance

Biffen (1905) was the first to report on the genetics of resistance to a plant pathogen. In his investigation of the inheritance of resistance to stripe rust he established that in Rivet wheat resistance was conferred by a single recessive gene. This was an important conclusion in that it demonstrated that resistance to Puccinia striiformis in wheat conformed to Mendalian principles and as such was heritable.

Ward (1902) was the first to recognize that pathogenic organisms differed genetically in their ability to cause disease in particular host genotypes. That is, only certain pathogen genotypes were capable of parasistizing certain host genotypes; others were avirulent. Similarly, shortly after Biffen's report, Barrus (1911) was also able to demonstrate variability in a pathogen. He reported that isolates of Colletotrichum lindemuthianum (Sacc. and Magn.)Bri. and Cav. differed in their ability to produce disease on varieties of Phaseolus vulgare. A few years after Barrus's report, Stakman and Levine (1922) reported on the variability in Puccinia graminis f. sp. tritici and this formed the basis for the elucidation of the concept of physiologic race.

Flor (1946, 1947) examined the relationship between genetic variability in the pathogen species andvariability in the resistance of the host, and he was able to conclude that for each gene conditioning resistance in flax (Linum usitatissimum) there was a specific gene in the flax rust fungus (Melampsora lini (Pers.)Lev.) determining pathogenicity. Flor's experiments showed a very simple pattern of genetic interactions between this host and pathogen and these results led him,

in 1955, to formulate the gene-for-gene theory (Flor, 1942; 1955). Briefly, Flor's (1956) theory maintained that "for each gene conditioning rust reaction in the host there is a specific gene conditioning pathogenicity in the parasite". Day (1974), as well as other authors, (Person, 1959; Flor, 1971; Person and Sidhu, 1971; Nelson, 1978; Ellingboe, 1984), have subsequently reported on the widespread applicability of the gene-for-gene theory to many economically important host-parasite interactions.

Although the biochemical basis of host-pathogen interactions has yet to be elucidated, a very simple hypothesis suggests that whereas dominant genes have a positive function, recessive genes do not. This hypothesis assumes that incompatibility results from the specific recognition of gene products produced by dominant genes in both the host and pathogen. However, if either or both genes are recessive, no recognition takes place between the host and pathogen, and compatibility or susceptibility results (Ellingboe, 1976).

Van der Plank (1963,1968), having defined vertical and horizontal resistance genetically, suggested that vertical resistance was controlled by a few genes and was race-specific whereas horizontal resistance was determined by many genes, each of small effect, and was race-non-specific. He further implied that vertical resistance adhered to the principles defined by the gene-for-gene theory whereas horizontal resistance did not. Subsequently, many authors have objected to the genetic definitions of the terms vertical and horizontal as well as to their epidemiological implications (Day, 1974; Ellingboe, 1975; Browning et al., 1977; Parlevliet 1977; Parlevliet and Zadoks, 1977; Johnson, 1981).

Vertical or race-specific resistance generally behaves in a qualitative fashion as a single gene trait in which resistance is dominant and susceptibility recessive (Van der Plank, 1963). Examples of this type of resistance are common in the literature (Biffen, 1905; Lupton and Macer, 1962; Ullstrup, 1965; Green and Campbell, 1979; Yuen and Lorbeer, 1983). Yuen and Lorbeer (1983) found that resistance to Bremia lactucae Regel in the lettuce (Lactuca sativa L.) cultivar Vanguard 75 was conditioned by a single dominant gene, and Green and Campbell (1979) noted that many of the wheat cultivars grown during this century have possessed this type of resistance. Recently, DeJong and Rademaker (1986) reported that a single dominant gene conditions white rust (Puccinia horiana Henn.) resistance of chrysanthemum (Chrysanthemum morifolium Ramat.). In addition, Lupton and Macer (1962) found that resistance to yellow rust of wheat was under the control of single genes. They found that resistance was inherited commonly as a dominant trait although in a few cases, it was inherited in a recessive manner. Resistance conferred by a single completely dominant gene is common having been identified from almost all economically important hosts to nearly all rust species.

Resistance conditioned by a single recessive gene is also common, being known to occur in several hosts (Samborski, 1963). In the inheritance of resistance to Puccinia graminis f. sp. secalis in barley, Steffenson (1984) identified a single recessive gene that was responsible for the resistance. Bartos et al., (1969) have found that the wheat cultivars Thatcher and Marquis possess specific resistance to race 9 of Puccinia recondita which is determined by a single recessive gene. Similarly, Sawhney et al., (1978) have reported that the resistance of

the wheat cultivar Chhoti lerma to race 122 of P. graminis f. sp. tritici is determined by two recessive genes.

Most cases of race-specific resistance are under oligogenic rather than monogenic control. The oligogenes may be either dominant or recessive or a combination of both dominants and recessives (Hooker, 1967). At least eight loci are thought to be involved in the yellow-rust resistance of Aegilops comosa Sibth. and Sm. (Riley et al., 1966) and the genetic control of resistance to powdery mildew in some barley cultivars is thought to involve several alleles with some of them operating at the same locus on a single chromosome (Moseman, 1966).

Many exceptions to this rather simple qualitative mode of inheritance have been reported. However, the majority of these can be readily explained by Flor's gene-for-gene theory and by the model describing the specific recognition of gene products (Flor, 1971). For example, in cereal-rust interactions, seven or more infection types have been recognized by early workers and these are known to be governed by single major genes. These infection or interaction types can be explained on the basis of partially functioning genes, the products of which interact to varying degrees with pathogen gene products to give a range of phenotypic expression.

It is often observed that resistance to rusts in cereals is inherited as an incompletely dominant character which implies a quantitative interaction of gene products. Similarly, many resistance genes are temperature-sensitive and their expression may either increase or decrease with increasing temperatures (Udeoglalanya and Clifford, 1978). This implied either impaired production or activity of products at unfa-

vourable temperature. There are instances of resistance being governed by complementary dominant host genes as in the oat variety Bond with regard to Puccinia coronata (Baker, 1966). And this suggests that the specific recognition factor is a complex molecule formed from a conjugation of two gene products.

A significant aspect of vertical resistance with respect to breeding is that while it is generally relatively easy to manipulate, it is subject to collapse when new physiologic races of a pathogen arise or increase in frequency. In many cases, the pathogen requires only a single genetic change to overcome a single gene for resistance. As a result there are many examples of the instability of this form of resistance in cereals to stem rust (Puccinia graminis), and in potato to late blight (Phytophthora infestans), as well as in many other host-pathogen interactions (Van der Plank, 1978). There are, however, instances where resistance conditioned by a single gene has been effective for many years (Johnson, 1984). For example, DeJong and Rademaker (1986) state that since testing began in Holland, in 1975, no break-down of white rust resistance has been observed in chrysanthemum. Similarly, resistance to stripe rust in some wheat cultivars has been long-lived (Grama et al., 1984).

2.3.3 Rate-Reducing Resistance

Nelson(1978) has stated that Van der Plank (1963) should have defined horizontal resistance in epidemiological terms rather than genetically.

He has suggested that since it is a resistance that reduces the apparent infection rate it should be referred to as rate-reducing or rate-limiting resistance. Incomplete vertical resistance can also slow down an epidemic and therefore rate-reducing (slow-rusting) is not characteristic of one form of resistance or the other. Nevertheless he does suggest that at least some slow-rusting might be conditioned by horizontal resistance.

The literature on the inheritance of rate-reducing types of resistance indicates a polygenic or quantitative inheritance (Nelson, 1978; Simons, 1975; Hooker, 1969). Hooker (1963, 1967) has reported that general resistance to northern leaf blight and leaf rust in maize is conditioned by many genes. Other examples of quantitatively inherited rate-reducing types of resistance in maize include that for brown spot (Moll et al., 1963), southern corn leaf blight (Pate and Harvey, 1954), and stalk rot (Kappelman and Thompson, 1966). Van der Plank (1984) notes that estimates of gene pair numbers range from less than two to greater than twenty, although more commonly from two to six.

In their investigation of the general resistance of maize to Puccinia sorghi, Kim and Brewbaker (1977) have found that one to three gene pairs are involved and that this trait is highly heritable (83.4%). Skovmand et al., (1978b) have reported that 2 to 12 pairs of genes are involved in the inheritance of slow-rusting resistance in wheat to stem rust. They obtained abnormally high numbers of slow-rusting progeny in crosses involving the spring wheat cultivars Idaed 59 and Kenya 58, which indicated that only a few genes condition slow-rusting. Luke et al., (1975) found that the slow development of crown rust (Puccinia coronata Cda. f. sp. avenae Eriks.) on Red Rustproof oats (Avena byzantina C. Koch)

was controlled by 2.16 genes and they estimated the heritability to be 87%. Simons (1975) has also reported that field resistance to oat crown rust is under polygenic control. Hepler et al., (1957) found the slow development of asparagus rust was controlled by at least four to five factors, and Parlevliet (1978) has provided evidence that seven loci appear to be involved in the inheritance of partial resistance in barley to leaf rust (Puccinia hordei). Gavinletvatana and Wilcoxson (1978) have demonstrated that the number of genes affecting the slow development of leaf rust in crosses among the wheat cultivars Lee, Marquis, and Thatcher is between 3 and 21 genes. They, as well as Skovmand et al., (1978b), note that gene number estimates are conservative for many reasons, but especially so since in hill plantings, rust spread from fast to slow rusters leads to high inoculum densities and consequently an underestimation of the number of genes involved.

Specific resistance genes may be involved in the control of rate-reducing types of resistance. Nelson (1978) has proposed that race-specific, major gene resistance and non-race-specific minor gene resistance are conditioned by the same genes. Martinez-Gonzalez et al., (1983) reported that slow-rusting in Era wheat was due to the combined effects of the specific genes Sr5, Sr6, Sr8, Sr9a or 9b, Sr11, Sr12, Sr17, and perhaps others. They noted, however, that Era might, in addition, possess other factors that condition slow-rusting because many of its ancestors rusted slowly. Skovmand et al., (1978a) found that the genes Sr5, Sr7b, and Sr11 did not affect slow stem rust development on wheat. They noted, however, that the genes Sr6 and SrTt-1 interacted with the genes controlling slow rust development, but that these genes per se were not responsible for slow-rusting since a few lines

containing them rusted rapidly. Similarly, Ayers et al., (1981) reported that specific genes in the slow-rusting spring wheat line FKN had little effect on AUDPC which the authors used as a measure of slow-rusting ability. They observed, however, that progenies with the gene Sr9b either alone, or in combination with the genes Sr5 and Sr8 resulted in smaller AUDPC values, but fast-rusting progenies with Sr9b were also identified. The authors suggest that therefore factors other than gene Sr9b condition the slow-rusting trait. Rowell (1981) was unable to separate the resistance mechanisms in the wheat cultivar Idaed 59 which has specific resistance to P. graminis f. sp. tritici conferred by the gene SrTt-1. This gene or a dominant gene closely linked to it has been identified as one conditioning low receptivity and thus slow- rusting ability in Idaed 59 (Rowell and McVey, 1979).

In addition to Rowell's (1981) work in which he noted that the gene SrTt-1 conditioned slow-rusting resistance in Idaed 59, other authors have provided evidence for single gene control of this type of resistance. Habgood (1972) presented evidence to indicate that resistance to Rhynchosporium secalis in the winter barley cultivar Vulcan was due to a single gene. Similarly, Martin and Ellingboe (1976) showed that a single gene Pm4, was responsible for the observed slow-mildewing of wheat infected with cultures of Erysiphe graminis f. sp. tritici carrying the compatible virulence gene, p4. They demonstrated that differences in compatibility among the three possible compatible parasite/host genotypes (P4/pm4, p4/Pm4, and p4/pm4) could be detected and that the p4/Pm4 parasite/host genotype resulted in a slower rate of development. Their results indicated that gene-for-gene relationships are applicable to horizontal (rate-reducing) resistance.

Residual effects of 'defeated' major genes, i.e., resistance genes that have been overcome by a pathogen with matching virulence genes, have been suggested to contribute to rate-reducing types of resistance (Nass et al., 1981; Brodny et al., 1986; Leath and Pedersen, 1986). Martin and Ellingboe (1976) reported that the race-specific resistance gene, Pm4, reduced the infection efficiency of a powdery mildew isolate with virulence gene P4, compared to a near-isogenic winter wheat line with the recessive allele, pm4. Nass et al., (1981), working with near-isogenic winter wheat lines with mildew resistance genes Pm3c, Pm4, or MA observed that they had lower disease efficiency and sporulation than the recurrent parental line Chancellor, when inoculated with E. graminis isolate 144, possessing virulence against these genes. They suggested that these effects on isolate 144 were residual expressions of Pm3c, Pm4, and MA. Recently, Brodny et al., (1986) have demonstrated residual effects of the wheat stem rust resistance genes Sr6, Sr8, and Sr9a on pustule size and sporulation capacity. They also noted that residuality was greater when the three genes were combined in one line, than from either single genes or any paired gene combination. Additionally, residual effects of 'defeated' genes have been reported for northern leaf blight of maize caused by Exserohilum turcicum (Pass.)Leonard and Suggs (Leath and Pedersen, 1986). Anderson (1982) has suggested, however, that residual gene resistance may be attributable to near-isogenic lines that "were not as nearly isogenic as intended." Consequently, the possibility exits that unidentified quantitative resistance genes were transferred along with the qualitative genes during production of the near-isogenic lines. Royer et al., (1984) has shown that the near-isogenic wheat line CI 14118, with the resistance gene Pm2 from the cultivar Ulka, does not possess the same level of partial resistance to

compatible mildew races as does the near-isogenic line CI 14119, with Pm2 from CI 12632. The authors suggest that this result indicates the importance of background differences in the expression of resistance.

There is considerable evidence in the literature to indicate that most of the gene action conditioning rate-reducing types of resistance is additive (Caldwell et al., 1957; Pope, 1968; Parlevliet, 1976; Nelson, 1978; Grama et al., 1984). Caldwell (1968) and Caldwell et al., (1957) have noted that the collective action of minor genes conditions a resistance similar to major genes and Parlevliet (1976) has reported that partial resistance is conditioned by minor genes. Pope (1968) has suggested that wheat cultivars that were susceptible to stripe rust might possess minor genes that could be added to minor genes in other moderately resistant cultivars to enhance the level of resistance. Grama et al., (1984) observed additive gene action for stripe rust resistance in wild emmer, that was indicated by the occurrence of transgressive segregation towards resistance.

2.3.4 Components of Rate-Reducing Resistance

2.3.4.1 Infection Frequency (IF)

Infection frequency (Parlevliet, 1977; Parlevliet and Kuiper, 1977a; Jeger et al., 1983), also referred to as disease or infection efficiency (Shaner, 1973; Shaner et al., 1978; Rouse et al., 1980; Villareal et al., 1981; Ahn and Ou, 1982b), infectibility (Wahl et al., 1980), and

receptivity (Mortensen and Green, 1978; Nutter and Pederson, 1985), is defined by Parlevliet (1979) as the proportion of spores resulting in sporulating lesions. Ahn and Ou (1982b) have equated this component to the ratio between the number of lesions per unit area of leaf and the spore concentration of the inoculum (mathematically expressed as: IF=Y/X, where Y is the number of lesions per unit area of leaf and X is the proportion of spores in the inoculum).

In rust diseases, this component is usually recorded as uredinial number per unit area (Martin et al., 1979; Milus and Line, 1980; Neervoort and Parlevliet, 1978). In mildews, evaluation is contingent upon the number of conidia having formed elongating secondary hyphae (Carver and Carr, 1977; Rouse et al., 1980), and in diseases such as glume blotch of wheat, lesions are examined for the presence of Septoria nodorum (Berk.)Berk. pycnidia (Jeger et al., 1983; Lancashire and Jones, 1985).

Low infection frequency is considered to be a major contributing factor to rate-reducing types of resistance. Asher and Thomas (1984) noted that in addition to it being the easiest component to measure, IF made the greatest contribution to the slow-mildewing resistance of spring barley. Parlevliet and Kuiper (1977a) likewise found IF to be significantly correlated with the levels of partial resistance of barley cultivars to leaf rust (Puccinia hordei) in the field. Mortensen and Green (1978) reported that low receptivity was important in the resistance of the slow-rusting cultivars Glenwari, Warigo, Hopps, and Idaed 59, to wheat stem rust. Field trials have indicated that the observed low receptivity of the latter cultivar, at the heading stage, reduced infection to about 92 to 98% in comparison to that on the susceptible wheat Purdue 5481CI (Rowell, 1982; Rowell and McVey, 1979).

Although the importance of infection frequency has been established many researchers have noted difficulties with the use of this component as a measure of rate-reducing resistance. For instance, Villareal et al., (1981) have emphasized that IF is only a relative measure because a true ratio of the number of infection sites to the number of spores applied cannot be obtained since not all spores in the inoculum settle or stay on host tissues. Johnson and Wilcoxson (1979) have found that selection for IF in the slow-rusting of barley is ineffective since IF is often associated with a high variability. They suggest that this variability is most probably due to the non-uniform inoculation of plants. Others tend to agree. For example, Shaner and Finney (1980) have reported a large variation in uredinia numbers on the winter wheat cultivars Monon and CI 13227, which they attribute to difficulties in obtaining uniform spore deposition. Similarly, Parlevliet and Kuiper (1977a) have found that the number of uredinia varies greatly from one plant to another and from one leaf part to another giving a large error variance despite use of large numbers of replicates. They, too, suggest that this large error is due to difficulties in obtaining even inoculation and uniform dew formation. Parlevliet (1977) in his assessment of IF in the barley - leaf rust system found a coefficent of variation (C.V.) equal to 21% associated with this component. He hypothesized that this relatively high C.V. was responsible for his inability to discern a cultivar - isolate interaction although one was indicated for the cultivar Julia - isolate 18 combination.

As these examples from the literature suggest, measurement of IF necessitates the uniform inoculation of the plants under investigation. Ahn and Ou (1982a) reported that in the blast disease of rice, an

increase in spore concentration resulted in a concomitant increase in the number of lesions. Parlevliet and Kuiper (1977a) have indicated that cultivar effects on IF may be density dependent. They suggested that testing for cultivar differences should be done at low spore densities as this is more indicative of the field situation.

Other environmental and host effects have been shown to influence infection frequency. In a recent report, Nutter and Pederson (1985) observed that receptivity increased as the duration of leaf wetness was increased following inoculation of barley seedlings with spores of Pyrenophora teres. Wahl et al., (1980) observed no significant differences with IF in wheat seedlings infected with stem rust. In adult plants, however, significantly fewer uredinia developed on the slow-rusters than on their fast-rusting counterparts. They concluded that this component of resistance was strongly influenced by differences in plant growth stage and was thus inappropriate for use in the detection of slow-rusting in wheat seedlings. Similarly, Martin et al., (1977) found that some wheat lines exhibited low numbers of stem rust uredinia in both seedlings and adult plants whereas in other lines only adult plants or portions of these plants showed reduced receptivity. They indicated that caution should be exercised when extrapolating conclusions from one stage of plant development to another.

Interactions between infection frequency and other components of resistance have been reported. Neervoort and Parlevliet (1978) noted that the components IF, spore production, and infectious period showed compensatory effects. A high IF tended to reduce the infectious period and the spore production per lesion per day. The compensatory effects between IF and spore production were especially pronounced. Leonard

(1969) observed decreased sporulation per pustule of P. graminis f. sp. avenae, as the number of pustules increased per leaf in partially resistant oats. Similarly, Rouse et al., (1984) have demonstrated an exponential decrease in the cumulative number of spores produced per mildew colony as the number of colonies increased on primary leaves of three wheat cultivars. Parlevliet and Kuiper (1977a) have reported a correlation between IF and latent period (r=0.80), in the adult plant stage. They suggested that this association was most likely responsible for the observed connection between IF and partial resistance of barley cultivars to leaf rust in the field. In addition, Jeger et al., (1983) have reported that IF was significantly correlated with lesion cover and incubation period in the glume blotch of wheat.

Evidence concerning the nature of the genetic control of infection frequency is at present inconclusive. Rowell (1982) reported that a single dominant gene conditions low receptivity to infection by stem rust in the wheat cultivars Idaed 59 and W2691SrTt-1. This gene is either very closely linked or identical to the specific resistance gene SrTt-1. Rowell and McVey (1979) reported that low receptivity is controlled by one recessive gene in the wheat cultivar Lee, and two recessive genes in Thatcher. On the other hand, Parlevliet (1977) has hypothesized that IF is under polygenic control. Recently, Modawi et al., (1985) demonstrated the lower receptivity of wheat lines possessing the gene Lr2c, as compared to those lines without Lr2c, when inoculated with cultures 6 and 17 of P. recondita, but the absence of such a difference in lines having Lr1 or Lr3a suggests that there is a residual effect of specific genes that relate to low infection type in some cases, but not in others.

2.3.4.2 Latent Period (LP)

Incubation period, defined as the time from inoculation to the initial appearance of symptoms, and latent period, the time between inoculation and sporulation (Parlevliet, 1979), are resistance components that have been studied extensively since they can be measured reliably and are found to correlate well with performance in the field (Parlevliet, 1975; Jones, 1978; Shaner, 1980; Subrahamanyam et al., 1983; Asher and Thomas, 1984). Parlevliet et al., (1985) state that LP is by far the most reproducible component and the easiest to measure. Other researchers tend to agree. Lancashire and Jones (1985) observed that LP had a lower variability (C.V.=12.4%) than all other components evaluated, except lesion width, in the glume blotch of winter wheat. They also point out that this low value is consistent with Lewontin's (1965) suggestion that opportunistic species should have short and stable generaton times. Parlevliet (1977) reported a C.V. for LP of 1.9% and he concluded that LP was the most sensitive component of the partial resistance of barley to leaf rust. Shaner and Finney (1980) also noted that in the leaf rust of winter wheat, LP was the component measured with the least error even when the percentage uredinia erupted was visually estimated. Parlevliet and Van Ommeren (1975) found that the LP of P. hordei, when measured in young flag leaves of barley, correlated very highly with levels of partial resistance in the field ($r = -0.94$ and $r = -0.91$, in 1973 and 1974, respectively). In fact, Neervoort and Parlevliet (1978) and Parlevliet et al., (1985) have shown that LP alone estimated the partial resistance as well as all the other components in combination.

Assessment of this component has, for the most part, been restricted to studies conducted in the greenhouse or in growth chambers. However, Parlevliet (1975) and Shearer and Zadoks (1972), in small-scale field studies, have estimated the LP of P. hordei and S. nodorum, respectively. In both these studies, as well as in others (Sztejnberg and Wahl, 1976; Martin et al., 1979; Osman-Ghani and Manners, 1985), the characterization of LP was based upon visual assessment of the time after inoculation at which the earliest lesion sporulated. Shaner (1980) has indicated, however, that this method does not necessarily provide an accurate estimation of LP because hosts may differ markedly in the time required for the same proportion of lesions to sporulate, although differences in minimum LP may be small. Other researchers have characterized LP as the time between inoculation and the appearance of 50% of the lesions (Parlevliet, 1975; Johnson and Wilcoxson, 1979; Subrahmanyam et al., 1983; Nutter and Pederson, 1985). This approach, however, provides no information about the minimum LP nor about the rate at which lesions become infectious (Shaner, 1980). Shaner et al., (1978) have attempted to overcome these problems with estimation of LP by the calculation of a weighted average latent period, using the formula:

$$LP = \sum_{i=0}^{n} P_i \; t_i$$

where Pi is the proportion of sporulating lesions in relation to the final number of sporulating lesions that appear on the ith day after inoculation; ti is the ith day after inoculation, and n is equal to the number of days after inoculation when the maximum number of lesions are sporulating. A modified expression of LP as the time at which 50% of the lesions are sporulating is obtained by the regression of the probit

of the proportion of lesions erupted on the number of days following inoculation. From this, T_{50} (the day by which 50% of the uredinia had erupted), an estimate of LP, can be obtained with the advantage that daily observations are not as necessary as they are for the calculation of the weighted average latent period.

There are numerous examples of the effectiveness of latent period as a method of distinguishing rate-reducing types of resistance. Ohm and Shaner (1976) reported that the LP for P. recondita f. sp. tritici was longer by a factor of 1.2 to 1.8 in slow-rusting winter wheats when compared to fast-rusters. Similar results have also been noted by Milus and Line (1980); Nutter and Pederson (1985); and Shaner and Finney (1980); as well as others. Subrahmanyam et al., (1983) found that the LP of P. arachidis in peanuts decreased substantially from highly resistant to resistant to moderately resistant genotypes whereas the moderately susceptible and suceptible groups differed very little with respect to this component. Similarly, Wahl et al., (1980) reported that while they did not observe differences in infectibility in wheat seedlings inoculated with P. graminis f. sp. tritici, they did find that uredinia developed much more rapidly in Prelude, a fast-rusting cultivar as compared to the slow-rusting wheat Thatcher.

Parlevliet (1979) has stated that when measuring latent period, plants should be compared at the same stage of development since this can greatly influence results. For example, the high correlations between this component and levels of partial resistance in the field refer primarily to those situations where LP is measured on adult plants. Correlation coefficients between partial resistance and LP measured on seedlings are typically very much smaller. Parlevliet et

al., (1985) have found that measurement of latent period in the young flag leaf is a very reliable selection criterion for partial resistance to barley leaf rust. Similar results have been obtained for yellow rust of barley (Parlevliet, 1980) as well as in rye for P. recondita f. sp. tritici (Parlevliet, 1977) and in wheat for P. recondita f. sp. tritici (Parlevliet, 1980). Such results have not been restricted to the cereal rusts. Jones (1978) observed that oat cultivars infected with powdery mildew caused by Erysiphe graminis f. sp. avenae showed small differences in incubation period at the seedling stage (from 4.5 to 6 days) but large differences at the adult stage (from 4.0 to 12 days).

Parlevliet (1975), in his examination of the partial resistance of barley to leaf rust, observed that all cultivars showed an increase in LP from the primary leaf up to the flag leaf. The LP of the flag leaf then decreased with aging. This pattern, although discernible in susceptible cultivars, was much more pronounced in resistant cultivars. Parlevliet concluded that not only does LP vary with developmental stage and leaf age, but also with the leaf position on the plant and the location on the leaf itself. He observed that LP appears to be shorter at the leaf margins. This observation has also been noted by Yarwood (1961) with bean rust, and with brown rust of wheat by Mehta and Zadoks (1970). Osman-Ghani and Manners (1985) have reported that latent periods were longer on flag leaves than on seedling leaves.

Parlevliet (1975) has examined the effect of temperature as well as light intensity and daylength on LP in the barley - leaf rust system. He has concluded that there are no indications of these environmental factors influencing the cultivar effect on LP. Kochman and Brown (1975) have also reported that the development of P. coronata f. sp. avenae on

oat cultivars is insensitive to temperature effects. However, they did observe that for P. graminis f. sp. avenae, LP was shorter at 30 - 35°C than at 20 - 25°C. Shearer and Zadoks (1972, 1974) examined the effects of temperature and the duration of leaf wetness on the latent period of S. nodorum. They observed that under field conditions and in growth chamber experiments, an increase in temperature and an increase in the duration of leaf wetness both caused LP to decrease. The magnitude of the response was similar (up to seven days) under both sets of conditions.

Latent period has been shown to be associated with many other components of rate-reducing resistance. As previously indicated, there is a strong association between latent period and the level of partial resistance in the field (Parlevliet and Van Ommeren, 1975; Neervoort and Parlevliet, 1978; Parlevliet et al., 1980; Parlevliet et al., 1985; Statler and Parlevliet, 1987). Parlevliet et al., (1985) have hypothesized that genes that control latent period most likely also govern partial resistance to a large extent. Parlevliet (1980) has also found a strong association between infection frequency and latent period in the barley - yellow rust system. Recently, in further investigations of this system, Parlevliet (1986) has observed that these components are governed by the same genes and are pleiotropically associated.

Latent period has been estimated to be controlled by three to six genes acting in an additive manner in the barley cultivars Sultan, Volla, Julia, and Vada (Parlevliet, 1978), and three to four in Cebada Capa (Parlevliet and Kuiper, 1977b). Parlevliet (1980) found that the cultivar L94 carries no genes for a longer LP, whereas Vada carries five to six minor genes, and Cebada Capa possibly three to four. These

authors have demonstrated that recombination and accumulation of these genes for a longer LP is possible. Parlevliet et al., (1985) have shown that lines obtained through selection for a longer LP in the greenhouse possess a very high level of partial resistance. They have concluded that genes governing LP also govern partial resistance to a large extent. Lee and Shaner (1985) have indicated that the long LP of P. recondita on some slow-rusting wheats is determined by two to three recessive genes showing additive effects. They suggest that wheats with a very long LP can be selected for by making crosses among different slow-rusting cultivars, since all crosses that they examined displayed transgressive segregation.

2.3.4.3 Spore Production (SP)

The estimation of spore production, expressed variously as SP per unit leaf area, SP per lesion or pustule, SP per unit area of lesion, or SP per unit area of sporulating area (Parlevliet, 1979), is a sensitive method of assessing resistance. Johnson and Taylor (1976) have indicated that not only does SP measure the sum of the effect of all components, but that it is also a much more precise estimate than that of the other components. The use of SP makes it possible to detect differences often overlooked by the use of other components. For example, Mortensen and Green (1978) reported that the resistance of the wheat cultivar Exchange was due to its low urediniospore production per pustule despite its relatively high receptivity to the three stem rust races tested.

The slow-mildewing resistance of the wheat cultivar Knox is also partly attributable to its low spore production (Shaner, 1973).

Sharma and Heather (1979) found that resistant clones of Populus resistant to leaf rust produced fewer urediniospores per uredinium than the moderately susceptible clones. This pattern of higher numbers of urediniospores per pustule on more susceptible tissues is in agreement with similar observations for P. graminis on oat cultivars (Leonard, 1969) and P. hordei on four cultivars of barley (Clifford and Clothier, 1974). Recently, Osman-Ghani and Manners (1985) reported substantial differences between cultivars in spore production per unit area of leaf. They observed that more spores of yellow rust were produced on leaves of the spring barley cultivars Astrix and Senta than on Sultan and Zephyr.

Attempts by various researchers to quantify differences in SP in susceptible and resistant hosts has yielded varying results. Jeger et al., (1983), for instance, observed that twice as many spores of S. nodorum per square centimeter diseased tissue were produced on the winter wheat cultivar Maris Ranger than on the more resistant cultivar Maris Huntsman. Shaner et al., (1978) found that P. recondita produced two to three times more inoculum on the winter wheat cultivars Monon and Suwon 92 than on the slower-rusting cultivars Suwon 85 and P6028. Villareal et al., (1981) have reported a much greater, sixfold to seven-fold, increase in the number of spores produced on a susceptible rice cultivar than on two cultivars possessing slow-blasting resistance.

Spore production is a very difficult component to measure accurately, primarily because of its dependency upon many factors. Lancashire and Jones (1985,) working with S. nodorum found that components associated

with sporulation (mean spore density, growth of spore density, mean number of spores, and growth of spore number) had the greatest variability (e.g., 64.9% for the increase of spore density). Rouse et al., (1980) observed that the wheat cultivar Vermillion had reduced sporulation compared with the cultivar Knox. Shaner (1973), however, observed less sporulation on Knox than on Vermillion. Rouse et al., (1980) suggested that this inconsistency was due to differences in the developmental stage of the plants used. Furthermore, they noted that the use of screening methods involving only seedlings could lead to erroneous conclusions. Other workers have observed similar results. Mortensen and Green (1978) found that with respect to SP, results with seedlings conducted in growth chambers did not correlate well with slow-rusting in the field, nor with SP on adult plants under controlled conditions. Other studies involving wheat stem rust (Martin and Miller, 1974; DePauw and Bucannon, 1975) and barley leaf rust (Parlevliet, 1975; Neervoort and Parlevliet, 1978) also support these conclusions. On the other hand, Johnson and Taylor (1976) cite a number of examples where measurement of SP in seedlings has adequately assessed resistance levels.

Spore production is dependent on many factors in addition to differences in plant age. Jeger et al., (1983) reported that spore production per square centimeter diseased tissue was linearly related to the product of maximum temperature and the duration of leaf wetness. Osman-Ghani and Manners (1985) reported that in all barley cultivars examined except for one, spore production was significantly lower at higher temperatures. Mehta and Zadoks (1970) have observed a dependency of SP on inoculum density. A high spore deposit leads to high pustule density and high pustule density causes a short LP, a high rate of

pustule opening, a steep increase of daily SP, an early and high maximum of daily SP, a relatively rapid decrease of daily SP and a relatively short sporulation period. They found, however, that total SP is independent of inoculum density and pustule density. These conclusions agree with the results of Yarwood (1961) with bean rust. Johnson and Taylor (1976) attribute this independence to the fact that with few pustules per unit area of leaf, the pustules were larger and sporulation occurred over a longer period than with many pustules per unit area. On the other hand, Shaner et al., (1978) observed that P. recondita of a common size on the winter wheat culivars Monon, Suwon 92, and Suwon 85 produced essentially equal numbers of spores. The observed lower productivity of uredinia on Suwon 85 was due almost entirely to their smaller size. The authors showed also that uredinia on P6028, which has greater slow-rusting resistance than Suwon 85, were not only smaller than uredinia on Monon and Suwon 92, but also produced few spores per square millimeter of uredinium.

In general there tends to be a negative correlation between SP per pustule and pustule size, as well as between pustule density and infection frequency. Nelson (1975) has suggested that in order to compare the SP of various lines, similar infection frequencies must be used, but this is very difficult to do in practice due to the typically high variability of this component. Good results often can be obtained by examining total SP because this is often less dependent upon inoculum density, however, since SP can occur over a period of 65 days under near optimal conditions, this too can be difficult to estimate accurately (Johnson and Wilcoxson, 1970). Neervoort and Parlevliet (1978) did, however, measure total SP per unit leaf area in the barley - P. hordei

system and found that it, like LP, was highly correlated with levels of partial resistance in the field (r=0.85). They suggested, however, that the LP is the preferable measure since it is estimated more easily, more accurately, and sooner after inoculation.

Spore production appears to be influenced by a number of minor genes. Mortensen and Green (1978) indicated that low urediniospore productivity in conjunction with low receptivity is probably inherited in a complex manner in wheat cultivars to stem rust, and as a result would probably be difficult to breed for.

2.3.4.4 Infectious Period (IP)

Very little work has been done on examining the significance of the length of the infectious period, defined as the period during which an infected leaf produces a demonstrable amount of spores (Mehta and Zadoks, 1970), on the rate of epidemic development. This is attributable to the fact that the majority of spores tend to be produced soon after pustule maturation and also because infectious period shows a negative correlation with infection frequency (Mehta and Zadoks, 1970; Parlevliet, 1979). There is, however, at least one example in the literature which indicates clear differences in infectious period among susceptible and resistant cultivars. In the barley - leaf rust interaction in which the resistant cultivar Vada has been shown to have a shorter infectious period relative to the susceptible variety L94. Parlevliet (1979) notes, however, that this shorter infectious period

can in part be explained by a longer latent period and the earlier termination of spore production in the more resistant cultivar.

Mehta and Zadoks (1970) showed that in primary leaves of wheat, P. recondita f. sp. triticina had an infectious period that in one experiment lasted for up to 72 days, when pustule densities were low. They observed, however, that maximum sporulation occurred on days 9 to 13 and that this was dependent upon pustule density. Eyal and Peterson (1967), working with the same pathogen, saw maximum sporulation from 13 to 14 days but also observed a long sporulation period. Mehta and Zadoks (1970) speculated on whether sporulation periods of over two months would occur in nature. A long sporulation period, they suggested, would enable the fungus to survive when the chances of infection were temporarily low. Neervoort and Parlevliet (1978) described an infectious period in the barley - leaf rust interaction that varied from about four to five weeks for the cultivars L94, Zephyr, and Sultan, to about three weeks for the resistant cultivar Vada.

Neervoort and Parlevliet (1978) observed compensatory effects between the components infection frequency, spore production and infectious period. This, they pointed out, agreed with the results of Yarwood (1961) with bean rust.

2.3.4.5 Colony Size and Lesion Size (LS)

Parlevliet (1979) has noted that many host-parasite interactions have demonstrated differences in colony size, which he defines as the area actually invaded by the pathogen, in addition to differences in lesion size, which is defined as the area showing disease symptoms. Lesion size can be measured in terms of area, diameter, and length, or it can be assessed using a scale especially devised for the particular host-parasite system under investigation.

Many researchers have suggested that lesion or colony size is an indicator of the growth rate of the pathogen in the host (Shaner et al., 1978; Parlevliet, 1979; Villareal et al., 1981). Jeger et al., (1983) found that this component was inadequate to distinguish varying resistance levels of two wheat cultivars to the glume blotch pathogen. Habgood (1977) observed that LS was similar for all barley cultivars tested for resistance to leaf blotch (Rhynchosporium secalis (Oud.) J. J. Davis). This result is in agreement with a number of other workers (Marshall, 1972; Williams and Owen, 1975). In contrast to the above examples, there are many instances where LS has been shown to be an effective component of resistance. Lancashire and Jones (1985) measured a variety of factors associated with this component and looked at mean values as well as rates of change of lesion length, lesion width, and lesion area, as well as shape factor which they calculated as the ratio of lesion length to width. They considered that lesion area as well as shape factor and rates of change of lesion area and shape factor were the most biologically meaningful and independent (in addition to three other components examined), giving significant differences between the

cultivars at p<5%. Of the 11 components examined, they recorded the lowest coefficent of variation for lesion width (8.0%). Martin et al., (1979) reported that size of uredinia, in addition to differences in receptivity, were the characters that most clearly separated slow-rusting wheats from fast-rusters in their reaction to P. graminis f. sp. tritici. Similarly, Ohm and Shaner (1976) showed that in the resistance of winter wheat to leaf rust, pustule size on the two slow-rusters was four- to six-tenths of that of the two fast-rusters examined. In addition, they noted that pustule size was most restricted on plants inoculated in the boot stage compared to plants inoculated at six other plant growth stages. Villareal et al., (1981) found that LS was an important component contributing to a reduced r-value in the slow-blasting resistance of five rice cultivars.

Ohm and Shaner (1976) found correlations between latent period and uredinium size and they suggested that linkage or pleiotropic effects of genes might control these components. Milus and Line (1985) reported that for stripe rust on the winter wheat cultivars Gaines, Nugaines, and Luke, uredinium size was postively correlated with rust intensity and lesion length, but negatively with latent period. They suggested that pleiotropic gene effects were involved, and that selection for one component should enhance resistance in terms of the others. Mehta and Zadoks(1970) found that pustule density negatively influenced the size of pustules. Similarly, Shaner (1983) observed a significant negative correlation between uredinium growth rate and the number of uredinia of P. recondita per 16 square milimeters of tissue in flag leaves of wheat. He found consistent differences in the growth rates of uredinia in this system with the average rates for the fast-rusting cultivars Morocco,

Monon, and Suwon 92 being 0.07, 0.05, and 0.04 mm^2/day, respectively, and for the slow-rusters 0.03 and 0.02 mm^2/day. Shaner (1983) concluded that the slow growth rate of uredinia would be a significant factor in retarding disease development in the field.

Environmental factors have been reported to affect LS. Milus and Line (1980) observed that differences in LS among cultivars in the seedling stage were more evident at diurnal temperatures of 10-30°C than at 2-18°C. Nutter and Pederson (1985) found that although LS was not greatly affected by increasing leaf wetness duration up to 24 hours, it almost doubled after 40 hours of treatment.

MANUSCRIPT I

Characterization of the components of rate-reducing resistance and assessment of population performance in field-grown faba beans (*Vicia faba* L.) to rust (*Uromyces viciae-fabae*).

ABSTRACT

Four faba bean mass-selected (MS) populations, three bulk (BK) populations, and the rust-susceptible population 2N40 were evaluated in field studies for the following components of rate-reducing resistance: fleck number (FKN), uredinia number (UDN), infection type (IT), range of infection types (ITR), and latent period (LP and LP_{50}). The populations were artificially inoculated, at one of three developmental stages, with either rust race 3 or 4 of Uromyces viciae-fabae. Significant differences (p-value<0.01) among the faba bean populations were found for all components although there was considerable variation in the expression of these components among the populationse. On the basis of these components, the populations were readily separated into those that were derived by mass-selection and those that were bulk populations, a result confirmed with cluster analysis. In general the MS populations demonstrated the greatest overall resistance to rust. The best slow-ruster was the MS population 2N43, with low mean values for FKN and UDN, a small IT and ITR, and a long latent period. The components were not equally effective in differentiating among the faba bean populations for levels of rate-reducing resistance. Principal component analysis indicated that components were equally effective in assessing rate-reducing resistance adequately enough to be useful for identifying breeding material. The most consistent results were obtained for the components LP_{50}, ITR, and UDN; the components FKN and LP, were the least useful.

Population performance in the field was compared using the following indicators: mean and final rust severity (RS and FRS, respectively), individual weekly assessments of rust severity (RS1 - RS4), apparent infection rate (AIR), area under the disease progress curve (AUDPC), and LPSM, a standardized disease index combining latent period and rust severity information. Although significant differences among the populations were found for all performance indicators, LPSM was the most efficient, followed by AUDPC, RS2, FRS, and RS.

The components of resistance as well as the performance indicators were variously affected by plant development stage at the time of inoculation, rust race, and year of testing. Only the components LP_{50} and UDN, and the performance indicators RS and AIR did not show a significant race or developmental stage effect. However, they in addition to all other parameters were influenced by year of testing. The resistance components were related to each other and to the population performance indicators, as demonstrated by significant Kendall's tau-b coefficients of concordance.

INTRODUCTION

Rust of faba beans, caused by Uromyces viciae-fabae, is one of the most common and potentially serious diseases of faba beans. It is especially severe in the Middle East and North Africa where disease severity can range up to 100 % (Mohamed, 1981), although losses of 5 to 20 % are more typical (Mansour et al., 1968). In Europe, Berthelem (1980) and Lapwood et al., (1984) have reported that rust is increasingly important on spring-sown faba beans, more so than on winter beans. In Western Canada, reports of rust from the major faba bean growing areas have been common since the introduction of this crop in 1972 (McKenzie and Morrall, 1973,1975; Bernier, 1975; Conner and Bernier, 1982a).

Recent studies have shown that U. viciae-fabae exists as numerous races (Conner and Bernier, 1982b). In Manitoba, native species of Vicia and Lathyrus may function as important sources of inoculum, in addition to being sources of new races. Faba bean accessions with specific resistance to races 1 and 3 (Conner and Bernier, 1982b) have been identified (Rashid and Bernier, 1984). However, due to high pathogen variability and the paritially out-crossing nature of this crop, it has been suggested that cultivars possessing this type of resistance may provide only short-term rust control (Bernier and Conner, 1983). Therefore, faba beans have recently also been evaluated for more durable types of resistance such as the polygenically inherited generalized resistance (Hooker, 1969) also referred to here as slow-rusting or rate-reducing

resistance. This type of resistance has been demonstrated to occur in faba beans. Conner and Bernier (1982d) evaluated open-pollinated faba beans for their ability to retard development of rust. In field trials, they recognized three bulk populations which consistently had low area under the disease progress curve (AUDPC) scores as well as six others which had AUDPC scores that varied from low to intermediate during three years of testing. Rashid (1983) recognized eight other faba bean selections as slow-rusters and an additional four as moderate-rusters over three to four years of mass-selection. The slow-rusting selections were characterized on the basis of AUDPC and final rust severity scores.

This study was undertaken to obtain information on the nature and stability of the slow-rusting character in faba beans. Despite the large number of reports on the components of slow-rusting, there is little information exists concerning these for crops other than the cereals, particularly under field conditions. The objectives of this study were to: (1) evaluate the components of rate-reducing resistance for each of several field-grown faba bean populations inoculated at three developmental stages with two races of Uromyces viciae-fabae; (2) compare population performance in the field using measures of rate-reducing resistance based upon weekly assessments of uredinial frequency; and (3) determine relationships among resistance components and performance indicators in the field, to establish methods of evaluating and screening rate-reducing resistance to Uromyces viciae-fabae. A sub-objective of this study was to examine the utility of two statistical multivariate techniques (principal component and cluster analysis) for the handling of disease resistance data.

MATERIALS AND METHODS

Four faba bean mass-selected populations (MS), three bulk populations (BK), and the rust-susceptible population 2N40 (P.I.222128) were evaluated for the components of rate-reducing resistance in field experiments, in 1982 and 1983, at the University of Manitoba Campus Farm. In three to four years of preliminary field evaluations, the mass-selected and bulk populations consistently had low area under the disease progress curve (AUDPC) and final rust severity scores (Conner and Bernier, 1982d; Rashid and Bernier, 1985).

6.1 EXPERIMENTAL DESIGN

In each year, three well-isolated sites at two locations, 2.5 km apart, were selected for evaluating the resistance of faba bean populations at three developmental stages to two races of Uromyces viciae-fabae. Each site was assigned one of six treatment combinations involving plants at one of three developmental stages (2.9, 4.5, and 5.3) and either rust race 3 or 4 (Conner and Bernier, 1982b). Plots at each site were arranged as a randomized complete block design with six replications. Each replication consisted of twenty plants of each of the eight populations, sown in single, 1.2 m rows, 15 cm apart. The three stages of development refer to plants 35, 50, and 65 days from sowing, respectively, and are based on the developmental key for beans developed in Britain by the Ministry of Agriculture (Anon, 1976) and

modified subsequently by Liew and Gaunt (1982). Since there did not appear to be large differences in maturity among the faba bean populations, no attempt was made to stagger dates of data collection.

6.2 METHOD OF INOCULATION

Plants were inoculated with urediniospores of U. viciae-fabae, during cool evenings with a high relative humidity. To facilitate infection following inoculation, each replication was enclosed by polyethylene sheeting for 12 hr.

Urediniospores required for inoculation were increased under greenhouse conditions on two-week-old seedlings of the rust susceptible population 2N40. Spores were collected with a cyclone spore collector (Browder, 1971) and stored at 5°C for one to two months, prior to use (Appendix A).

In 1982, inoculum consisting of urediniospores in talc was dusted onto leaflet surfaces with a modified atomiser (Rowell and Olien, 1957). Prior to inoculation, plants were sprayed with water containing a few drops of Tween 20 (Polyoxyethylene sorbitan monolaurate). In 1983, urediniospores were suspended in the water - Tween 20 solution and this was applied to leaflets with a controlled droplet sprayer (FLAK, Micron Corporation, Houston, Texas). Rows were sprayed uniformly by walking alongside each row at a set pace, with the sprayer aimed towards the plants at a fixed angle. In both years, the inoculum concentration was adjusted so that approximately 50 urediniospores were deposited per square centimeter of leaflet area. During the inoculation of each replicate, two Petri plates containing water agar were placed within the plots to monitor inoculum deposition.

6.3 EVALUATION OF THE COMPONENTS OF RESISTANCE AND ASSESSMENT OF POPULATION PERFORMANCE

One week after inoculation, and subsequently at weekly intervals for four to six weeks, leaflets at node six, on six randomly selected plants per population in each replicate were evaluated for the following components of resistance: (1) number of flecks, (2) number of uredinia, (3) infection type and range of infection types, (4) urediniospore production, and (5) latent period.

In addition to the above, populations were compared in terms of rust severity and final rust severity, apparent infection rate, area under the disease progress curve, and LPSM, a new disease index combining latent period and rust severity information.

6.4 MEASUREMENT AND STATISTICAL ANALYSES

6.4.1 Numbers of flecks and uredinia

Numbers of flecks and uredinia were estimated by counting their occurrence on leaflets. A pale chlorotic zone of cells on the leaf surface constituted a fleck. Pin-point sized necrotic areas thought to indicate hypersensitivity were not included. In the determination of uredinia number only erupted lesions were considered. Mean leaflet area was estimated for each faba bean population at each developmental stage with a LI-COR model 3000 area meter (Lambda Instrument Corporation, Lincoln, NE). These values were used to calculate the numbers of flecks and uredinia per square centimeter of leaflet area. To correct for heterogeneous error variance, data were transformed to square roots.

Fleck frequency (the proportion of the spores applied per square centimeter of leaflet area that result in flecks) and uredinial frequency (the proportion of the spores applied per square centimeter of leaflet area that result in erupted uredinia), were also calculated. These data were transformed to square roots. The frequency data, however, will not be presented since population rankings did not differ appreciably from those for numbers of flecks and uredinia.

6.4.2 Infection type and range of infection types

Infection type and range of infection types were classified on the basis of pustule size (Table 2). Infection type represents the predominant rust reaction whereas the parameter range indicates the extent of the variability in infection type per leaflet.

Data were assigned a numerical value ranging from 1 to 10 which corresponded to infection types 1 to 4, and the ranges 1 to 2, 1 to 3, 1 to 4, 2 to 3, 2 to 4, and 3 to 4. These categorical data were analyzed without transformation.

6.4.3 Urediniospore production

This component was assessed under field conditions, but was found to be extremely variable and ineffective to distinguish the faba bean populations. It was eliminated from all analyses and will not be presented.

TABLE 2. Infection types of Uromyces viciae-fabae on Vicia faba.

Infection type	Host reaction	Reaction category
0	No visible sign of infection	Immune
;	Necrotic fleck	Hypersensitive
1	Uredinia minute (little sporulation)	Very resistant
2	Uredinia small (~0.5 mm in diameter)	Resistant
3	Uredinia large (~1.0 mm in diameter)	Susceptible
4	Uredinia very large (>1.0 mm in diameter)	Very susceptible

(modified from Conner, 1981).

6.4.4 Latent period

Latent period was estimated as either the period of time after inoculation when sporulation was observed on at least one uredinium per leaflet (LP), or as the time at which 50% of the erupted uredinia sporulated (LP_{50}). Both LP and LP_{50} were expressed in terms of days. LP_{50} is similar to Shaner's T_{50} (Shaner, 1980) but, unlike T_{50}, which is calculated from the linear regression coefficient and y-intercept of the regression of probit percent of uredinia erupted on time after inoculation, LP_{50} is determinded on an individual plant basis by estimation of the time at which the maximum number of uredinia erupt. LP_{50} is thought to provide a better estimate of latent period because those situations where there are either few or many erupted uredinia are given equal weight. In the estimation of T_{50}, however, more weight is given to plants with many erupted uredinia and this tends to underestimate the latent period. Like T_{50}, LP_{50} has the advantage over other methods of calculating latent period in that daily data collection on percent uredinia erupted is not required since it can be adequately estimated by interpolation of values. LP_{50} was assigned a value of 31.5 days as a conservative estimate of latent period for those situations where no erupted uredinia were observed over the sampling period.

6.4.5 Leaflet area infected by Uromyces viciae-fabae

The percent leaflet area infected by rust was visually assessed using a pictorial key of 1, 5, 10, and 25% leaflet area covered by erupted uredinia. Logit transformation of these data, calculated as indicated below, was necessary to stabilize variances:

$$\text{logit}(X) = \log_e [\, X \,/\, (1-X) \,]$$

where X is equal to the proportion of leaflet area infected by rust. To avoid taking the logarithm of zero, all values of percent leaflet area infected (X) were replaced by (X+1), prior to transformation.

These transformed data were utilized in several ways to compare the performance of the faba bean populations. Mean values of leaflet area infected by rust over a four week period were determined as were mean values of leaflet area infected at the final sampling time or at the sampling time just prior to leaflet senescence (final rust severity). In addition, the values of leaflet area infected over time were summarized as area under the disease progress curve (AUDPC), using the formula:

$$AUDPC = \sum_{i=1}^{k} [(S_i + S_{i-1})/2]$$

where S is equal to the rust severity at week i, and k is the number of successive observations (Wilcoxson et al., 1975). The apparent infection rate for each population was estimated as the slope of the regression line of logit disease severity on time.

6.4.6 LPSM - a standardized severity measure

It was noted that although estimation of latent period provided information about the time for infected tissue to become infectious and consequently the rate of disease development, it provided little information about the intensity of infection. Two populations could differ marginally with respect to latent period, but differ substantially with respect to the number of erupted uredinia. To facilitate identification of populations with a long latent period and few erupted uredinia a standardized disease index was developed that combined LP_{50} data with the number of erupted uredinia.

6.4.7 Statistical Analyses

All data were analyzed using the GLM, PRINCOMP, and CLUSTER subprograms of the Statistical Analysis System Version 82.2 (SAS Institute Inc., 1982) running on the Amdahl 580/5850 installation of the University of Manitoba.

6.4.7.1 Analysis of variance

One-way analysis of variance of unweighted means was performed for each resistance parameter using transformed data (non-transformed data for IT and ITR) to test for the significance of population differences. Additional analyses of variance were done to examine the significance of year, race, and developmental stage differences. Each analysis was then repeated after elimination of all insignificant effects to improve precision of the error term. Scheffé's significant difference procedure was used to identify subsets of mean values that were not significantly different (p-value<0.01; Neter et al., 1985). Transformed means were converted back to actual values for presentation in the tables.

6.4.7.2 Kendall's tau-b coefficients of concordance

Kendall's tau-b coefficients were computed to identify possible inter-relationships among the components of resistance. This is a valid test for non-normal data and is invariant under all order-preserving transformations. Kendall's tau-b is a non-parametric statistic based on concordances and discordances. Concordance is determined for pairs of observations by observing whether values of two variables vary together (in concord) or differently (in discord). In the calculation of these

coefficients, data are ranked in order according to values of the first variable and then re-ranked according to values of the second variable. The number of interchanges that occur with respect to the first variable are tabulated and used in the calculation of this statistic (Noether, 1967).

6.4.7.3 Principal component analysis

This is a multivariate technique for examining relationships among several variables. The purpose of this technique is to derive a number of linear combinations (principal components or eigenvectors) of the variables while retaining as much information as in the original variables. This analysis extracts the eigenvalues and the eigenvectors from the correlation matrix of the the components of resistance. The eigenvectors are composed of the weights of the resistance components contributing to each principal component. Each principal component has associated with it an eigenvalue representing the amount of the total variation that the principal component accounts for. The eigenvalues sum to the number of variables analyzed. The principal components are orthogonal to each other. The first principal component has the largest variance associated with any linear combination of the observed variables (Harris, 1985).

6.4.7.4 Cluster analysis

Cluster analysis was used to determine whether the eight faba bean populations formed groups having distinct combinations of resistance components. To prevent one component of resistance dominating the

others because it is numerically larger, standardized variables with a mean of zero and a standard deviation of one were calculated from each of the components of resistance. The components, mean infection type and range were excluded due to their categorical nature. The standardized variables were used in the cluster analysis.

The purpose of cluster analysis is to place objects into groups or clusters suggested by the data, such that objects in a given cluster tend to be similar to each other, and objects in different clusters tend to be dissimilar. This technique finds hierarchical clusters using Ward's minimum variance clustering method. In very simple terms, this is a method that follows a series of steps begining with t clusters each consisting of one object and ending with one cluster containing all objects. At each step in the procedure a merger of two clusters results in the smallest increase in the sum of squares index (E). This index is computed from the differences between each object in a given cluster and its cluster mean (Romesburg, 1984). The advantages of this clustering algorithm are discussed by Kuiper and Fisher (1975), Goodall (1978), and Milligan (1980).

RESULTS AND DISCUSSION

7.1 CHARACTERIZATION OF THE COMPONENTS OF RATE-REDUCING RESISTANCE

7.1.1 Number of flecks per square centimeter of leaflet area (FKN)

On the basis of the mean number of flecks produced per square centimeter of leaflet area, Scheffé's significant difference procedure categorized the eight faba bean populations into three distinct groups (Table 3). The rust-susceptible population 2N40 had the highest mean FKN (25.74), and it differed significantly from the other populations with respect to this component. The three bulk faba bean populations 2N34, 2N430, and 2N52, with values of 11.45, 12.77, and 14.44, respectively, were indistinguishable statistically. These three populations comprised the second group. Group three consisted of the four mass-selected populations 2N319, 2N122, 2N43, and 2N29, with values ranging from 2.21 for 2N29 to 5.13 for 2N319.

Comparisons among populations inoculated at the three developmental stages were significant indicating that developmental stage affects expression of this component as reported for other resistance components by Ohm and Shaner (1976). Plants inoculated at stage 4.5 had the highest mean FKN (13.28) whereas those inoculated at stage 5.3 had the lowest (5.12). Additionally, significant differences were observed between races; higher values for mean FKN were seen in plants inoculated with urediniospores of race 3 (10.33) than in those inoculated with

TABLE 3. Effect of host population, developmental stage, rust race, and year on the number of flecks and uredinia per square centimeter of leaflet area of eight field-grown faba bean populations.

		Flecks	Uredinia
Population[1]	2N40 (BK)	25.74 a[5]	45.28 a
	2N34 (BK)	11.45 b	21.22 b
	2N430 (BK)	12.77 b	20.23 b
	2N52 (BK)	14.44 b	21.80 b
	2N319 (MS)	5.13 c	7.27 c
	2N29 (MS)	2.21 c	5.56 c
	2N43 (MS)	2.23 c	4.51 c
	2N122 (MS)	3.13 c	4.59 c
Developmental Stage[2]	2.9	8.75 b	15.27 a
	4.5	13.28 a	18.90 a
	5.3	5.12 c	12.41 a
Race[3]	3	10.33 a	16.66 a
	4	8.30 b	14.83 a
Year[4]	1982	11.72 a	22.49 a
	1983	7.30 b	9.96 b
Mean square error		1.09	1.94

[1]Data are means for 432 observations combined over developmental stages, races, and years.
[2]Data are means for 1152 observations combined over populations, races, and years. The three stages of development: 2.9, 4.5, and 5.3, refer to plants 35, 50, and 65 days from planting, respectively, and are based on Liew and Gaunt's (1982) developmental key for beans.
[3]Data are means for 1728 observations combined over populations, developmental stages, and years.
[4]Data are means for 1728 observations combined over populations, developmental stages, and races.
[5]Comparisons among means were made using square root transformed data. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

TABLE 4. Number of flecks per square centimeter of leaflet area of eight faba bean populations, at seven and fourteen days after inoculation, with two rust races, in 1982 and 1983.

Seven days after inoculation

		1982		1983	
		Race 3	Race 4	Race 3	Race 4
Population	2N40 (BK)	75.06 a[1]	14.72 a	22.10 a	48.03 a
	2N34 (BK)	27.32 bc	9.70 ab	9.01 bcd	15.79 b
	2N430 (BK)	31.55 b	6.44 ab	10.24 bc	13.78 b
	2N52 (BK)	30.89 bc	11.30 ab	16.61 ab	16.99 b
	2N319 (MS)	6.96 cd	4.28 ab	6.44 cde	4.86 b
	2N29 (MS)	2.13 d	3.06 ab	1.61 de	2.69 b
	2N43 (MS)	3.09 d	1.64 bc	1.17 e	3.00 b
	2N122 (MS)	2.63 d	1.38 bc	2.84 cde	4.29 b
Mean square error		1.91	1.32	1.03	2.24

Fourteen days after inoculation

		1982		1983	
		Race 3	Race 4	Race 3	Race 4
Population	2N40 (BK)	2.82 a	15.18 a	2.35 a	8.25 a
	2N34 (BK)	12.12 a	8.44 a	2.84 a	5.84 a
	2N430 (BK)	17.71 a	19.15 a	2.87 a	3.79 a
	2N52 (BK)	17.53 a	16.00 a	2.40 a	3.77 a
	2N319 (MS)	4.28 a	11.25 a	2.07 a	0.89 a
	2N29 (MS)	2.98 a	1.80 a	1.65 a	1.60 a
	2N43 (MS)	4.58 a	1.67 a	1.23 a	1.72 a
	2N122 (MS)	8.69 a	3.01 a	1.37 a	0.63 a
Mean square error		1.60	2.49	0.39	1.05

[1]Data are means for 108 observations combined over developmental stages. Comparisons among means were made using square root transformed data. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

urediniospores of race 4 (8.30). Furthermore, significantly higher values for FKN were observed in 1982 (11.72) than in 1983 (7.30).

When year-race combinations of the data, at 7 days after inoculation (d.p.i.), were analyzed (Table 4), only plants inoculated in 1982, with urediniospores of race 3, gave results similar to those observed with the combined data. High values for FKN (75.06) were observed on leaflets of 2N40 and this was in contrast to the relatively few seen on, for example, 2N29 (2.13) or on the other mass-selected populations. However, unlike with the combined data, the mass-selected population 2N319, could not be clearly distinguished from the bulk populations.

When plants were inoculated with urediniospores of race 4, the three population categories observed with urediniospores of race 3, and with the combined data, were not readily distinguishable. Although, as with the latter combinations, population 2N40 had the largest number of flecks (14.72), it did not differ significantly from the three bulk populations nor from the mass-selected populations 2N319 and 2N29. However, the mass-selected populations 2N43 and 2N122 were distinguishable statistically from 2N40. No other significant differences among populations were detected with urediniospores of race 4.

In 1983, more significant differences were observed with race 3 than with urediniospores of race 4. The rust-susceptible population 2N40 had the largest values for FKN with both race 3 and 4, although values were higher with urediniospores of race 4. In contrast, in 1982, race 3 had higher values for FKN. In 1983, when plants were inoculated with urediniospores of race 3, population 2N52 did not differ significantly from 2N40. Although the bulk populations 2N34 and 2N430 could be

distinguished statistically from 2N40, they were not significantly different from the mass-selected populations with the exception of 2N43. With race 4, all populations were significantly different from the rust-susceptible population 2N40, although no other differences were observed.

At 14 d.p.i., no significant differences were observed among populations in either 1982 or 1983, with either race 3 or race 4. This possibly was due to the very high coefficient of variation (C.V.) associated with this component at 14 d.p.i. (C.V. = 112.19 %; Appendix D).

The race x population interaction was significant at 7 d.p.i., but not at 14 d.p.i. perhaps because at 7 d.p.i., higher FKN values occurred with urediniospores of race 3 for 2N40, the bulk populations, and 2N29, whereas lower values were observed for the other three mass-selected populations (Appendices C and D). Similarly, the developmental stage x population interaction was significant at 7 d.p.i. but not at 14 d.p.i. However, the interaction between populations and the year of testing was not significant at either 7 or 14 d.p.i. The coefficient of variation for this component, at 7 d.p.i., was 63.32 %, almost one-half the C.V. for this component at 14 d.p.i. These high C.V.'s may have resulted from the inclusion in these analyses, of data for the fast-rusting population 2N40, with its comparatively large values for FKN, and at 14 d.p.i., also to the presence of flecks from secondary infections (both auto- and allo-infections), as well as to the varying rates at which the flecks present at 7 days formed uredinia. Shaner (1980) has reported that hosts may differ markedly in the time required for the same proportion of lesions to sporulate.

FKN, which has not previously been looked at as a component of resistance was effective in discriminating among the faba bean populations in this investigaion, especially at 7 days after inoculation, in 1982, and particularly with urediniospores of race 3. It was less effective with urediniospores of race 4, in 1982, and with both races in 1983. These results tend to suggest that FKN was most proficient under conditions most favourable for rust as was the situation in 1982 (Appendix B).

7.1.2 Number of uredinia per square centimeter of leaflet area (UDN)

The number of uredinia per square centimeter of leaflet area categorized the eight faba bean populations into three groups (Table 3). The first group consisted of the rust-susceptible population 2N40 with a mean value for UDN of 45.28. The three bulk populations comprised group 2 with values for this component ranging from 21.80 for population 2N52 to 20.23 for 2N430. The four mass-selected populations, with values for UDN ranging from 7.27 for population 2N319 to 4.51 for population 2N43, made up group 3.

In general the populations were ranked similarly with respect to this component as they were with FKN. The mass-selected populations had significantly fewer uredinia per square centimeter than the bulk populations which, in turn, had fewer uredinia than the rust-susceptible population. These results are in agreement with reports from various authors who have noted that this component is important in rate-reducing resistance and that resistant cultivars have fewer infections per unit area (Parlevliet and Kuiper, 1977a; Mortensen and Green, 1978; and Rowell, 1982).

The populations behaved similarly in terms of this component when inoculated with either race 3 or 4, although greater mean numbers of uredinia were observed with urediniospores of race 3 (16.66) than with urediniospores of race 4 (14.83). However, these differences were not statistically significant. In 1982, values for UDN were higher (22.49) than in 1983 (9.96); this difference was significant and similar to the results obtained with FKN. Unlike with FKN, however, there were no significant race or plant age effects although trends were similar in that race 3 was the most aggressive, and plants inoculated at stage 5.3, the most resistant, and those at flowering, the most susceptible. This lack of significance is in agreement with the results of Parlevliet and Kuiper (1977a) who observed that for barley leaf rust, correlations between infection in the seedling stage and partial resistance in the field were as high as those between infection in the adult plant stage and partial resistance. They suggested that selection for partial resistance among seedlings might be as feasible as selection among individual adult plants in the field. Somewhat later, Parlevliet and Van Ommeren (1985) pointed out that there is no need to evaluate partial resistance at the same stage of development. On the other hand, Martin et al., (1977) advised caution when extrapolating conclusions from one stage of plant development to another. Similarly, Wahl et al., (1980) concluded that this component was inappropriate for use in the detection of slow-rusting in seedlings because no significant differences were observed, whereas in adult plants, they found that significantly fewer uredinia developed on the slow-rusters than on the fast-rusters.

At 7 d.p.i., UDN was not as efficient at differentiating among populations as was FKN (Table 5). For all year-race combinations, at 7

d.p.i., the rust-susceptible population 2N40 had the largest values for UDN, however, with urediniospores of race 4 in both 1982 and 1983, 2N40 was not significantly different from some or all of the bulk populations. In both test years, when plants were inoculated with urediniospores of race 3, no significant differences were observed among populations other than those for 2N40. Ranking of the populations within each year-race combination, however, was relatively consistent, although, population 2N319 demonstrated some variability in that in 1982, with urediniospores of race 4, it had the fewest uredinia, whereas with urediniospores of race 3 it had more than any of the other mass-selected populations. In 1982, more uredinia were observed on plants inoculated with race 4 than with urediniospores of race 3, however, the opposite was true in 1983. In general higher values for UDN were seen in 1982 than in 1983.

The C.V. associated with UDN at 7 days was very high (104.36 %; Appendix E) and this may account for the relatively few significant differences observed. Parlevliet (1977) reported a very large coefficient of variation associated with this component, as have Johnson and Wilcoxson (1970). This high degree of variation may be due to the relatively few uredinia present at 7 days, and to the observation by Parlevliet and Kuiper (1977a) that the number of uredinia varied greatly from one plant to another and also from one leaf to another.

More significant differences were observed among the populations with this component at 14 days after inoculation (Table 5). The coefficient of variation was much smaller (47.08 %; Appendix F), perhaps because by 14 days, the majority of uredinia produced from the initial inoculum had matured. In all year-race combinations at 14 d.p.i., population 2N40

TABLE 5. Number of uredinia per square centimeter of leaflet area of eight faba bean populations, at seven and fourteen days after inoculation, with two rust races, in 1982 and 1983.

Seven days after inoculation

		1982		1983	
		Race 3	Race 4	Race 3	Race 4
Population	2N40 (BK)	6.85 a[1]	51.57 a	10.95 a	0.82 a
	2N34 (BK)	0.82 b	23.95 ab	0.69 b	0.01 b
	2N430 (BK)	2.33 b	18.99 ab	1.58 b	0.02 ab
	2N52 (BK)	0.28 b	20.46 ab	2.58 b	0.02 ab
	2N319 (MS)	0.23 b	2.56 b	0.15 b	0 b
	2N29 (MS)	0.08 b	6.23 b	0.03 b	0 b
	2N43 (MS)	0.08 b	4.53 b	0.04 b	0 b
	2N122 (MS)	0 b	4.53 b	0.22 b	0 b
Mean square error		0.15	2.63	0.22	0.03

Fourteen days after inoculation

		1982		1983	
		Race 3	Race 4	Race 3	Race 4
Population	2N40 (BK)	135.93 a	99.40 a	59.38 a	60.46 a
	2N34 (BK)	54.47 bc	47.46 b	27.12 bc	33.84 abc
	2N430 (BK)	57.44 bc	33.48 bcd	25.00 abc	34.05 abc
	2N52 (BK)	70.21 b	39.04 bc	38.54 ab	20.33 bcd
	2N319 (MS)	23.37 cd	11.06 bcd	15.37 bcd	9.58 cd
	2N29 (MS)	17.46 cd	8.40 cd	9.27 cd	5.44 d
	2N43 (MS)	17.53 cd	6.75 d	4.42 d	6.12 d
	2N122 (MS)	12.25 d	6.19 d	10.61 cd	5.62 d
Mean square error		4.38	3.77	2.85	3.19

[1]Data are means for 108 observations combined over developmental stages. Comparisons among means were made using square root transformed data. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

had the most uredinia, and in 1982, it was significantly different from the other populations when inoculated with either race 3 or 4. In the inoculation with urediniospores of race 3, population 2N52 had a mean value for UDN of 70.21 and this was significantly different from 2N40 with a mean of 135.93, and from the four mass-selected populations. However, population 2N52 could not be distinguished from either 2N430 and 2N34, with values for UDN of 57.44 and 54.47, respectively. The latter pair of populations was significantly different from 2N122 with a mean value for UDN of only 12.25, but not from the other mass-selected populations.

Results for race 4 were similar to those with urediniospores of race 3, in 1982, except that population 2N34 had the highest mean value for UDN (47.46) followed by 2N52 and 2N430, with 39.04 and 33.48, respectively. These populations were indistinguishable from the mass-selected population 2N319. As with urediniospores of race 3, population 2N122 had the fewest uredinia, but this was not significantly different from the other mass-selected populations and from the bulk population 2N430.

In 1983, results paralleled those observed in 1982 except that when populations were inoculated with urediniospores of race 3, 2N43 rather than 2N122, had the smallest value for this component. When inoculated with urediniospores of race 4, population 2N52 shifted from being the bulk population with the most uredinia, in 1982, to being the one with the least, in 1983. In addition, the mass-selected populations 2N29 and 2N122 exchanged positions in 1983, with the result that 2N29, rather than 2N122, had the fewest UDN.

Unlike with FKN, the interaction between populations and races was not significant at either 7 or 14 d.p.i. (Appendices E and F, respectively). Parlevliet (1977) pointed out that this could result from the high C.V.'s typically associated with uredinia number. Rouse et al., (1980) reported a significant isolate x cultivar interaction for this component of slow-mildewing resistance. They were concerned that resistance based solely on this component could at least to some extent, erode over time. The interactions between populations and year of testing, and between races and the developmental stage at the time of inoculation were significant at both 7 and 14 d.p.i. However, the interactions between races or developmental stages and year of testing were significant only at 7 d.p.i. The C.V. for this component was larger at 7 d.p.i. (104.36 %) than at 14 d.p.i. (47.08 %); this perhaps was due to the inclusion of the rust-susceptible popultion in these analyses.

7.1.3 Infection type (IT)

In this study, IT was effective in differentiating among the faba bean populations, and on the basis of this component the eight faba bean populations were categorized into four significantly different groups (Table 6). The rust-susceptible population 2N40 had the largest mean IT (1.76) and this was significantly larger than the IT's of 2N52 and 2N34, which comprised the second group of populations. Group three consisted of the mass-selected population 2N319 with a mean IT of 1.05; the other mass-selected populations 2N29, 2N43, and 2N122, with the smallest mean

IT (0.91; approximately one-half of the size of 2N40), made up the fourth group. The remaining population, 2N430, with a mean IT of 1.31 could not be distinguished from the populations in either group two or three. These population differences in mean infection type indicated that populations with rate-reducing resistance had low infection types (resistant). This is contrary to the traditional definition of rate-reducing resistance which presupposes a high or susceptible infection type (Parlevliet, 1979; Van der Plank, 1982). The results of this study are, however, consistent with those of Ohm and Shaner (1976) who observed that on slow-rusting winter wheats, pustule sizes were about one-half that of the fast- rusting cultivars. Shaner et al., (1978) working with the same four winter wheats as the previous authors, noted that average uredinia on the fast-rusters were 2.0 and 1.7 times larger than uredinia on the slow-rusting wheats. Kuhn et al., (1978) observed a similar difference in pustule size between fast and slow-rusters, however, he attributed this to differences in the latent periods of these cultivars since no differences were seen in final pustule size.

No significant differences were observed in IT among populations inoculated at either of the two earliest developmental stages. However, plants inoculated at the latest developmental stage had significantly smaller infection types (1.27 and 1.37 for stages 2.9 and 4.5, respectively, versus 0.98 for developmental stage 5.3). Plant developmental stage therefore, had a significant effect on uredinial size. This is in agreement with Ohm and Shaner's (1976) observation that pustule size was more limited when plants were inoculated in the boot stage than at one of six other plant growth stages. Similarly, Martin et al., (1979) concluded after examining uredinial size in both seedling and adult

plants that caution should be exercised in extrapolating conclusions from one stage of plant development to another. Milus and Line (1980) reported that evaluation of cultivars for resistance in the seedling stage does not always agree with similar evaluations in the adult stage. They observed many differences in infection type among seedling and adult plants inoculated with P. recondita. On the other hand, Parlevliet and Van Ommeren (1985) have suggested that there is no need to evaluate partial resistance at the same stage of development.

Significant differences in infection type were observed between races. Race 3 resulted in a mean IT of 1.36, and race 4, a mean of 1.05. Milus and Line (1980) have reported a difference in this component among wheat cultivars inoculated with one of two cultures of P. recondita. In addition, differences in IT between the two test years were significant, with a larger IT observed in 1982 (1.30) than in 1983 (1.11). These differences may have resulted from the markedly different test years (Appendix B) since infection type has been shown to be subject to environmental influences. Milus and Line (1980) concluded that temperature can influence the expression of this component after they observed that differences in infection type were more evident at 10 - 30 ^{o}C than at 2 - 18 ^{o}C. The effect of duration of leaf wetness on this component has been investigated by Nutter and Pederson (1985). They observed that in the net blotch of barley, lesions caused by Pyrenophora teres were not greatly affected by increasing leaf wetness duration up to 24 hr, but that lesion size nearly doubled after 40 hr of treatment.

At 7 d.p.i., the number of statistically significant differences due to IT was less than those observed when these data were combined with the data at 14 d.p.i. (Table 7). In the 1982-race 4 combination, no

TABLE 6. Effect of host population, developmental stage, rust race, and year on infection type and range of infection types of eight field-grown faba bean populations.

		Infection type	Range of infection types
Population[1]	2N40 (BK)	1.76 a[5]	4.98 a
	2N34 (BK)	1.37 b	3.57 b
	2N430 (BK)	1.31 bc	3.46 b
	2N52 (BK)	1.38 b	3.67 b
	2N319 (MS)	1.05 c	2.45 c
	2N29 (MS)	0.98 d	2.27 c
	2N43 (MS)	0.94 d	1.89 c
	2N122 (MS)	0.91 d	1.93 c
Developmental Stage[2]	2.9	1.27 a	3.39 a
	4.5	1.37 a	3.36 a
	5.3	0.98 b	2.27 b
Race[3]	3	1.36 a	2.59 b
	4	1.05 b	3.41 a
Year[4]	1982	1.30 a	3.39 a
	1983	1.11 b	2.62 b
Mean square error		0.16	1.21

[1]Data are means for 432 observations combined over developmental stages, races, and years.
[2]Data are means for 1152 observations combined over populations, races, and years. The three stages of development: 2.9, 4.5, and 5.3, refer to plants 35, 50, and 65 days from planting, respectively, and are based on Liew and Gaunt's (1982) developmental key for beans.
[3]Data are means for 1728 observations combined over populations, developmental stages, and years.
[4]Data are means for 1728 observations combined over populations, developmental stages, and races.
[5]Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

TABLE 7. Infection type of eight field-grown faba bean populations at seven and fourteen days after inoculation with two rust races in 1982 and 1983.

Seven days after inoculation

		1982		1983	
		Race 3	Race 4	Race 3	Race 4
Population	2N40 (BK)	1.35 a[1]	1.68 a	1.44 a	2.07 a
	2N34 (BK)	1.01 abc	1.55 a	0.76 b	1.63 ab
	2N430 (BK)	1.02 abc	1.15 a	0.61 b	1.55 ab
	2N52 (BK)	1.16 ab	1.40 a	0.83 b	1.25 bc
	2N319 (MS)	0.94 abc	1.07 a	0.49 b	0.95 bc
	2N29 (MS)	0.72 bc	1.50 a	0.36 b	0.57 c
	2N43 (MS)	0.97 abc	1.07 a	0.33 b	0.76 c
	2N122 (MS)	0.56 c	1.32 a	0.31 b	0.95 bc
Mean square error		0.15	0.20	0.16	0.28

Fourteen days after inoculation

		1982		1983	
		Race 3	Race 4	Race 3	Race 4
Population	2N40 (BK)	1.83 a	1.89 a	2.05 a	2.00 ab
	2N34 (BK)	1.41 a	1.86 a	1.48 ab	1.62 a
	2N430 (BK)	1.65 a	1.72 ab	1.60 ab	2.00 a
	2N52 (BK)	1.79 a	1.97 a	1.68 ab	1.84 a
	2N319 (MS)	1.23 a	1.55 ab	1.63 ab	1.61 ab
	2N29 (MS)	1.23 a	1.77 ab	1.23 b	1.20 ab
	2N43 (MS)	1.42 a	1.52 ab	1.15 b	0.83 b
	2N122 (MS)	1.17 a	1.30 b	1.03 b	0.92 b
Mean square error		0.32	0.13	0.23	0.16

[1]Data are means for 108 observations combined over developmental stages. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

significant differences were seen among the populations. Similarly, when the data for race 3 were analyzed, the rust-susceptible population 2N40 differed significantly from only the mass-selected populations 2N29 and 2N122. One other significant difference was observed in 1982; that between the populations 2N52 and 2N122, with the latter having a mean IT of 0.56 as compared to 1.16 for 2N52.

In 1983, in the inoculation with urediniospores of race 3, population 2N40 (with a mean IT type of 1.44) differed significantly from the remaining populations. No other differences were observed. In the inoculation with urediniospores of race 4, population 2N40 had a mean IT of 2.07, the largest value obtained for this component. It differed significantly from the mass-selected populations and from the bulk population 2N52. The mean IT of 2N40 was almost four times that of 2N29 (0.57), the population with the smallest mean IT.

The largest values for this component were observed in the 1983-race 4 combination for populations 2N40, 2N34, and 2N430, and in the 1982-race 4 combination for the other populations. Conversely, the smallest IT for all populations excluding 2N40, was found in the 1983-race 3 combination. The smallest value for the rust-susceptible population 2N40 was observed with urediniospores of race 3, in 1982.

At 14 d.p.i., few statistically significant differences were seen among the populations, regardless of the year-race combination analyzed. No significant differences were observed in 1982, with urediniospores of race 3; however, in the inoculation with race 4, population 2N40, in addition to populations 2N34 and 2N52 were found to differ significantly from only 2N122.

In the 1983-race 3 combination, population 2N40 differed significantly from the mass-selected populations 2N29, 2N43, and 2N122. No other statistically significant differences were observed. When the faba beans were inoculated with urediniospores of race 4, the bulk populations were found to differ significantly from the mass-selected populations 2N43 and 2N122, but not from 2N319 and 2N29. In this year-race combination, the rust-susceptible population 2N40 could not be distinguished statistically from the other populations.

The coefficients of variation for IT at 7 d.p.i. (42.74%) and at 14 d.p.i. (31.17%) were large, although much smaller (Appendices G and H, respectively), than for those components measuring lesion number. Many workers have reported that the interaction of IT with receptivity may be responsible for some of the varibility associated with this component (Shaner and Finney, 1980). Although precautions were taken to ensure uniform deposition of inoculum on leaf surfaces, differences in the infectibiliy of the populations may have affected pustule size.

7.1.4 Range of infection types (ITR)

The eight faba bean populations were categorized into three groups based upon significant differences in range of infection types (Table 6). The rust-susceptible population 2N40 displayed the greatest range with a value of 4.98. The three bulk populations 2N34, 2N430, and 2N52, comprised the second category, and the four mass-selected populations made up the third. The mass-selected population 2N43 had the smallest value for this component (1.89), and it was much smaller than the range observed for 2N40.

All of the populations used in this study exhibited a range of infection types. This is in contrast to Milus and Line's (1980) observations, who in their investigation of this component on winter wheat infected with P. recondita, found that only those race-cultivar combinations that were resistant as determined by one or more other components demonstrated a range of infection types. They noted that range of infection types is similar to the race-specific mesothetic or 'X' infection type of P. graminis described by Stakman et al., (1962), although it may not consist of the complete range of infection types.

No significant differences were observed among populations inoculated at either developmental stage 2.9 or 4.5, however, populations inoculated at developmental stage 5.3 had a significantly smaller ITR (2.27), and IT. Likewise, during the two test years, the populations behaved similarly in terms of IT and ITR, with significantly smaller values for both components occurring in 1983. However, the populations differed, in terms of IT and ITR, in their reactions to the two races. While race 3 produced a significantly larger mean infection type than did race 4, the latter race generated a significantly greater range of infection types than did race 3. This race-specificity is in agreement with the culture-specificity described by Milus and Line (1980) for both ITR and IT, but it is in contrast to the evidence for nonspecificity of resistance to P. striiformis in wheat cultivars grown in the northwestern United States (Line et al., 1976).

At 7 d.p.i., statistically significant differences among populations were less obvious than they were with the combined data (Table 8). In the 1982-race 3 combination, the rust-susceptible population 2N40 with a value for ITR of 3.55 differed significantly from only the mass-selected

populations 2N29, 2N43, and 2N122, with values for ITR of 1.64, 1.90, and 0.92, respectively. In addition, the bulk populations could not be distinguished from the mass- selected populations 2N319, 2N29, and 2N43, except for 2N52 which was significantly different from 2N29. In 1983, populations inoculated with urediniospores of race 3, with the exception of 2N40, did not differ significantly on the basis of this component.

In the 1982-race 4 combination, 2N40 did not differ significantly from the bulk populations and from the mass-selected population 2N29. In addition, with the exception of population 2N34, these populations had significantly greater ranges than the mass-selected populations 2N319, 2N43, and 2N122. In 1983, population 2N40 with a value for ITR of 5.73, differed significantly from the other populations. The mass-selected population 2N29 had the smallest value for this component (1.32), although it did not differ significantly from the other mass-selected populations.

At 14 days after inoculation, no statistically significant differences in ITR were observed among the populations in the 1982-race 3 combination. In the 1983-race 3 combination, however, population 2N40 with a mean value for ITR of 5.99, was found to differ significantly from the mass-selected populations, with the exception of 2N319. Populations 2N43 and 2N122, with the smallest values for this component (1.93 and 2.03, respectively) could not be distinguished statistically from each other, but were found to be significantly different from the bulk population 2N52 and from the mass-selected population 2N29.

In the 1982-race 4 combination, population 2N40 (5.99) was different only from 2N43 and 2N122 with values for ITR of 3.93 and 4.02, respec-

TABLE 8. Range of infection types of eight field-grown faba bean populations at seven and fourteen days after inoculation with two rust races in 1982 and 1983.

Seven days after inoculation

		1982		1983	
		Race 3	Race 4	Race 3	Race 4
Population	2N40 (BK)	3.55 a[1]	4.86 a	3.80 a	5.73 a
	2N34 (BK)	2.91 abc	3.76 ab	1.56 b	3.54 b
	2N430 (BK)	2.93 abc	3.31 a	1.32 b	3.58 b
	2N52 (BK)	3.29 ab	3.69 a	1.68 b	3.35 bc
	2N319 (MS)	2.24 abcd	2.70 b	0.95 b	1.77 bcd
	2N29 (MS)	1.64 c	2.96 a	0.62 b	1.32 d
	2N43 (MS)	1.90 bcd	1.92 b	0.59 b	1.44 cd
	2N122 (MS)	0.92 d	2.77 b	0.73 b	1.46 cd
Mean square error		0.89	1.83	1.07	1.78

Fourteen days after inoculation

		1982		1983	
		Race 3	Race 4	Race 3	Race 4
Population	2N40 (BK)	5.62 a	5.99 a	5.99 a	7.00 abc
	2N34 (BK)	4.28 a	5.35 ab	4.04 abc	5.69 a
	2N430 (BK)	3.68 a	5.33 ab	4.13 abc	5.21 ab
	2N52 (BK)	4.87 a	5.47 ab	4.73 ab	5.75 a
	2N319 (MS)	2.97 a	4.18 ab	4.09 abc	3.17 abc
	2N29 (MS)	3.26 a	4.92 ab	2.68 b	2.94 abc
	2N43 (MS)	3.15 a	3.93 b	1.93 c	1.92 bc
	2N122 (MS)	3.28 a	4.02 b	2.03 c	2.23 c
Mean square error		3.15	1.21	2.19	1.81

[1]Data are means for 108 observations combined over developmental stages. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

tively. No other significant differences were seen. In 1983, population 2N40 had a range of 7.00, the highest value observed for this component. While 2N40 was not found to differ significantly from any of the others, two of the bulk populations, 2N34 and 2N52, were different from the mass-selected populations 2N43 and 2N122. In addition, the bulk population 2N430 differed significantly from 2N122, but not from 2N43.

The C.V.'s for ITR (Appendices I and J), were similar to those for IT, and likewise considerably smaller than those for the components measuring lesion number. Few interactions were significant with this component. At 14 d.p.i., the interaction between populations and year of testing was significant as was the interaction between populations and developmental stage. The significant population x year interaction may have arisen because for five of the populations, larger values for ITR were seen in 1983, whereas for the remaining populations, larger values occurred in 1982. No interactions involving the populations were significant at 7 d.p.i.

7.1.5 Latent period (LP)

When populations were compared across developmental stages, races, and years for LP (Table 9), the rust-susceptible population 2N40 had the shortest mean LP (9.66 days). It differed significantly from two of the bulk populations, 2N430 and 2N52, and from the four mass-selected populations. The three bulk populations were indistinguishable statistically, in terms of this component, as were the four mass-selected popu-

lations. However, these two groups were significantly different from each other, with the exception of population 2N319. The mass-selected population 2N319 with a latent period of 11.83 days was significantly different from 2N34, but could not be distinguished from the other two bulk populations. The mass-selected population 2N29 had the longest mean LP (12.81 days) and this was 1.3 times longer than that for the fast-rusting 2N40.

Plants inoculated at developmental stage 2.9 were found to differ significantly on the basis of LP (11.76 days) from those inoculated at stage 4.5 (11.20 days), but not from plants inoculated at stage 5.3 (11.62 days). Plants inoculated at developmental stage 4.5 had the shortest mean LP.

No significant differences were observed between the two races. However, differences between the two test years were significant. Plants inoculated with rust in 1982 had a significantly shorter LP (10.50 days) than those inoculated in 1983 (12.25 days).

The populations were compared within each year with either race for mean LP (Table 10). In 1982, when inoculated with urediniospores of race 3, population 2N40 had the shortest mean LP (9.59 days). It differed significantly from only the following three mass- selected populations: 2N319 (11.83 days), 2N122 (12.25 days), and 2N29 (12.81 days). The bulk populations were significantly different from only 2N29, the population with the longest mean LP.

No significant differences were observed in mean LP among populations inoculated with urediniospores of race 4, in 1982. In 1983, when plants were inoculated with urediniospores of race 3, the susceptible popula-

TABLE 9. Effect of host population, developmental stage, rust race, and year on latent period and LP_{50} of eight field-grown faba bean populations.

		Latent period	LP_{50}
Population[1]	2N40 (BK)	9.66 a[5]	11.06 a
	2N34 (BK)	10.64 ab	13.44 a
	2N430 (BK)	10.85 bc	13.72 b
	2N52 (BK)	10.85 bc	13.37 b
	2N319 (MS)	11.83 cd	15.12 c
	2N29 (MS)	12.81 d	16.10 c
	2N43 (MS)	12.60 d	16.03 c
	2N122 (MS)	12.32 d	15.61 c
Developmental Stage[2]	2.9	11.76 a	14.56 a
	4.5	11.20 b	14.21 a
	5.3	11.62 ab	14.56 a
Race[3]	3	11.48 a	14.28 a
	4	11.48 a	14.56 a
Year[4]	1982	10.50 a	13.23 a
	1983	12.25 b	15.33 b
Mean square error		0.17	0.19

[1]Data are means for 432 observations combined over developmental stages, races, and years.
[2]Data are means for 1152 observations combined over populations, races, and years. The three stages of development: 2.9, 4.5, and 5.3, refer to plants 35, 50, and 65 days from planting, respectively, and are based on Liew and Gaunt's (1982) developmental key for beans.
[3]Data are means for 1728 observations combined over populations, developmental stages, and years.
[4]Data are means for 1728 observations combined over populations, developmental stages, and races.
[5]Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

TABLE 10. Latent period of eight field-grown faba bean populations inoculated with two rust races in 1982 and 1983.

		1982		1983	
		Race 3	Race 4	Race 3	Race 4
Population	2N40 (BK)	9.59 a[1]	8.68 a	9.80 a	10.50 a
	2N34 (BK)	10.50 ab	9.45 a	10.85 ab	11.41 ab
	2N430 (BK)	10.78 ab	9.45 a	11.20 abc	11.48 ab
	2N52 (BK)	10.71 ab	9.87 a	10.08 a	12.39 abc
	2N319 (MS)	11.83 bc	9.52 a	11.97 abc	13.30 bcd
	2N29 (MS)	12.81 c	9.03 a	13.09 c	15.26 d
	2N43 (MS)	11.13 abc	10.43 a	13.16 c	14.28 cd
	2N122 (MS)	12.25 bc	10.15 a	12.46 bc	13.72 cd
Mean square error		0.11	0.20	0.18	0.17

[1]Data are means for 108 observations combined over developmental stages. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

tion 2N40 had the shortest LP (9.80 days). It, as well as the bulk population 2N52 (LP of 10.08 days) differed significantly from the following three mass-selected populations: 2N29 (13.09 days), 2N43 (13.16 days), and 2N122 (12.46 days). Additionally, the bulk population 2N34 had a significantly shorter LP (10.85 days) than either of the mass-selected populations 2N29 and 2N43. No other significant differences were observed for this year-race combination.

When plants were inoculated with urediniospores of race 4, in 1983, the rust-susceptible population 2N40, with the shortest mean LP (10.50 days) was significantly different from the mass-selected populations, but not from the bulk populations. The bulk populations 2N34 and 2N430 with LPs of 11.41 and 11.48 days, respectively, were significantly different from three of the four mass-selected populations. Additionally, population 2N52 had a significantly shorter LP (12.39 days) than 2N29, the population with the longest LP (15.26 days).

7.1.6 Latent period (LP_{50})

Populations were compared across developmental stages, races, and years for mean values of LP_{50} (Table 9). The rust-susceptible population 2N40 had the smallest mean LP_{50} value and it differed significantly, on the basis of this component from the remaining populations according to Scheffé's procedure. The other populations were categorized into two groups based on their mean LP_{50} values. The bulk populations 2N34, 2N430, and 2N52, with mean values of 13.44, 13.72, and 13.37 days, respectively, were statistically indistinguishable by Scheffé's

procedure. Similarly, the mass-selected populations which had the longest mean values for this component (ranging from 15.12 days for population 2N319 to 16.10 days for population 2N29), did not differ significantly from each other. They were statistically different from the bulk populations, however.

LP_{50} was longer by a factor of 1.4 to 1.5 in the mass-selected populations than in the rust-susceptible population. The magnitude of this increase is consistent with the observations of Ohm and Shaner (1976), who reported that slow-rusting winter wheats had latent periods that were 1.2 to 1.8 times longer than their fast-rusting counterparts. In addition, Wahl et al., (1980) and Statler and Parlevliet (1987) have reported similar differences in latent period between slow and fast-rusting populations.

Comparisons among plants inoculated at the three developmental stages were not significant. In addition, plants inoculated with urediniospores of race 3 did not differ significantly from those inoculated with urediniospores of race 4. Differences between the two test years were, however, significant. Plants inoculated with rust in 1982 possessed a mean latent period of 13.23 days and this was significantly shorter than those inoculated in 1983 (15.33 days).

The populations were compared within each year with either race 3 or 4 on the basis of their mean values for LP_{50} (Table 11). These values represent the average for plants over all developmental stages. In 1982, when plants were inoculated with urediniospores of race 3, the rust-susceptible population 2N40, had the smallest mean value for LP_{50} (10.15 days). This differed significantly from the mean values for the

TABLE 11. LP_{50} of eight field-grown faba bean populations inoculated with two rust races in 1982 and 1983.

		1982		1983	
		Race 3	Race 4	Race 3	Race 4
Population	2N40 (BK)	10.15 a[1]	10.43 a	10.64 a	13.37 a
	2N34 (BK)	13.44 bc	11.69 ab	13.37 bc	14.91 ab
	2N430 (BK)	14.00 bcd	11.48 ab	13.93 bcd	14.98 ab
	2N52 (BK)	12.46 b	12.25 ab	12.32 ab	15.89 bc
	2N319 (MS)	15.33 cde	12.53 ab	14.98 cde	16.80 bcd
	2N29 (MS)	16.31 e	11.69 ab	16.59 e	18.76 d
	2N43 (MS)	14.63 bcde	13.58 b	16.66 e	17.78 cd
	2N122 (MS)	15.75 de	13.02 b	15.75 de	17.22 cd
Mean square error		0.15	0.18	0.24	0.17

[1]Data are means for 108 observations combined over developmental stages. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

other populations. The three bulk populations, in addition to the mass-selected population 2N43, were statistically indistinguishable with values ranging from 12.46 days for 2N52 to 14.63 days for population 2N43. The mass-selected population 2N29, possessed the largest mean value for LP_{50} (16.31 days). It differed significantly from the bulk populations, but was statistically indistinguishable from the other mass-selected populations.

With race 4, as with urediniospores of race 3, the rust-susceptible population 2N40 possessed the shortest mean LP_{50} (10.43 days). However, unlike with urediniospores of race 3, 2N40 differed significantly from only two mass-selected populations, 2N43 and 2N122, with mean values for LP_{50} of 13.58 and 13.02 days, respectively. Both 2N43 and 2N122 were indistinguishable statistically from the other populations.

In 1983, when inoculated with urediniospores of race 3, population 2N40 had the smallest mean value for LP_{50} (10.64 days). Although it was statistically indistinguishable from population 2N52 (12.32 days), it differed significantly from the others. The mass-selected populations 2N29 and 2N43, with mean values of 16.59 and 16.66 days, respectively, possessed the largest values for this component. They were not, however, significantly different from the remaining mass-selected populations. The bulk populations were indistinguishable on the basis of this component.

When inoculated with race 4, the rust-susceptible population 2N40 had the smallest value for LP_{50} (13.37 days). Population 2N40 did not differ significantly from the bulk populations, 2N34 and 2N430 (with values of 14.91 and 14.98 days, respectively), but it was statistically

distinguishable from the bulk population 2N319, in addition to the four mass-selected populations. The latter populations had values for this component that ranged from 15.89 days for population 2N52 to 18.76 days for population 2N29.

LP_{50}, which has the advantage of being easier to measure (Shaner, 1980), was superior to LP in distinguishing among the faba bean populations when the data for this study was pooled. LP_{50} separated the populations into three groups, whereas with LP, these groups were less distinct.

Comparisons among plants inoculated at the three developmental stages were not significant for LP_{50}. For LP, however, plants inoculated at developmental stage 2.9 were found to differ significantly from those inoculated at stage 4.5, but not from those inoculated at stage 5.3. Plants inoculated at stage 4.5 had the smallest mean LP and LP_{50} values. Parlevliet (1977;1979), Jones (1978), Parlevliet et al., (1985), and Johnson (1986) have reported that latent period is greatly influenced by the growth stage of the plants. They have stressed the importance of measuring latent period on plants at the same stage of development. Results from this study for LP tend to support their conclusions.

No significant differences in LP_{50} and LP were observed with the two rust races used in this study. Rouse et al., (1980) found that when they inoculated four wheat cultivars with one of six isolates of Erysiphe graminis f. sp. tritici, all cultivar-isolate combinations possessed latent periods that were less than 24 hours of each other. However, Parlevliet (1977) reported that there was a significant interaction between cultivars and isolates for the latent period of barley, but in most cases the interaction was of small magnitude.

Significant differences were found between the two test years. With both LP and LP_{50}, significantly longer latent periods were found in 1983, and this may be explained by the less favourable conditions for rust development in that year (Appendix B). This is in contrast to the results of Parlevliet and Van Ommeren (1975) who reported that despite seasons that were very different from each other, no year effect on the latent period of barley was discernable. On the other hand, Shearer and Zadoks (1972;1974) and Asher and Thomas (1984) have found that temperature and the duration of leaf wetness are important environmental factors which influence the length of the latent period.

When year-race combinations of the data were analyzed, LP_{50} was more effective in differentiating among the populations than was LP, and this was the case for every combination. The interaction between races and populations was not significant for LP and neither was the interaction between the year of testing and populations. The C.V. for LP_{50} (21.26 %; Appendix L), was smaller than for LP (24.93 %; Appendix K)), and this, along with the superior differentiating ability and relative ease of measurement of LP_{50} suggests that it is preferred over LP as a method of assessing rate-reducing resistance.

7.2 ASSESSMENT OF POPULATION PERFORMANCE

7.2.1 Rust severity (RS)

The rust-susceptible population 2N40 had the greatest mean leaflet area infected with rust (6.53 %) during the four week period following inoculation. It differed significantly from the other populations according to Scheffé's significant difference procedure (Table 12). The bulk populations 2N34, 2N430, and 2N52, with mean values for RS of 1.97,

1.61, and 1.86 %, respectively, were indistinguishable statistically. Population 2N34 was significantly different from all mass-selected populations whereas 2N52 differed from three of the four (2N29, 2N43, and 2N122), and 2N430 from only population 2N122. Comparisons among the mass-selected populations were not significant.

No significant differences were observed on the basis of this component among plants inoculated at the different developmental stages. Similarly, comparisons between the two races were not significant. However, differences between the test years were significant with populations inoculated in 1982 having a higher overall RS (2.64 %) than those inoculated in 1983 (1.25 %). Differences in rust severity among cultivars inoculated with different isolates of rust were observed by Wilcoxson et al., (1975) in wheat infected with stem rust and by Parlevliet (1977) in barley infected with leaf rust. On the other hand, both of these reports in addition to a study by Groth et al., (1983) did not observe any significant differences over two to three years of testing. Differences in rust severity between the two test years in this study may be attributable to the heterogeneous nature of the faba bean populations and to the magnitude of the environmental variation represented by the two seasons (Appendix B).

The populations were compared within each year with either race, (Table 13), and when plants were inoculated with urediniospores of race 3, in 1982, population 2N40 had the greatest mean RS (8.05 %); it differed significantly from the other populations. Mean RS values for the remaining populations ranged from 2.09 % for the bulk population 2N34 to 0.69 % for the mass-selected population 2N122 and these were statistically indistinguishable.

TABLE 12. Effect of host population, developmental stage, rust race, and year on mean and final rust severity of eight field-grown faba bean populations.

		Mean rust severity	Final rust severity
Population[1]	2N40 (BK)	6.53 a[5]	21.78 a
	2N34 (BK)	1.97 b	6.63 b
	2N430 (BK)	1.61 bcd	5.92 bc
	2N52 (BK)	1.86 bc	6.35 b
	2N319 (MS)	1.05 cde	4.09 cd
	2N29 (MS)	0.92 de	3.84 d
	2N43 (MS)	0.92 de	3.81 d
	2N122 (MS)	0.75 e	3.30 d
Developmental Stage[2]	2.9	2.01 a	6.62 ab
	4.5	2.09 a	7.04 a
	5.3	1.71 a	5.68 b
Race[3]	3	1.80 a	5.93 a
	4	2.80 a	6.89 a
Year[4]	1982	2.64 a	8.32 a
	1983	1.25 b	4.61 b
Mean square error		0.09	0.25

[1]Data are means for 432 observations combined over developmental stages, races, and years.
[2]Data are means for 1152 observations combined over populations, races, and years. The three stages of development: 2.9, 4.5, and 5.3, refer to plants 35, 50, and 65 days from planting, respectively, and are based on Liew and Gaunt's (1982) developmental key for beans.
[3]Data are means for 1728 observations combined over populations, developmental stages, and years.
[4]Data are means for 1728 observations combined over populations, developmental stages, and races.
[5]Comparisons among means were made using logit transformed data. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

TABLE 13. Rust severity of eight field-grown faba bean populations inoculated with two rust races in 1982 and 1983.

		1982		1983	
		Race 3	Race 4	Race 3	Race 4
Population	2N40 (BK)	8.05 a[1]	10.49 a	3.35 a	3.91 a
	2N34 (BK)	2.09 b	2.80 b	1.63 bc	1.36 b
	2N430 (BK)	1.52 b	2.55 b	1.22 bcd	1.20 bc
	2N52 (BK)	1.98 b	2.17 b	2.05 b	1.22 bcd
	2N319 (MS)	1.11 b	1.85 b	0.94 bcd	0.33 cd
	2N29 (MS)	0.86 b	1.89 b	0.67 cd	0.27 d
	2N43 (MS)	1.43 b	1.39 b	0.58 d	0.29 cd
	2N122 (MS)	0.69 b	1.30 b	0.71 cd	0.30 cd
Mean square error		0.17	0.12	0.05	0.05

[1]Data are means for 108 observations combined over developmental stages. Comparisons among means were made using logit transformed data. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

In 1982, when plants were inoculated with urediniospores of race 4, comparisons among the populations gave results similar to those with urediniospores of race 3. Population 2N40 had the greatest mean value for RS (10.49 %) and 2N122, the lowest (1.30 %). Population 2N40 was significantly different from the others, however, no other comparisons were significant. Mean values for RS were greater for plants inocuated with urediniospores of race 4 than for those inoculated with urediniospores of race 3, but these differences were not significant.

In 1983, comparisons among populations inoculated with race 3 indicated that population 2N40 had the largest mean value for this component (3.35 %), and that it differed significantly from the other populations. The bulk populations 2N34, 2N43, and 2N52, with mean values for RS of 1.63 %, 1.22 %, and 2.05 %, respectively, and the mass-selected population 2N319 with a mean value of 0.94 % were indistinguishable statistically. However, population 2N52 was significantly different from the mass-selected populations 2N29, 2N43, and 2N122; moreover, population 2N34 differed from 2N122. The four mass-selected populations were indistinguishable statistically on the basis of this component.

When comparisons were made among populations inoculated with urediniospores of race 4, population 2N40, with a value of 3.91 percent had the largest value for RS, and population 2N29, the smallest (0.27%). Population 2N40 was significantly different from the other faba bean populations. The bulk populations 2N34, 2N43, and 2N52, with mean values of 1.63 % , 1.22 % , and 2.05 %, respectively were indistinguishable statistically as were the mass-selected populations.

The interaction between test years and races was significant for this component (Appendix M). This is possibly due to the higher values for this component with urediniospores of race 4 than with urediniospores of race 3 in 1982 whereas in 1983, higher values were found with urediniospores of race 3 for all populations, except 2N40. The coefficient of variation for RS was low (7.49 %).

Individual analyses of rust severity at weekly intervals (one to four weeks following inoculation) were also conducted. The results from these analyses are not presented here, because as suggested by Bailey et al., (1987), difficulties in establishing the timing of individual weekly assessments could hamper their usefulness since small differences between slow- and fast-rusters may only be identifiable for short periods of time. However, tables of the effects of host population, developmental stage, rust race, and year on the rust severity of the faba bean populations, at each of the four assessment periods are available in Appendices O - V.

7.2.2 Final rust severity (FRS)

Final rust severity, a measure of the percent leaflet area infected with rust just prior to leaflet senescence, was used to differentiate among the faba bean populations. The populations were compared over developmental stages, races, and years on the basis of this component (Table 12). The rust-susceptible population 2N40, had the highest mean final rust severity (21.78 %) and this value was significantly higher than the values for the other populations. The smallest value for FRS

was observed for the mass-selected population 2N122 (3.30 %), however, it was not significantly different from the values for the other three mass-selected populations. The bulk populations 2N34, 2N430, and 2N52, with mean values of 6.63 %, 5.92 %, and 6.35 % respectively, were indistinguishable statistically, and had significantly higher values for FRS (except for 2N430) than did the mass-selected populations.

When plants were inoculated at the different developmental stages the largest mean value for FRS was observed at developmental stage 4.5 (7.04 %). The smallest value occurred for those plants inoculated at stage 5.3 (5.68 %), and it was significantly different from those at stage 4.5. Subrahmanyam et al., (1983), reported that there was a decline in the susceptibility of plants to peanut rust with age, and his results are in agreement with the results from this study.

Plants inoculated with urediniospores of race 4 had a greater FRS (6.89 %), however, this was not significantly different from those inoculated with urediniospores of race 3 (5.93 %). Comparisons between test years were significant. The mean FRS for plants inoculated in 1982 was 8.32 %, considerably higher than for those inoculated in 1983 (4.61 %).

The populations were compared within each year with either race on the basis of their mean FRS (Table 14). In 1982, in the inoculation with urediniospores of race 3, population 2N40, had the largest mean value for this component (21.60 %), and it differed significantly from the other populations. The smallest mean value was observed for population 2N122 (3.96 %), however, it did not differ significantly from any of the other populations, with the exception of 2N40.

TABLE 14. Final rust severity of eight field-grown faba bean populations inoculated with two rust races in 1982 and 1983.

		1982		1983	
		Race 3	Race 4	Race 3	Race 4
Population	2N40 (BK)	21.60 a[1]	29.03 a	14.88 a	15.83 a
	2N34 (BK)	7.23 b	8.84 b	5.04 bc	5.32 b
	2N430 (BK)	5.57 b	7.79 bc	5.23 bc	4.96 b
	2N52 (BK)	7.17 b	6.67 bc	6.21 b	5.34 b
	2N319 (MS)	4.96 b	5.89 bc	3.51 bc	1.79 bc
	2N29 (MS)	4.33 b	6.14 bc	3.41 c	0.93 c
	2N43 (MS)	6.02 b	4.62 bc	3.02 c	1.66 bc
	2N122 (MS)	3.96 b	3.94 c	3.92 bc	1.39 c
Mean square error		0.32	0.23	0.13	0.27

[1]Data are means for 108 observations combined over developmental stages. Comparisons among means were made using logit transformed data. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

When the populations were inoculated with urediniospores of race 4, the largest value for this component, as with urediniospores of race 3, occurred with population 2N40 (29.03 %). Population 2N40 was significantly different from the others in terms of FRS. The bulk population 2N34 had the next largest value for this component (8.84%), however, it differed significantly from only the mass-selected population 2N122 (3.94%). No other significant differences were observed.

In the 1983-race 3 combination, population 2N40 had the highest value (14.88 %) for FRS, and it differed significantly from the other populations. The mass-selected populations 2N29 and 2N43 had the smallest values (6.14 % and 4.62 %, respectively). These populations, however, differed significantly from only the bulk population 2N52, and from 2N40.

In the inoculation with urediniospores of race 4, population 2N40 had the largest value for this component (15.83 %) and it was significantly different from the others. The mass-selected population 2N29, as with urediniospores of race 3, and population 2N122 had the smallest values for FRS (0.93 % and 1.39 %, respectively). Although these differed significantly from the bulk populations, they were indistinguishable from the other mass-selected populations 2N319 and 2N43, with values of 1.79 % and 1.66 %, respectively.

The C.V. for FRS was 17.46 % (Appendix N), very much greater than the C.V. for RS (7.49 %). However, final rust severity was more useful than mean rust severity in differentiating among the populations. Conner and Bernier (1982d) and Rashid and Bernier (1986) have reported that FRS was beneficial in assessing the levels of slow-rusting resistance in faba bean accessions and that it correlated well with AUDPC scores.

7.2.3 Apparent infection rate (AIR)

When populations were compared across developmental stages, races, and years for mean apparent infection rates, the rust-susceptible population 2N40 had the highest rate (0.13) although this did not differ significantly from the rates for the bulk populations (Table 15). The four mass-selected populations all possessed the same rate (0.06). They differed significantly on the basis of this component from population 2N40, but they were indistinguishable from the bulk populations. Poyntz and Hyde (1985), Shaner (1973), Shaner and Finney (1980), and Villareal et al., (1981), have all reported significant differences among cultivars in terms of apparent infection rate.

No significant differences for r-values were observed among plants inoculated at the different developmental stages nor were differences seen with the two races. This may be due to the fact that the analyses were conducted using mean r-values which when averaged over the season did not vary substantially for the different populations. Plaut and Berger (1981) reported that low levels of disease early on in the season were compensated for by accelerated rates of increase later in the season which tended to negate the effects of the slower-rusting populations. Additionally, the use of small adjacent plots may have resulted in high levels of interplot interference which masked differences between developmental stages and races.

Significant differences for r-values were observed between the two test years. Higher mean r-values were found in 1982 than in 1983. This difference probably reflects the difference in these two seasons in terms of favorability for rust development (Appendix B).

TABLE 15. Effect of host population, developmental stage, rust race, and year on the apparent infection rate and AUDPC score of eight field-grown faba bean populations.

		Apparent infection rate	AUDPC
Population[1]	2N40 (BK)	0.13 a[5]	25.46 a
	2N34 (BK)	0.08 ab	7.49 b
	2N430 (BK)	0.08 ab	5.71 bc
	2N52 (BK)	0.09 ab	6.20 bc
	2N319 (MS)	0.06 b	3.90 bc
	2N29 (MS)	0.06 b	3.16 c
	2N43 (MS)	0.06 b	3.28 c
	2N122 (MS)	0.06 b	2.60 c
Developmental Stage[2]	2.9	0.08 a	7.52 a
	4.5	0.08 a	7.64 a
	5.3	0.08 a	6.07 b
Race[3]	3	0.08 a	7.59 a
	4	0.08 a	6.71 a
Year[4]	1982	0.10 a	8.63 a
	1983	0.06 b	5.35 b
Mean square error		<0.01	20.60

[1]Data are means for 432 observations combined over developmental stages, races, and years.
[2]Data are means for 1152 observations combined over populations, races, and years. The three stages of development: 2.9, 4.5, and 5.3, refer to plants 35, 50, and 65 days from planting, respectively, and are based on Liew and Gaunt's (1982) developmental key for beans.
[3]Data are means for 1728 observations combined over populations, developmental stages, and years.
[4]Data are means for 1728 observations combined over populations, developmental stages, and races.
[5]Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

TABLE 16. Apparent infection rate of eight field-grown faba bean populations inoculated with two rust races in 1982 and 1983.

		1982		1983	
		Race 3	Race 4	Race 3	Race 4
Population	2N40 (BK)	0.16 a[1]	0.17 a	0.08 a	0.12 a
	2N34 (BK)	0.10 a	0.11 ab	0.06 a	0.06 ab
	2N430 (BK)	0.10 a	0.10 b	0.07 a	0.06 ab
	2N52 (BK)	0.11 a	0.09 b	0.08 a	0.08 ab
	2N319 (MS)	0.08 a	0.09 b	0.05 a	0.04 b
	2N29 (MS)	0.07 a	0.10 b	0.05 a	0.02 b
	2N43 (MS)	0.09 a	0.08 b	0.05 a	0.04 b
	2N122 (MS)	0.07 a	0.07 b	0.06 a	0.03 b
Mean square error		<0.01	<0.01	<0.01	<0.01

[1]Data are means for 108 observations combined over developmental stages. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

The populations were compared within each year with either race on the basis of their mean AIR (Table 16). In the inoculation with urediniospores of race 3, in 1982, rates ranged from a high of 0.16 for the rust-susceptible population 2N40 to 0.07 for the mass-selected populations 2N29 and 2N122. However, no differences among the populations were considered significant by Scheffé's significant difference procedure.

With race 4, population 2N40 possessed the highest mean infection rate (0.17) and it differed significantly on the basis of this component from the other populations, but with the exception of the bulk population 2N34, which had a mean rate of 0.11. Additionally, 2N34 was indistinguishable from the other populations which had mean infection rates ranging from 0.10 for populations 2N430 and 2N29 to 0.07 for population 2N122.

Results obtained with urediniospores of race 3, in 1983, were similar to those obtained with this race in 1982, in that no significant differences were seen among the populations. Rates for the populations ranged from 0.08 for 2N40 and 2N52, to a low of 0.05 for the mass-selected populations 2N319, 2N29, and 2N43.

In 1983, in the inoculation with urediniospores of race 4, population 2N40 possessed the highest mean infection rate (0.12). It was significantly different from the mass-selected populations which had mean rates ranging from 0.04 for 2N319 and 2N43 to 0.02 for the population 2N29. However, 2N40 was found to be indistinguishable statistically from the bulk populations 2N34 and 2N430 with a mean infection rate of 0.06, as well as from 2N52, with a value for this component of 0.08.

Additionally, the bulk populations could not be distinguished from the mass-selected populations.

The C.V. associated with AIR was 22.07 % (Appendix W). All interactions were significant except for the interaction between year of testing and developmental stage.

7.2.4 Area under the disease progress curve (AUDPC)

AUDPC was effective in distinguishing among the faba bean populations. The rust-susceptible population 2N40 had the largest mean AUDPC value (25.46) and it was found to differ significantly from the other populations (Table 15). Population 2N34, a bulk population, had the second largest mean AUDPC value (7.49). This population could not be distinguished statistically from either 2N430 and 2N52, also bulk populations, nor from 2N319, a mass-selected population. However, 2N34 was found to differ significantly from the mass-selected populations 2N29, 2N43, and 2N122. These, however, could not be distinguished from any of the others except 2N40.

Area under the disease progress curve has been used extensively to assess levels of resistance in plant populations because as Palmer and Wilcoxson (1982) have stated, it summarizes the effects of all those factors that contribute to the development of rust over the season. Previously, Rashid and Bernier (1986) and Conner and Bernier (1982d) have noted the usefulness of AUDPC in differentiating among faba bean accessions. Rashid and Bernier (1986) found differences at the 1 %

TABLE 17. Area under the disease progress curve (AUDPC) values of eight field-grown faba bean populations inoculated with two rust races in 1982 and 1983.

		1982		1983	
		Race 3	Race 4	Race 3	Race 4
Population	2N40 (BK)	25.15 a[1]	36.34 a	22.01 a	15.30 a
	2N34 (BK)	9.35 b	8.32 b	7.16 b	5.23 b
	2N430 (BK)	5.25 b	7.20 b	6.37 b	4.00 bc
	2N52 (BK)	7.28 b	5.91 b	7.20 b	4.77 bc
	2N319 (MS)	5.06 b	4.84 b	4.72 b	1.42 bc
	2N29 (MS)	3.48 b	5.13 b	2.91 b	0.98 c
	2N43 (MS)	5.36 b	3.54 b	2.72 b	1.59 bc
	2N122 (MS)	3.76 b	2.96 b	2.39 b	1.41 bc
Mean square error		12.29	39.39	11.52	6.21

[1]Data are means for 108 observations combined over developmental stages. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

level of significance between accessions for AUDPC. Similarly, Wilcoxson et al., (1975), Southern (1978), and Singleton et al., (1982), have found AUDPC a reliable and convenient method for observing differences among cereal cultivars infected with rust; Johnson (1986) came to the same conclusion in his study of the rust of asparagus.

No significant differences were observed in mean AUDPC values among populations inoculated at either developmental stage 2.9 (7.52) or 4.5 (7.64). Plants inoculated at the latest developmental stage, however, had mean AUDPC values that were significantly less (6.07), thus indicating the importance of using plants at the same stage of development when screening for rate-reducing resistance in artificially inoculated plots.

AUDPC values were not found to be influenced by race in that the overall mean for populations inoculated with race 3 was indistinguishable statistically (7.52) from those inoculated with urediniospores of race 4 (6.71). In addition, the interaction between populations and races was not significant. These results are in agreement with those of Rashid and Bernier (1986) who reported that mass-selected faba bean populations reacted similarly to races 1 and 3 of U. viciae-fabae. Wilcoxson et al., (1975) noted that over three years of testing with different stem rust races, used individually, or in mixtures, differences among cultivars as measured by AUDPC were distinct and stable. On the other hand, Southern (1978) and Cox (1977) found that the slow-rusting ability, as determined by AUDPC, of certain spring wheat cultivars varied with the races of Puccinia graminis f.sp. tritici used in the inoculation. It is possible, however, that the presence of the temperature-sensitive Sr6 gene (Green and Johnson, 1955) may have been responsible for these differences.

Mean AUDPC values for the populations in this study were significantly different between the two test years. Higher AUDPC values were observed in 1982 (8.63) than in 1983 (5.35). The interaction between populations and year of testing was significant, probably because AUDPC values were approximately equal in both years for populations 2N430, 2N52, and 2N122, but were greater in 1982 for the other populations. Wilcoxson et al., (1975), Southern, (1978), and Singleton et al., (1982) all reported that testing over a number of years indicates that AUDPC is generally a stable character. However, it is subject to environmental influences (Southern, 1978 and Johnson, 1986). Southern (1978) noted that precipitation, in addition to other factors such as host growth stage, minimum and maximum temperatures, hours of free moisture, sunlight intensity as well as infection rate and spore numbers probably contributed to the higher mean AUDPC values observed in some locations.

When analyses of variance for AUDPC were done on year-race combinations of the data, only a very few statistically significant differences among the populations were observed (Table 17). This may be due to the general heterogeneity of the populations resulting from their partially outcrossing nature (Holden and Bond, 1960) as well as to varying levels of interplot interference. In three of the four year-race combinations (1982-race 3, 1982-race 4, and 1983-race 3), only the rust-susceptible population 2N40 could be distinguished.

In the 1983-race 4 combination, 2N40, with a mean AUDPC value of 15.3 was found to be significantly different from the other populations. Only one other difference was significant; population 2N34 (5.23) was found to differ from population 2N29 (0.98). The largest values were observed with either race 3 or race 4, in 1982, and the smallest values, with race 4, in 1983.

The coefficient of variation associated with AUDPC was 64.15 % (Appendix X). This value was considerably higher than the C.V. for apparent infection rate (Appendix W), however, AUDPC was a more effective measure of rate-reducing resistance. The superiority of AUDPC values over AIR has also been reported by Shaner and Finney (1980) and by Wilcoxson et al., (1975). The two-way interactions that were significant were those between year of testing and rust race, and between year of testing and populations. In addition, the interaction between developmental stage and populations was significant, as was the triple interaction between year of testing, race, and populations.

7.2.5 LPSM

LPSM proved to be very useful in the evaluation of rate- reducing resistance in faba bean populations. When populations were compared across developmental stages, races, and years for LPSM (Table 18), the rust-susceptible population 2N40 had the smallest mean value for this index (0.36), and it differed significantly from the other populations. The bulk populations, 2N34, 2N430, and 2N52, with mean values for this component of 1.71, 1.80, and 1.66, respectively, were indistinguishable statistically. No significant differences were observed among the mass-selected populations with mean values for LPSM ranging from 2.47 for population 2N319 to 2.72 for 2N29. The mass-selected populations had significantly higher values for LPSM than the bulk populations.

Faba bean plants inoculated at developmental stages 2.9 and 5.3, with values for LPSM of 2.18 and 2.16, respectively, were indistinguishable

TABLE 18. Effect of host population, developmental stage, rust race, and year on the LPSM values of eight field-grown faba bean populations.

		LPSM
Population[1]	2N40 (BK)	0.36 a[5]
	2N34 (BK)	1.71 b
	2N430 (BK)	1.80 b
	2N52 (BK)	1.66 b
	2N319 (MS)	2.47 c
	2N29 (MS)	2.72 c
	2N43 (MS)	2.71 c
	2N122 (MS)	2.63 c
Developmental Stage[2]	2.9	2.18 a
	4.5	1.88 b
	5.3	2.16 a
Race[3]	3	1.98 a
	4	1.15 b
Year[4]	1982	1.70 a
	1983	2.32 b
Mean square error		0.93

[1]Data are means for 432 observations combined over developmental stages, races, and years.
[2]Data are means for 1152 observations combined over populations, races, and years. The three stages of development: 2.9, 4.5, and 5.3, refer to plants 35, 50, and 65 days from planting, respectively, and are based on Liew and Gaunt's (1982) developmental key for beans.
[3]Data are means for 1728 observations combined over populations, developmental stages, and years.
[4]Data are means for 1728 observations combined over populations, developmental stages, and races.
[5]Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

TABLE 19. LPSM values of eight field-grown faba bean populations inoculated with two rust races in 1982 and 1983.

		1982		1983	
		Race 3	Race 4	Race 3	Race 4
Population	2N40 (BK)	-0.92 a[1]	-0.03 a	0.94 a	1.21 a
	2N34 (BK)	1.45 b	1.21 b	1.95 bc	2.03 b
	2N430 (BK)	1.41 b	1.45 bc	2.07 cd	2.04 b
	2N52 (BK)	1.03 b	1.62 bcd	1.44 ab	2.44 bc
	2N319 (MS)	2.39 c	2.17 d	2.44 cde	2.80 cd
	2N29 (MS)	2.74 c	2.05 cd	2.76 e	3.15 d
	2N43 (MS)	2.42 c	2.30 d	2.86 e	2.99 cd
	2N122 (MS)	2.67 c	2.20 d	2.61 de	2.92 cd
Mean square error		1.42	0.79	0.93	0.71

[1]Data are means for 108 observations combined over developmental stages. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

statistically, but significantly different from those inoculated at stage 4.5 (mean LPSM value of 1.88).

Differences between races for mean values of LPSM were significant. Plants inoculated with urediniospores of race 3 had a larger mean value for LPSM (1.98) than those inoculated with urediniospores of race 4 (1.15). Differences between the two test years were also significant. Plants inoculated in 1982 had a smaller mean value for LPSM (1.70) than those inoculated in 1983 (2.32).

The populations were compared within each year with either race for mean LPSM (Table 19). In 1982, when plants were inoculated with race 3, population 2N40 had the smallest mean value (-0.92), and it differed significantly from the other populations. The three bulk populations with mean values for LPSM ranging from 1.03 for population 2N52 to 1.45 for 2N34, were indistinguishable statistically. Similarly, no significant differences were observed among the four mass-selected populations which had mean values for this index ranging from 2.39 for population 2N319 to 2.74 for 2N29. The mass-selected populations had significantly higher values for LPSM than did the bulk populations.

When plants were inoculated with urediniospores of race 4 population 2N40 had the smallest value for LPSM (-0.03). This population differed significantly from the others on the basis of this component. The bulk population 2N34 had the next smallest value for LPSM (1.21). It differed significantly from the four mass- selected populations but was indistinguishable from the other bulk populations. The mass-selected populations were indistinguishable not only amongst themselves, but also from the bulk population 2N52. Additionally, the mass-selected popula-

tion 2N29 with a LPSM value of 2.05 could not be distinguished from the bulk population 2N430 (mean LPSM value of 1.45).

In 1983, when plants were inoculated with urediniospores of race 3, the rust-susceptible population 2N40 had the smallest value for LPSM (0.94). It differed significantly from the other populations, with the exception of 2N52 (1.44). The bulk populations, 2N34 and 2N430, with mean values for LPSM of 1.95 and 2.07, respectively, were indistinguishable. The four mass-selected populations with mean values ranging from 2.44 for 2N319 to 2.86 for population 2N43 were also indistinguishable statistically. The separation between bulk and mass-selected populations was not definitive as both 2N34 and 2N430 were statistically similar to the mass-selected population 2N319, and in the case of 2N430, also to the mass-selected population 2N122.

When plants were inoculated with urediniospores of race 4, in 1983, population 2N40 had the smallest value for LPSM (1.21). This population differed significantly from the other populations in terms of this index. The bulk populations, with values for LPSM ranging from 2.03 for population 2N34 to 2.44 for 2N52, were indistinguishable according to Scheffé's significant difference procedure. Likewise, the four mass-selected populations were similar on the basis of LPSM. For the latter group of populations, the mean values for LPSM ranged from 2.80 for population 2N319 to 3.15 for population 2N29. With race 4, the bulk populations 2N34 and 2N430 were clearly distinguishable from the mass-selected populations. The bulk population 2N52, was found not to be significantly different from three of the mass-selected populations. It differed significantly only from population 2N29.

The coefficient of variation associated with LPSM was 46.88 % (Appendix Y), and this was considerably greater than the C.V.'s for either LP or LP_{50}. However, LPSM was at least as effective as LP_{50} in differentiating among the populations. It differed from LP_{50} in that differences between the races used to inoculate the populations were significant and comparisons among the developmental stages were significant.

7.2.6 Kendall's tau-b coefficients of concordance (t)

There was no consistently strong association between any single pair of resistance parameters in the year-race combinations (Appendices Z - AC). This suggests that no one component was a definitive predictor of this epidemic. Parlevliet et al., (1985) observed that there was a tendency for the components of partial resistance to vary in association. Clifford (1972) noted that seedlings of the barley cultivar Vada had a lower infection frequency and that this was associated with a longer latent period, a lower rate of sporulation, and a shorter infectious period than the rust-susceptible L94. It is possible that because these analyses were performed on data combined over developmental stages and populations, some of these associations were under-estimated. Parlevliet et al., (1985) noted, however, that sampling at the same developmental stage as opposed to not taking this factor into consideration, did not improve the value of the correlation coefficient between latent period and the level of barley leaf rust.

TABLE 20. Kendall's tau-b coefficients of concordance for the components of rate-reducing resistance for field-grown faba beans inoculated with rust races 3 and 4 in 1982-83.

	Components[1]									
Components	FKN	UDN	IT	ITR	LP_{50}	LPSM	RS	FRS	AUDPC	AIR
FKN	1.000	0.374**[2]	0.171*	0.228**	-0.241**	-0.320**	0.270**	0.311**	0.340**	0.291**
UDN		1.000	0.354**	0.462**	-0.538**	-0.602**	0.451**	0.483**	0.475**	0.489**
IT			1.000	0.723**	-0.219**	-0.286**	0.385**	0.422**	0.350**	0.409**
ITR				1.000	-0.280**	-0.357**	0.413**	0.479**	0.419**	0.471**
LP_{50}					1.000	0.604**	-0.485**	-0.415**	-0.432**	-0.473**
LPSM						1.000	-0.433**	-0.410**	-0.413**	-0.436**
RS							1.000	0.618**	0.625**	0.679**
FRS								1.000	0.713**	0.644**
AUDPC									1.000	0.609**
AIR										1.000

[1]FKN = Number of flecks per square centimeter of leaflet area
UDN = Number of uredinia per square centimeter of leaflet area
IT = Infection type
ITR = Range of infection types
LP_{50} = Latent period (time after inoculation until sporulation on 50 % of uredinia)
LPSM = Standardized rust severity measure
RS = Mean rust severity
FRS = Final rust severity
AUDPC= Area under the disease progress curve
AIR = Apparent infection rate
[2]Asterisks (* and **) indicate statistical significance at p-value <0.05 and p-value<0.01, respectively.

Analysis of the complete data matrix (Table 20), revealed that all associations between the characters of resistance were significant at either the 1 % or 5 % probability level. The 1983-race 4 combination (Appendix AC) also demonstrated this. Fewer significant associations occurred in the 1982-race 3 combination (Appendix Z); the weakest relationships were found in the 1982-race 4 combination (Appendix AA), as well as with the 1983-race 3 combination (Appendix AB).

The strongest associations were found between the components IT and ITR; this was the case for all year-race combinations. This was not unexpected since IT contributes, in part, to ITR. Milus and Line (1980) noted an association between ITR and other components such as latent period, infection frequency, and sporulation rate. They suggested that this component might be useful in screening breeding material for the selection of lines with longer latent periods, fewer uredinia, and low sporulation. This study would tend to support their conclusions particularly with the 1982-race 3 and 1983-race 4 analyses, where IT and ITR were the components most strongly associated with the characters measuring disease intensity. With the other year-race combinations and with the pooled data, only the component UDN was more strongly associated with the disease intensity variables. Good correspondence was also observed between UDN and LPSM, and to a lesser extent between LP_{50} and LPSM. In the latter case, the two components were negatively associated with the other characters, but positively with each other except in the 1982-race 4 analysis where the associations between IT and ITR and LP_{50} and between IT and LPSM were positive.

Among the disease intensity variables, stronger relationships were evident between AIR and the components of resistance, in 1982, and

between AUDPC and the components, in 1983. Wilcoxson et al., (1975) and Shaner and Finney (1980) have indicated that apparent infection rate is a less reliable measure than AUDPC. In this study, the apparent superiority of AIR, in 1982, may be due to the higher levels of disease present that year. Assessments for AIR and many of the resistance components were made earlier in the course of the epidemic and would therefore be less affected by the high disease levels at season-end which resulted in inflated AUDPC values. Good correspondence was also observed between FRS and AUDPC. This has been previously noted by Rashid (1983) and Conner (1981). These authors have suggested that FRS would be an appropriate indicator of slow-rusting in faba beans in preliminary tests since it is a less labour-intensive measure than AUDPC. Unfortunately, however, severity measured at a single time at epidemic-end may indicate adult plant resistance, which at least for the cereal rusts has been identified as being race-specific (Parlevliet and Van Ommeren, 1975).

7.2.7 Principal component analysis

The number of principal components (PC) estimated in these analyses is dependent upon the ability of each additional component to explain the variation in the dependency structure of the response variables and upon the somewhat subjective decision as to the proportion of the total variation that it is felt necessary to explain. Generally, for all of the PC analyses (analyses for the year-race combinations are not presented), three to five principal components were necessary to explain between 86 % to 95% of the total variation among the original response variables. All analyses indicated that the first principal component

(PC1), which accounted for 53 % (for the 1983-race 4 data matrix) to 72 % (for the 1982-race 4 data matrix) of the total variation, had factor loadings which were approximately equivalent for the constituent variables. This suggested that all variables were equally useful in assessing levels of rate-reducing resistance in the faba bean populations.

When the complete dataset for this study was submitted for PC analysis, the sum of squares of the coefficients for each response variable (eigenvalues) indicated that at least four principal components were necessary to provide a good summary of the data (each PC accounted for more than 5 % of the total variation). This implied that the disease reaction of the faba bean populations in the presence of rust races 3 and 4, was adequately described in four dimensions rather than in the original ten. Coefficients for each principal component and the communalities for this analysis are presented in Table 21. Communality estimates indicate the proportion of the variance of each response variable which is accounted for by those components that contribute greater than 5% of the total variation in the dependency structure. The proportion of the total variation among the original variables which was absorbed by the first principal component (PC1) was 61%. The second PC which is uncorrelated with PC1 absorbed an additional 11% of the total variance of the original response variables. PC3 contributed 8%, and PC4, 6%. The latter three components were trivial compared to PC1. The sum of the variation exhausted by the four components extracted in this analysis was 86%.

The interpretation of each PC was based upon the magnitude and algebraic sign of the coefficients corresponding to each response variable

TABLE 21. Principal component coefficients, communalities, and the proportion of the total variance explained by each component for ten disease resistance variables.

Variable[1]	Comm.[2]	Coefficients for principal component number									
		1	2	3	4	5	6	7	8	9	10
FKN	0.99	0.23	0.34	0.36	-0.82	0.01	-0.00	0.01	0.07	0.12	0.05
UDN	0.72	0.34	-0.12	0.08	0.09	0.69	0.24	0.55	-0.02	-0.08	0.13
LP_{50}	0.91	-0.22	0.66	0.28	0.28	0.36	-0.11	-0.29	-0.31	-0.24	0.14
LPSM	0.85	-0.31	0.45	0.09	0.19	-0.29	0.25	0.58	0.32	0.25	-0.11
IT	0.95	0.29	0.34	-0.60	0.04	-0.03	-0.13	-0.03	0.06	0.27	0.58
ITR	0.94	0.32	0.35	-0.44	-0.04	0.07	-0.06	0.03	-0.06	-0.20	-0.73
RS	0.81	0.34	0.02	0.28	0.19	-0.37	-0.52	0.38	-0.45	-0.37	0.05
FRS	0.85	0.37	0.06	0.14	0.14	-0.30	0.17	-0.08	0.48	-0.66	0.19
AUDPC	0.88	0.34	0.03	0.33	0.35	0.19	-0.25	-0.29	0.44	0.48	-0.20
AIR	0.81	0.36	-0.00	0.09	0.14	-0.26	0.70	-0.20	-0.40	0.28	-0.03
Proportion of total variance explained											
	0.87	0.61	0.11	0.08	0.06	0.04	0.02	0.02	0.02	0.01	0.01

[1]FKN = Number of flecks per square centimeter of leaflet area
UDN = Number of uredinia per square centimeter of leaflet area
IT = Infection type
ITR = Range of infection types
LP_{50} = Latent period (time after inoculation until sporulation on 50 % of uredinia)
LPSM = Standardized rust severity measure
RS = Mean rust severity
FRS = Final rust severity
AUDPC= Area under the disease progress curve
AIR = Apparent infection rate

[2]Communality estimates indicate the proportion of the variance of each variable which is accounted for by those components that contribute greater than 5 % of the total variation.

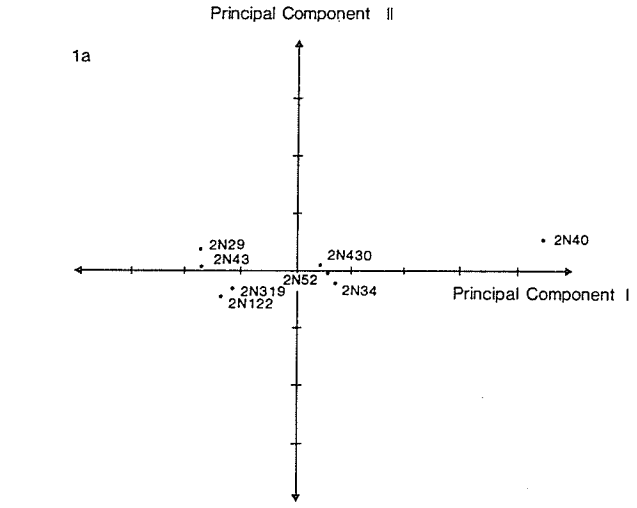
and in the proportion of the total variation in the dependency structure explained by each component. On this basis, PC1 could be interpreted as an index of overall disease. All response variables contributed approximately equally to the determination of overall disease. All coefficients were positive except for those corresponding to the response variables LP_{50} and LPSM, which received negative emphasis. This difference in sign implies that these measures varied together and in a manner in constrast to the others.

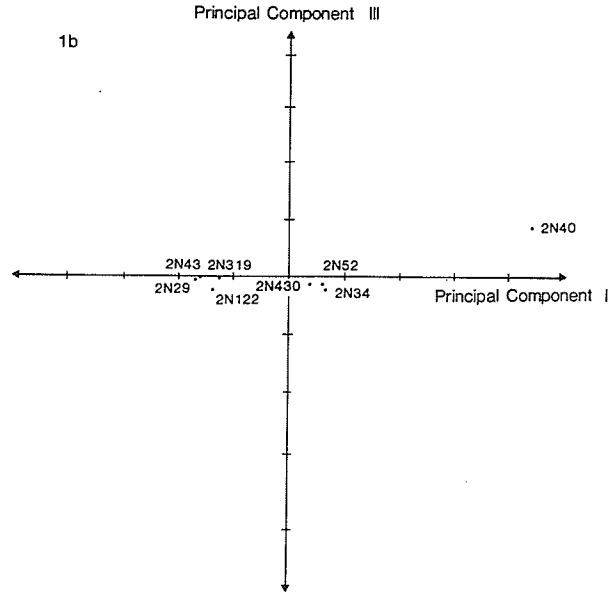
Large, positive values for PC2 were given to faba beans with long latent periods (0.66) and high values for the LPSM index (0.45). Somewhat less emphasis was given to FKN, IT, and ITR (0.34, 0.34, and 0.35, respectively). Three of the four disease intensity variables (RS, FRS, and AUDPC) received positive accent although very near zero whereas, the fourth, AIR, was very slightly negative. PC2 appears to measure the host effect on overall disease levels. The third component has large, negative values for those plants with large infection types (0.60) and range of infection types (-0.44). The other variables have coefficients that are positive with values ranging from 0.09 for AIR and LPSM to 0.36 for fleck number per square centimeter. PC4 has a very large negative value (-0.82) for FKN. Interpretations of components 3 and 4 are unclear.

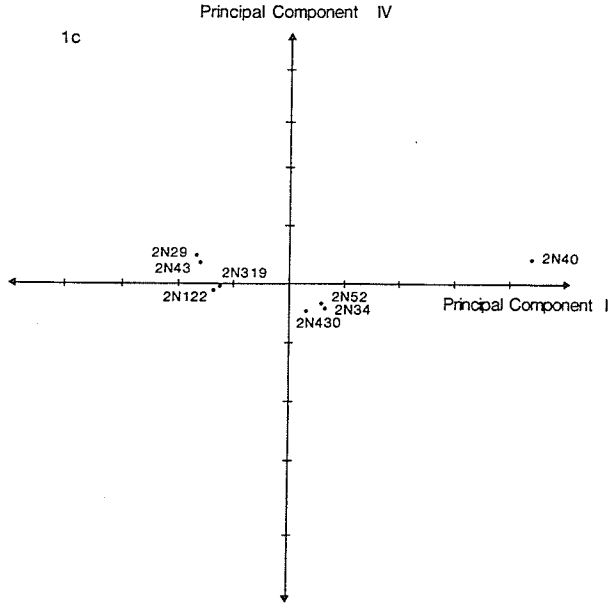
Communality estimates for this analysis ranged from 0.99 for FKN to 0.72 for UDN. The mean communality for this analysis was 0.87. High estimates were also seen for LP_{50} and LPSM, in addition to infection type and range of infection types. For the disease intensity variables, principal components 1 to 4 accounted for most of the variation in the variable, AUDPC.

Mean population scores for each of principal components two, three, and four were calculated and plotted against scores for PC1, and are presented in Figure 1. The three graphs revealed similar trends. The populations are arranged in groups corresponding to the type of selection technique that they were derived by. The mass- selected populations are clustered together as are the bulk populations. The rust-susceptible population was distinct from the other populations in having the highest positive score for PC1.

Figure 1. Mean population scores for principal components two, three, and four plotted against the scores for principal component one.


Principal Component II
1a
2N29
2N43
2N430
2N40
2N52
2N319
2N34
2N122
Principal Component I

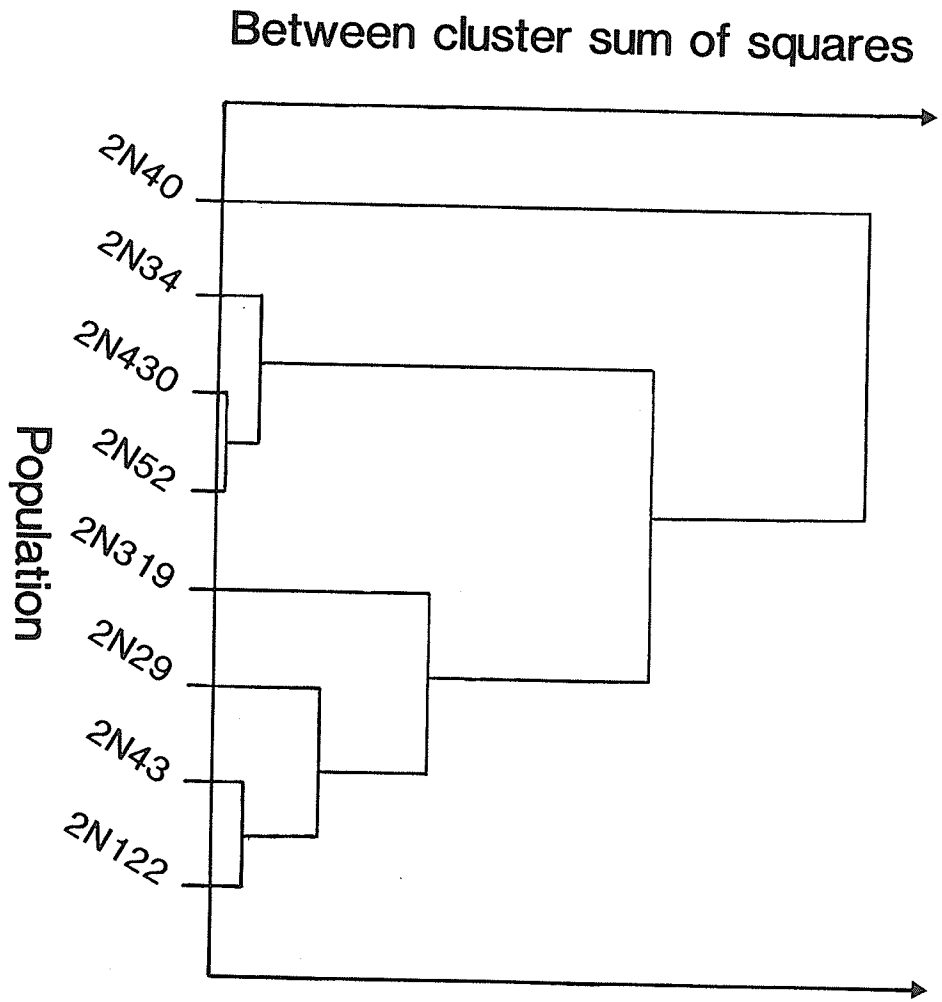

Principal Component III
1b
2N40
2N43 2N319
2N52
2N29
2N430
2N34
2N122
Principal Component I


Principal Component IV
1c
2N29
2N43
2N40
2N319
2N122
2N52
2N34
2N430
Principal Component I

7.2.8 Cluster analysis

The cluster analysis dendrogram for the complete data matrix is presented in Figure 2. When this dendrogram was examined for changes of level, merging of the faba bean bulk populations 2N430 and 2N52 caused the smallest increase in the sum of squares index, E, (0.012). This indicated that these populations were close together as shown by their reactions to the resistance parameters included in this analysis. The next smallest increase in E, (0.052) occurred when the mass-selected populations 2N43 and 2N122 were combined. When population 2N34 was merged with the other bulk populations, E increased to 0.054, and when population 2N29 was merged with 2N43 and 2N122, the index increased to 0.095. When population 2N319 was joined with the other mass-selected populations, the index increased to 0.494. A large increase (10.74) in the index, implying greater dismilarity among consitutents, was observed when the bulk populations was merged with the mass-selected populations. The sum of squares index increased to 27.21 when the rust-susceptible population was merged with the other populations. This analysis appeared to group the bulk populations in one cluster and the mass-selected populations 2N29, 2N43, and 2N122 in another. The addition of population 2N319 to the mass-selected cluster caused the sum of squares index to increase from 0.095 to 0.494. Large increases in E occurred when the mass-selected and bulk populations were combined and when the rust-susceptible population was joined with the resistant populations.

Figure 2. Sum of squares agglomeration dendrogram of eight faba bean populations inoculated at three developmental stages with two rust races in 1982 and 1983.


Between cluster sum of squares
Population
2N40
2N34
2N430
2N52
2N319
2N29
2N43
2N122

The field study indicated that the components of rate-reducing resistance were effective in identifying rate-reducing resistant populations of faba beans. On the basis of these components, the populations were readily distinguishable into those that were derived by mass-selection and those that were bulk populations. In general the mass-selected populations had more rate-reducing ability than the bulk populations, which in turn had more than the rust-susceptible population 2N40. The mass-selected and bulk populations were also distinguished by the population performance indicators. Therefore, it would appear that these results confirm the previous findings of Rashid and Bernier (1986) who noted the benefits of mass-selection for faba bean improvement. They observed that faba bean populations derived from mass-selection became increasingly homogeneous for rust reaction and that the coefficients of variation associated with AUDPC and final rust severity decreased after only a few cycles of mass-selection.

The resistance components were not equally effective in differentiating among the faba bean populations for levels of rate-reducing resistance. UDN, ITR, and LP_{50} were the most efficient. These components ranked the populations in the order predicted by all the components when taken together (Figure 1a), with only one change in ranking (for ITR). The components FKN, IT, and LP were less effective as were the performance indicators except LPSM.

Comparisons among the developmental stages were significant for all components except UDN and LP_{50}, and for all indicators except RS and AIR. This suggests that for these resistance parameters, screening for rate-reducing resistance might be equally effective with faba beans of

differing maturity. Plants inoculated at developmental stage 4.5 (equivalent to 50 days from planting) were either the most susceptible according to all indicators and components (except ITR), or were equal in susceptibility to the other stages (AIR). In addition, plants inoculated at developmental stage 5.3 (equivalent to 65 days from planting) were the most resistant according to all indicators and components (except ITR and LP), or were equal to the other developmental stages (AIR). Comparisons between the rust races indicated that race 3 was more aggressive than race 4 for all components. These differences were significant for the components FKN, IT, and ITR, but not for the components UDN, LP, and LP_{50}. Conversely, comparisons between the races for the population performance indicators indicated that race 4 was more aggressive for RS, FRS, and LPSM, but not for AUDPC. These results suggest that although race 4 was less aggressive than race 3 during the initial stages of the epidemic, it became more aggressive (than race 3) towards season-end. Evidence for this is reflected in the dependency of RS, FRS, and LPSM, moreso than for the components and AUDPC, on late-season rust severity levels.

The best slow-ruster in the field was the mass-selected population 2N43. It had low mean values for FKN and UDN, a small IT, and the smallest value for ITR. In addition, it possessed a long latent period (LP=12.60 days and LP_{50}=16.03 days). These values were only slightly shorter than for the MS population 2N29, which had the longest latent period in addition to having the smallest value for FKN. The MS population 2N122 also had high rate-reducing ability. It possessed the smallest IT, a very small ITR, and a low value for UDN. The mass-selected population 2N319 and the bulk population 2N430 had intermediate

levels of rate-reducing resistance as indicated by intermediate values for all components.

The rate-reducing ability of these populations was based upon several components, all of which appeared to be associated. These associations were verified by Kendall's tau-b analysis and by principal component analysis which indicated that all variables were equally useful in assessing rate-reducing resistance in the faba bean populations. These results agree with those of Parlevliet (1979) who observed that the components of resistance were associated and that they varied in association. This indicates an underlying genetic complexity that might confer durability (Nelson, 1984).

MANUSCRIPT II

Studies in controlled environments to identify the components of rate-reducing resistance in faba beans (*Vicia faba* L.) to rust (*Uromyces viciae-fabae*) and comparison with field evaluations.

ABSTRACT

Five faba bean mass-selected (MS) populations, four bulk (BK) populations, and the rust-susceptible population 2N40 were evaluated in growth cabinet studies for reaction to Uromyces viciae-fabae. The plants were inoculated at three developmental stages with either rust race 3 or 4. Significant differences among the populations were observed for fleck number (FKN), uredinia number (UDN), infection type (IT), range of infection types (ITR), latent period (LP and LP_{50}), and for LPSM, a standardized disease index combining latent period and pustule density data. On the basis of these components, the populations could be separated into those that were derived by mass-selection, or from bulk populations. The mass-selected populations 2N122, 2N43, 2N29, and ILB(332x133)B were the best slow-rusters. The MS population 2N319 and the BK population 2N430 were intermediate, and the BK populations 2N3, 2N34, and 2N52, were low in their rate-reducing abilities.

The resistance components were not equally effective in differentiating among the faba bean populations for levels of rate-reducing resistance. UDN was the most efficient followed by the components LP, LP_{50}, and the disease index, LPSM. The components FKN and IT were ineffective. The components of rust development were related to each other as indicated by significant Kendall tau-b coefficients of concordance, and as well, they tended to vary in association. The strongest associations were observed between LP_{50} and LPSM, and also between the latent period

measures and UDN. The developmental stage of the plants at the time of inoculation influenced all of the components, significantly. In general there was an increase in rust resistance with increasing plant age, attesting to the necessity of using plants at the same development stage when screening for rate-reducing resistance. Comparisons between components evaluated in the field (Manuscript I), and those evaluated in growth cabinets indicated that estimation of uredinia number in growth cabinets best corresponded with field performance and could be of use for identifying faba beans with urediniospores of rate-reducing resistance to Uromyces viciae-fabae.

INTRODUCTION

Disease resistance in plants has been categorized as either race-specific or generalized (Clifford and Clothier, 1974; Simmonds, 1983; and Pataky, 1986). Race-specific resistance which is based upon host hypersensitivity, is characterized by little or no sporulation and is qualitative in expression (Nelson, 1977). It is frequently dominant, and monogenic or oligogenic in inheritance (Van der Plank, 1963; and Ellingboe, 1975). Generalized resistance, also referred to as partial, rate-reducing, or slow-rusting (Parlevliet, 1976; Nelson, 1978; and Skovmand et al., 1978), is quantitative in expression and is typically polygenically inherited (Parlevliet, 1979). It is considered to be more durable than resistance of the race-specific type, which can often be transitory (Clifford, 1972; Parlevliet and Van Ommeren, 1975).

Slow-rusting resistance to Uromyces viciae-fabae has recently been demonstrated in open-pollinated faba bean accessions (Conner and Bernier, 1982d; Rashid and Bernier, 1986). In small adjacent plots, they identified 11 selections which had low area under the disease progress curve (AUDPC) scores, as well as 10 others which had AUDPC scores that varied from low to intermediate during three to four years of testing. Shaner and Finney (1980) and Wilcoxson et al., (1975) have shown that AUDPC is a more sensitive and reliable criterion for evaluating rate-reducing types of resistances than apparent infection rate or final disease severity. Others have reported that AUDPC is correlated

with such components of resistance as infection frequency (Singleton et al., 1982; and Dreiseitl and Hlavac, 1984) and latent period (Johnson and Wilcoxson, 1979; Shaner and Finney, 1980; and Johnson, 1986). The good correlations between AUDPC and the components of resistance suggest the possibility of screening for more durable forms of resistance in greenhouse or growth cabinet facilities. This would be potentially valuable in breeding programs.

The objectives of the investigation reported here were to: (1) evaluate the components of rate-reducing resistance in controlled environment facilities for each of ten faba bean populations inoculated at three developmental stages with either race 3 or 4 of Uromyces viciae-fabae; (2) determine the relationships among the resistance components using Kendall's tau-b coefficients of concordance; and (3) determine the relationships between resistance components measured in the field and in controlled environment facilities in order to compare these environments for the evaluation and screening of faba beans for rate-reducing resistance.

MATERIALS AND METHODS

In addition to the eight faba bean populations utilized in the field experiments (Materials and Methods, Thesis section 1), the mass-selected population ILB(332x133)B (abbreviated as ILB-B), and the bulk population 2N3, were evaluated for the components of rate-reducing resistance in controlled environment facilities at the Winnipeg Research Station, Agriculture Canada. Based upon three to four years of preliminary field screening, population ILB-B had been designated as slow-rusting (Rashid and Bernier, 1985) and population 2N3 as fast-rusting (Conner and Bernier, 1982d).

11.1 EXPERIMENTAL DESIGN AND METHOD OF INOCULATION

Four seeds of each of the 10 populations were planted in 15 cm clay pots filled with a 2:1:1 (v/v) mixture of soil, sand, and peat moss. Populations were fertilized with 16-20-0 at the time of planting and 20-20-20 after germination. They were arranged in a randomized complete block design with four replications, and incubated in a growth chamber with alternating day/night temperatures of 20° C and 15° C, respectively, and a photoperiod of 18 hr.

One week following germination, populations were thinned leaving one seedling per pot, and at 20 days after germination, these were trimmed so that paired leaflets at nodes five and six were uppermost. The seedlings were sprayed, to the point of dripping, with water containing

a few drops of Tween 20 (Polyoxyethylene sorbitan monolaurate) prior to inoculation in a settling tower where they were exposed to a 10 minute shower of urediniospores (10 mg/replicate) of either race 3 or 4 of U. viciae-fabae. One replicate was inoculated at a time (during each inoculation, four Petri plates of water agar were placed at leaf height within the settling tower, to monitor the uniformity of inoculum deposition). All plants were removed to a dew chamber for 24 hr, after which they were returned to the growth chamber for further incubation.

Urediniospores for the inoculations were increased under greenhouse conditions on two week-old seedlings of the rust susceptible population 2N40. Spores were collected with a cyclone spore collector (Browder, 1971) and stored at 5^0 C for one to two months prior to use (Appendix A). A germination test on water agar was performed on all spore samples before use.

Experiments were repeated two to three times for plants inoculated with either race 3 or 4 of U. viciae-fabae, at each of three developmental stages (2.9, 4.5, or 5.3). These stages refer to plants at 20, 35, and 45 days after germination, respectively, and are based upon a developmental key for beans developed in Britain by the Ministry of Agriculture (Anon, 1976), and subsequently modified by Liew and Gaunt (1982). As there did not appear to be large differences in maturity among the faba bean populations, no attempt was made to stagger the dates of inoculation. other than for developmental stage.

11.2 CHARACTERIZATION OF THE COMPONENTS OF RATE-REDUCING RESISTANCE

One week after inoculation and subsequently on alternate days until either leaf senescence or until the appearance of secondary infections, the number of flecks and uredinia were counted for the entire leaflet if less than 20, or if greater than 20, then the number in three 1 cm^2 areas were computed per leaflet. Mean leaflet area was estimated for each faba bean population at each developmental stage, using plants grown under conditions similar to those described above, with a LI-COR model 3000 area meter (Lambda Instrument Corporation, Lincoln, NE). These values were used to calculate the numbers of flecks and uredinia per square centimeter of leaflet area.

Infection type and range of infection types based upon pustule size (Table 2, Manuscript I) were determined for each plant. Infection type is a measure of the predominant rust reaction whereas range represents the extent of the variability in infection type per leaflet. In addition, latent period, estimated as either the period of time after inoculation when sporulation was observed on at least one uredium per leaflet (LP), or as the time at which 50 % of the erupted uredinia sporulated (LP_{50}), and LPSM, a standardized disease severity measure, combining LP_{50} and pustule density data, were calculated on an individual plant basis and are described in detail elsewhere (Materials and Methods, Manuscript 1).

Transformation of the data, one-way analysis of variance, and mean separation for each of the above resistance components were conducted as outlined previously (Materials and Methods, Manuscript 1). Kendall's tau-b coefficients of concordance were computed to identify possible inter-relationships among the components.

RESULTS AND DISCUSSION

12.1 CHARACTERIZATION OF THE COMPONENTS OF RATE-REDUCING RESISTANCE

12.1.1 Number of flecks per square centimeter of leaflet area (FKN)

When the data were combined over developmental stages and rust races, no significant differences for the number of flecks per square centimeter of leaflet area (FKN) were observed among populations grown under controlled environment conditions (Table 22). Values for FKN ranged from a high of 2.38 for the rust-susceptible population 2N3 to 1.11 for the mass- selected population 2N29.

Plants inoculated at the earliest developmental stage (2.9) were the most resistant to rust in terms of mean FKN (1.36), while those at the intermediate growth stage (4.5) were the most susceptible (2.02). These differences were significant, indicating that plants under controlled conditions should be compared only if they are at the same stage of development. Also, the race x stage and population x stage interactions were significant underlining further the necessity of using plants of the same age. Parlevliet (1975), Osman-Ghani and Manners (1985), and Johnson (1986) have all demonstrated that plant-growth stage has a significant effect on the components of rate-reducing resistance.

Comparisons between the rust races were significant. Populations inoculated with urediniospores of race 3 had larger mean values for FKN (2.93) than those inoculated with urediniospores of race 4 (0.58).

When the data were analyzed as race- developmental stage combinations, no significant differences were observed at any of the three developmental stages among populations inoculated with urediniospores of race 3 (Table 23). Mean FKN values for the bulk populations were higher than for the mass-selected populations when the faba beans were inoculated at developmental stages 2.9 and 5.3; this did not hold true for those inoculated at stage 4.5, however.

When the populations were inoculated with urediniospores of race 4, significant differences were observed unlike with urediniospores of race 3. At developmental stage 2.9, the mass-selected population 2N319 which had the highest mean value for FKN (1.86) was significantly different from the mass-selected populations 2N43 and ILB-B, with mean FKN values of 0.27 and 0.12, respectively, and from the bulk population 2N52 with a mean value for FKN of 0.22. At developmental stage 4.5, no significant differences among populations could be discerned. However, at stage 5.3, the bulk population 2N52, with the largest mean value for FKN (1.57) was significantly different from the mass-selected populations 2N43, 2N122, and ILB-B, with values of 0.01, 0.05, and 0.01, respectively.

The population x race interaction was not significant (Appendix AD), whereas the population x developmental stage interaction was significant indicating that the rust reaction of the populations was not consistent with respect to developmental stage. The coefficient of variation for this component was high (116.00 %).

TABLE 22. Effect of host population, developmental stage, and rust race on the number of flecks and uredinia per square centimeter of leaflet area of ten faba bean populations grown under controlled environment conditions.

		Flecks	Uredinia
Population[1]	2N40 (BK)	1.97 a[4]	18.37 a
	2N3 (BK)	2.38 a	13.68 b
	2N34 (BK)	1.82 a	12.80 ab
	2N430 (BK)	1.69 a	10.46 b
	2N52 (BK)	1.86 a	10.92 b
	2N319 (MS)	2.00 a	4.70 c
	2N29 (MS)	1.11 a	1.86 cd
	2N43 (MS)	1.58 a	1.50 d
	2N122 (MS)	1.91 a	1.64 d
	ILB-B (MS)	1.35 a	0.54 d
Developmental Stage[2]	2.9	1.36 a	8.72 a
	4.5	2.02 b	8.30 a
	5.3	1.93 ab	5.77 b
Race[3]	3	2.93 a	9.36 a
	4	0.58 b	5.84 b
Mean square error		7.98	83.17

[1]Data are means for 1152 observations combined over developmental stages, and races.
[2]Data are means for 3840 observations combined over populations and races. The three stages of development: 2.9, 4.5, and 5.3, refer to plants 20, 35, and 45 days from germination, respectively, and are based on Liew and Gaunt's (1982) developmental key for beans.
[3]Data are means for 5760 observations combined over populations and developmental stages.
[4]Comparisons among means were made using square root transformed data. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

TABLE 23. Number of flecks per square centimeter of leaflet area of ten faba bean populations, inoculated with two rust races at three developmental stages.

Inoculation with race 3

		Developmental Stage[1]		
		2.9	4.5	5.3
Population	2N40 (BK)	4.50 a[2]	1.27 a	2.73 a
	2N3 (BK)	3.62 a	3.82 a	4.69 a
	2N34 (BK)	2.93 a	1.18 a	5.21 a
	2N430 (BK)	2.91 a	1.94 a	4.04 a
	2N52 (BK)	2.67 a	4.07 a	2.06 a
	2N319 (MS)	0.96 a	2.18 a	4.95 a
	2N29 (MS)	0.24 a	4.57 a	1.15 a
	2N43 (MS)	0.45 a	3.30 a	5.24 a
	2N122 (MS)	1.64 a	5.49 a	1.73 a
	ILB-B (MS)	0.15 a	5.94 a	1.74 a
Mean square error		10.80	15.32	17.39

Inoculation with race 4

		Developmental Stage		
		2.9	4.5	5.3
Population	2N40 (BK)	1.17 ab[2]	1.20 a	0.65 ab
	2N3 (BK)	0.69 ab	0.54 a	0.93 ab
	2N34 (BK)	0.41 ab	0.43 a	0.74 ab
	2N430 (BK)	0.51 ab	0.48 a	0.38 ab
	2N52 (BK)	0.22 b	0.35 a	1.57 a
	2N319 (MS)	1.86 a	1.73 a	0.28 ab
	2N29 (MS)	0.37 ab	0.26 a	0.09 ab
	2N43 (MS)	0.27 b	0.19 a	0.01 b
	2N122 (MS)	1.60 ab	0.01 a	0.05 b
	ILB-B (MS)	0.12 b	0.10 a	0.01 b
Mean square error		1.25	1.79	1.22

[1]The three stages of development: 2.9, 4.5, and 5.3, refer to plants 20, 35, and 45 days from germination, respectively, and are based on Liew and Gaunt's (1982) developmental key for beans.
[2]Data are means for 192 observations.
Comparisons among means were made using square root transformed data. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

12.1.2 Number of uredinia per square centimeter of leaflet area (UDN)

Unlike FKN, analysis of the overall data for the number of uredinia per square centimeter of leaflet area (UDN) resulted in significant differences among the populations (Table 22). This component has previously been shown to be useful in the assessment of rate-reducing types of resistance (Mortensen and Green, 1978; Asher and Thomas, 1984; and Johnson, 1986). The rust-susceptible population 2N40, with a mean value for UDN of 18.37, was significantly different from all other populations, except the bulk population 2N34. Additionally, the bulk populations were significantly different from the mass-selected populations. The mass-selected population ILB-B had the smallest mean value for UDN (0.54), but it was statistically indistinguishable from three other mass-selected populations: 2N29, 2N43, and 2N122, with values of 1.86, 1.50, and 1.64, respectively.

As with FKN, comparisons among developmental stages were significant. However, no significant differences were observed for UDN among populations inoculated at either developmental stage 2.9 or 4.5. Populations inoculated at developmental stage 5.3 had a significantly smaller mean value for UDN (5.77) than those inoculated at either stage 2.9 or 4.5, however. In fact, there was a trend towards increasing resistance, as indicated by fewer uredinia per square centimeter of leaflet area, as faba bean plants matured. Headrick and Pataky (1987) have reported a similar pattern in the partial resistance of sweet corn to common rust. Johnson (1986) observed that in the partial resistance of asparagus to P. asparagi, the third shoot (youngest) had significantly more uredinia per square centimeter than the second and first shoots.

Comparisons between races for mean values of UDN were significant. Plants inoculated with urediniospores of race 3 had a larger mean value for UDN (9.36) than those inoculated with urediniospores of race 4 (5.84).

As with the overall data, more significant differences were observed with this component than with FKN when the data were analyzed as race-developmental stage combinations (Table 24). When plants at developmental stage 2.9 were inoculated with urediniospores of race 3, the rust- susceptible populations 2N40 and 2N3 were found to differ significantly from the mass-selected populations, although not from the other bulk populations. At developmental stage 4.5, differences between the bulk and mass-selected populations were more distinct than at stage 2.9. However, the mass-selected population 2N319 could not be distinguished from three of the bulk populations. In the inoculation with urediniospores of race 3, the mass-selected population ILB-B had the lowest value for UDN at all developmental stages whereas the rust-susceptible populations had the highest values for this component.

When plants were inoculated with urediniospores of race 4, more significant differences were apparent than in the inoculation with urediniospores of race 3. At developmental stage 2.9, differences between the bulk and mass-selected populations were distinct, with the exception of the populations 2N52 and 2N319. This was also the situation at stage 4.5. At developmental stage 5.3, population 2N52 had the highest mean value for UDN, and although it could not be distinguished from the bulk populations, it was significantly different from the mass-selected populations. Population 2N319, a mass-selected population, could only be distinguished from the bulk populations 2N34 and 2N52.

TABLE 24. Number of uredinia per square centimeter of leaflet area of ten faba bean populations, inoculated with two rust races at three developmental stages.

Inoculation with race 3

		Developmental Stage[1]		
		2.9	4.5	5.3
Population	2N40 (BK)	3.79 a[2]	17.89 a	27.81 a
	2N3 (BK)	3.84 a	14.63 ab	10.18 bc
	2N34 (BK)	2.74 ab	14.88 ab	12.91 ab
	2N430 (BK)	1.95 abc	19.32 ab	11.05 bc
	2N52 (BK)	2.17 abc	23.15 a	6.78 abc
	2N319 (MS)	1.00 bc	9.62 bc	5.68 bc
	2N29 (MS)	0.41 c	5.50 cd	1.66 c
	2N43 (MS)	0.99 bc	1.68 d	1.09 c
	2N122 (MS)	0.76 bc	2.24 d	1.02 c
	ILB-B (MS)	0.36 c	1.34 d	0.17 c
Mean square error		185.39	37.86	119.17

Inoculation with race 4

		Developmental Stage		
		2.9	4.5	5.3
Population	2N40 (BK)	21.88 a[2]	11.87 ab	3.41 abcd
	2N3 (BK)	18.37 ab	5.82 abc	6.85 ab
	2N34 (BK)	10.46 bc	18.76 a	6.64 a
	2N430 (BK)	17.22 ab	2.14 c	3.88 abc
	2N52 (BK)	4.63 cd	4.63 bc	12.30 a
	2N319 (MS)	3.13 cd	4.76 bc	2.38 bc
	2N29 (MS)	1.31 d	1.04 c	1.08 cd
	2N43 (MS)	2.12 d	1.66 c	0.02 d
	2N122 (MS)	3.24 cd	0.03 c	0.34 cd
	ILB-B (MS)	1.21 d	0.06 c	0.13 cd
Mean square error		86.86	45.12	23.02

[1]The three stages of development: 2.9, 4.5, and 5.3, refer to plants 20, 35, and 45 days from germination, respectively, and are based on Liew and Gaunt's (1982) developmental key for beans.
[2]Data are means for 192 observations.
Comparisons among means were made using square root transformed data. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

The mass-selected population ILB-B had low mean values for UDN at all three developmental stages, although population 2N122 had the lowest value at stage 4.5, and population 2N43 at stage 5.3.

The coefficient of variation for this component was 70.72 % (Appendix AE), considerably less than for FKN (116.00 %). The population x race interaction was significant for UDN as was the race x developmental stage interaction. Plants inoculated with urediniospores of race 3 had signficantly greater numbers of uredinia than did those inoculated with urediniospores of race 4 for the overall data, and also for developmental stages 4.5 and 5.3. At stage 2.9, however, race 4 had the higher number of uredinia.

12.1.3 Infection type (IT)

When the data were combined over developmental stages and rust races, the mass-selected population ILB-B had the largest infection type with a value for this component of 2.53 (Table 25). However, it was statistically distinguishable only from the bulk population 2N3 and the mass-selected population 2N122, both with values for IT of 2.02, the smallest observed for this component. In addition to these differences, the comparison between the mass-selected population 2N29, with a mean value for IT of 2.48, and the bulk population 2N3, was also significant.

Populations inoculated at developmental stage 2.9 had significantly larger infection types (2.44) than did populations inoculated at either stage 4.5 (2.20) or stage 5.3 (2.13). Populations inoculated at the

latter two stages were indistinguishable. Ohm and Shaner (1976) showed that plant growth stage had a significant effect on pustule size in wheat infected with P. recondita. Seedlings were found to be more susceptible on the basis of pustule size than wheat in the boot stage of growth. Additionally, differences between the rust races were significant; populations inoculated with urediniospores of race 3 had a larger mean infection type (2.37) than those inoculated with urediniospores of race 4 (2.14).

When the data were analyzed as race-developmental stage combinations (Table 26), populations inoculated at stage 2.9 had mean infection types that ranged in size from 1.62 for population 2N122 to 3.12 for population 2N29. The comparison between 2N122 and 2N29 was the only significant one in this race-developmental stage combination.

When plants were inoculated at developmental stage 4.5, the smallest mean values for IT were observed for the mass-selected populations 2N122 (1.81) and 2N319 (1.84). The bulk population 2N52 had the largest mean infection type (3.75). Only the comparisons between population 2N52 and 2N122, or 2N319 were statistically significant.

When the populations were inoculated at stage 5.3, the bulk populations 2N3 and 2N34 had the smallest IT values (1.78 and 1.72, respectively), and the mass-selected population ILB-B, the largest (3.19). Only the comparisons between population ILB-B and 2N3, or 2N34 were statistically significant in this race-developmental stage combination.

No significant differences were observed among the populations inoculated with urediniospores of race 4 at any of the three developmental stages. The C.V. for IT was 29.91 % (Appendix AF), and all interactions were significant except for the interaction between population and race.

TABLE 25. Effect of host population, developmental stage, and rust race on infection type and range of infection types of ten faba bean populations grown under controlled environment conditions.

		Infection type	Range of infection type
Population[1]	2N40 (BK)	2.49 a[4]	3.71 abc
	2N3 (BK)	2.02 c	2.79 d
	2N34 (BK)	2.18 abc	3.51 abcd
	2N430 (BK)	2.16 abc	3.06 bcd
	2N52 (BK)	2.30 abc	4.09 a
	2N319 (MS)	2.14 abc	2.90 cd
	2N29 (MS)	2.48 ab	3.87 ab
	2N43 (MS)	2.31 abc	3.00 cd
	2N122 (MS)	2.02 bc	3.02 bcd
	ILB-B (MS)	2.53 a	3.61 abcd
Developmental Stage[2]	2.9	2.44 a	3.77 a
	4.5	2.20 b	2.84 b
	5.3	2.13 b	3.13 b
Race[3]	3	2.37 a	2.78 b
	4	2.14 b	4.04 a
Mean square error		0.46	4.73

[1]Data are means for 768 observations combined over developmental stages, and races.
[2]Data are means for 2560 observations combined over populations and races. The three stages of development: 2.9, 4.5, and 5.3, refer to plants 20, 35, and 45 days from germination, respectively, and are based on Liew and Gaunt's (1982) developmental key for beans.
[3]Data are means for 3840 observations combined over populations and developmental stages.
[4]Comparisons among means were made using square root transformed data. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

TABLE 26. Infection type of ten faba bean populations inoculated with two rust races at three developmental stages.

Inoculation with race 3

		Developmental Stage[1]		
		2.9	4.5	5.3
Population	2N40 (BK)	2.19 ab[2]	2.97 ab	2.75 ab
	2N3 (BK)	2.22 ab	2.03 ab	1.78 b
	2N34 (BK)	2.47 ab	2.66 ab	1.72 b
	2N430 (BK)	2.25 ab	2.41 ab	1.88 ab
	2N52 (BK)	2.66 ab	3.75 a	1.75 abc
	2N319 (MS)	2.84 ab	1.84 b	2.19 ab
	2N29 (MS)	3.12 a	2.12 ab	2.88 ab
	2N43 (MS)	2.38 ab	2.12 ab	2.66 ab
	2N122 (MS)	1.62 b	1.81 b	2.72 ab
	ILB-B (MS)	2.09 ab	2.58 ab	3.19 a
Mean square error		0.60	0.75	0.67

Inoculation with race 4

		Developmental Stage		
		2.9	4.5	5.3
Population	2N40 (BK)	2.56 a[2]	2.25 a	2.00 a
	2N3 (BK)	2.25 a	1.88 a	2.00 a
	2N34 (BK)	2.19 a	2.00 a	2.00 a
	2N430 (BK)	2.50 a	2.00 a	1.94 a
	2N52 (BK)	2.62 a	1.67 a	1.75 a
	2N319 (MS)	2.31 a	1.69 a	1.94 a
	2N29 (MS)	2.38 a	1.64 a	2.50 a
	2N43 (MS)	2.88 a	1.92 a	1.81 a
	2N122 (MS)	2.38 a	1.67 a	1.75 a
	ILB-B (MS)	2.75 a	2.14 a	2.36 a
Mean square error		0.29	0.20	0.21

[1]The three stages of development:2.9, 4.5, and 5.3, refer to plants 20, 35, and 45 days from germination, respectively, and are based on Liew and Gaunt's (1982) developmental key for beans.
[1]Data are means for 128 observations.
Comparisons among means were made using square root transformed data. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

The results from this study indicate that infection type was not useful in distinguishing among the faba bean populations. The mass-selected and bulk populations had nearly equivalent values for mean IT. The mass-selected population ILB-B had the largest IT, but was the best slow-ruster when evaluated on the basis of the other components. On the other hand, the mass-selected population 2N122 had the smallest infection type (along with the bulk population 2N3), and was the best slow-ruster overall. These results, along with the reported monogenic inheritance of this component (Rashid and Bernier, 1986) suggests that selection on the basis of this component may not be indicative of rate-reducing resistance in faba bean populations. There are other reports of the inappropriateness of IT as a measure of rate-reducing resistance. Jeger et al., (1983) found that this component was inadequate to distinguish varying resistance levels of two wheat cultivars to the glume blotch pathogen. Habgood (1977) observed that lesion size was similar for all barley cultivars tested for resistance to leaf blotch. In contrast, Martin et al. (1979) reported that size of uredinia, in addition to differences in receptivity, were the characters that most clearly separated slow-rusting wheats from fast-rusters in their reaction to P. graminis f. sp. tritici. Similarly, Villareal et al., (1981) found that lesion size was an important component contributing to a reduced r-value in the slow-blasting resistance of five rice cultivars.

12.1.4 Range of infection types (ITR)

When the data were combined over developmental stages and rust races (Table 25), the bulk population 2N52 had the largest value for ITR (4.09). It differed significantly from the bulk populations 2N3 and 2N430, and from the mass-selected populations 2N319, 2N29, and 2N43. The bulk population 2N3, with the smallest value for ITR (2.79), was indistinguishable from the bulk populations 2N34 and 2N430, with values of 3.51 and 3.06, respectively, and from the mass-selected populations 2N319, 2N43, 2N122, and ILB-B, with values of 2.90, 3.00, 3.02, and 3.61, respectively.

Populations inoculated at developmental stage 2.9 had significantly greater values for ITR (3.77) than populations inoculated at developmental stages 4.5 (2.84) and 5.3 (3.13). Populations inoculated at the latter two stages were indistinguishable.

Differences between the rust races were significant; populations inoculated with urediniospores of race 4 had a significantly greater range of infection types (4.04) than did populations inoculated with urediniospores of race 3 (2.78).

In the inoculation with urediniospores of race 3, at developmental stage 2.9 (Table 27), the mass-selected population 2N122, with the smallest value of of ITR, differed significantly from the other populations. No other comparisons among the populations were significant. Values for ITR ranged from 1.52 for population 2N122 to 4.10 for population 2N29. When the plants were inoculated at developmental stage 4.5, the bulk population 2N52 had the largest value for ITR (5.62), although it was statistically indistinguishable from the rust-susceptible popula-

tion 2N40, the bulk population 2N34, and the mass-selected population ILB-B. The mass-selected population 2N319 had the smallest mean ITR value (1.76), but was significantly different from only the rust-susceptible population 2N40 and the bulk population 2N52.

At developmental stage 5.3, the mass-selected population ILB-B had the largest value for ITR (4.35) and it differed significantly from the bulk populations 2N3 and 2N430 with values for this component of 2.04 and 2.05, respectively, as well as from the mass-selected population 2N319, with a value of 2.09. No other comparisons among the populations were significant.

When populations at developmental stage 2.9 were inoculated with urediniospores of race 3, the bulk population 2N52 had the largest mean ITR value (5.52). It differed significantly from the rust-susceptible population 2N3, with a value for ITR of 3.66. No other comparisons among the populations were significant. At developmental stage 4.5, no significant differences were observed among the populations. Values for ITR ranged from 2.37 for the mass-selected population ILB-B to 3.66 for the rust-susceptible population 2N40. At developmental stage 5.3, the bulk population 2N52 and the mass-selected population 2N29 had the largest values for this component (4.42 and 4.75, respectively). These populations differed significantly from the mass-selected populations 2N319 and 2N43, with values for ITR of 2.57 and 1.86, respectively. No other comparisons among the populations were significant for this race-developmental stage combination.

Range of infection types has not been used extensively as a method of characterizing rate-reducing types of resistance. However, the results

TABLE 27. Range of infection type of ten faba bean populations inoculated with two rust races at three developmental stages.

Inoculation with race 3

		Developmental Stage[1]		
		2.9	4.5	5.3
Population	2N40 (BK)	2.28 a[2]	4.02 ab	3.50 ab
	2N3 (BK)	2.43 a	2.27 bc	2.04 b
	2N34 (BK)	3.20 a	3.19 abc	3.37 ab
	2N430 (BK)	2.19 a	2.64 bc	2.05 b
	2N52 (BK)	3.15 a	5.62 a	1.59 ab
	2N319 (MS)	3.03 a	1.76 c	2.09 b
	2N29 (MS)	4.10 a	2.67 bc	3.44 ab
	2N43 (MS)	2.77 a	2.07 bc	3.33 ab
	2N122 (MS)	1.52 b	1.85 bc	3.33 ab
	ILB-B (MS)	2.07 a	2.69 abc	4.35 a
Mean square error		5.59	5.17	5.50

Inoculation with race 4

		Developmental Stage		
		2.9	4.5	5.3
Population	2N40 (BK)	4.94 ab[2]	3.66 a	3.93 ab
	2N3 (BK)	3.66 b	2.83 a	3.67 ab
	2N34 (BK)	5.28 ab	2.87 a	3.40 ab
	2N430 (BK)	5.09 ab	2.74 a	3.55 ab
	2N52 (BK)	5.52 a	2.79 a	4.42 a
	2N319 (MS)	4.48 ab	3.00 a	2.57 b
	2N29 (MS)	4.59 ab	3.24 a	4.75 a
	2N43 (MS)	4.23 ab	3.45 a	1.86 b
	2N122 (MS)	5.00 ab	2.40 a	2.82 ab
	ILB-B (MS)	5.23 ab	2.37 a	3.67 ab
Mean square error		4.26	3.50	3.36

[1]The three stages of development: 2.9, 4.5, and 5.3, refer to plants 20, 35, and 45 days from germination, respectively, and are based on Liew and Gaunt's (1982) developmental key for beans.
[2]Data are means for 128 observations.
Comparisons among means were made using square root transformed data. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

from this study indicate that more differences were discernable with ITR than with IT. This was true not only for the pooled data, but also for most of the race-developmental stage combinations. Differences in ITR due to the developmental stage of the populations at the time of inoculation were as observed for IT. However, the populations differed in their reactions to the two races in this study in terms of IT and ITR. While race 3 produced a significantly larger mean infection type than did race 4, the latter race resulted in a significantly greater range of infection types than did race 3. This observed race-specificity is in agreement with the culture-specificity described by Milus and Line (1980) for both ITR and IT. The C.V. for ITR was 65.16 % (Appendix AG), and as with IT, all interactions, except for the population X race interaction, were significant.

12.1.5 Latent period (LP)

When the data were combined over developmental stages and rust races, significant differences for latent period (LP) were observed among the populations (Table 28). Differences between the bulk and mass-selected populations, with the exception of population 2N319, were pronounced. The rust-susceptible population 2N40 had the shortest mean LP (10.01 days), but it could not be statistically distinguished from the bulk populations 2N34 and 2N52, with mean values for LP of 10.92 and 11.27 days, respectively. The mass-selected population 2N319 could not be statistically distinguished from the bulk populations 2N3 and 2N40, although it was significantly different from the other mass-selected

populations, with the exception of 2N43. These results are in agreement with Ohm and Shaner (1976) who demonstrated that slow-rusting winter wheats have latent periods that are considerably longer than their fast-rusting counterparts. Similarly, Wahl et al., (1980) and Statler and Parlevliet (1987) have also observed differences in latent period between slow and fast-rusting populations. Consequently, latent period has been used frequently and with a good deal of reliability in the assessment of rate-reducing resistance (Parlevliet and Van Ommeren, 1975; Parlevliet, 1979; Asher and Thomas, 1984; and Lancashire and Jones, 1985).

Plants inoculated at the three developmental stages were found to differ significantly from each other in terms of this component. Those inoculated at stage 2.9 had the shortest mean LP (10.08 days) whereas plants inoculated at stage 5.3 had the longest (18.69 days). Parlevliet (1977;1979), Jones (1978), and Johnson (1986) have all reported that latent period is greatly influenced by the growth stage of the plants. Consequently, they have stressed the importance of measuring latent period on plants at the same stage of development.

Comparisons between races for mean LP values were significant. Plants inoculated with urediniospores of race 4 had a longer mean LP (15.05 days) than those inoculated with urediniospores of race 3 (12.81 days). Furthermore, the population x race interaction was significant (Appendix AH). Parlevliet (1977) has reported that there was a significant interaction between cultivars and isolates for the latent period of barley, although in most cases, the interaction was small.

When the data were analyzed as race-developmental stage combinations, differences among the populations in terms of this component were less apparent than with the overall data (Table 29). In the inoculation with urediniospores of race 3, at developmental stage 2.9, the mass-selected population 2N29 had the smallest mean value for this component (7.91 days), and was indistinguishable statistically from the mass-selected populations 2N43 and 2N122 with mean LP values of 9.66 and 11.69 days, respectively. The bulk population 2N3 had the longest mean LP at this developmental stage, but was not significantly different from the rust-susceptible population 2N40; from the bulk populations 2N34, 2N430, and 2N52; nor from the mass-selected populations 2N319 and ILB-B. At developmental stage 4.5, the rust-susceptible population 2N40 had the shortest mean LP (7.00 days) and was statistically indistinguishable from the other bulk populations and from the mass-selected population 2N319. The mass-selected population ILB-B had the largest mean value for this component (14.56 days), and was significantly different from the other mass-selected populations. At developmental stage 5.3, as at stage 2.9, the mass-selected population ILB-B had the longest mean LP (23.31 days), and differed significantly from the other populations with the exception of population 2N29 (20.86 days). The bulk population 2N52 had the shortest mean LP (9.03 days), and was significantly different from the other populations, with the exception of the rust- susceptible population 2N40 (9.66 days).

In the inoculation with urediniospores of race 4, fewer significant differences were observed among the populations than in the inoculation with urediniospores of race 3. At developmental stage 2.9, no significant differences were observed among the populations for LP. Values for

TABLE 28. Effect of host population, developmental stage, and rust race on the latent period of ten faba bean populations grown under controlled environment conditions.

		LP	LP_{50}
Population[1]	2N40 (BK)	10.01 a[4]	15.47 abc
	2N3 (BK)	12.67 bc	16.59 bc
	2N34 (BK)	10.92 ab	13.65 a
	2N430 (BK)	13.37 c	15.19 ab
	2N52 (BK)	11.27 ab	14.00 a
	2N319 (MS)	14.07 cd	17.78 cd
	2N29 (MS)	16.80 e	20.72 e
	2N43 (MS)	15.33 de	19.32 de
	2N122 (MS)	15.96 e	19.39 de
	ILB-B (MS)	19.11 f	20.72 e
Developmental Stage[2]	2.9	10.08 a	14.98 a
	4.5	13.09 b	16.17 b
	5.3	18.69 c	19.88 c
Race[3]	3	12.81 a	16.10 a
	4	15.05 b	17.99 b
Mean square error		0.47	0.67

[1]Data are means for 288 observations combined over developmental stages and races.
[2]Data are means for 960 observations combined over populations and races. The three stages of development: 2.9, 4.5, and 5.3, refer to plants 20, 35, and 45 days from planting, respectively, and are based on Liew and Gaunt's (1982) developmental key for beans.
[3]Data are means for 1440 observations combined over populations and developmental stages.
[4]Comparisons among means were made using square root transformed data. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

TABLE 29. Latent period of ten faba bean populations inoculated with two rust races at three developmental stages.

Inoculation with race 3

		Developmental Stage[1]		
		2.9	4.5	5.3
Population	2N40 (BK)	12.95 bcd[2]	7.00 a	9.66 ab
	2N3 (BK)	15.75 d	7.28 ab	13.72 cd
	2N34 (BK)	13.16 bcd	7.56 ab	13.16 bc
	2N430 (BK)	15.47 cd	8.47 abc	16.94 de
	2N52 (BK)	15.19 cd	7.00 a	9.03 a
	2N319 (MS)	13.44 bcd	7.84 ab	17.22 de
	2N29 (MS)	7.91 a	12.53 cd	20.86 fg
	2N43 (MS)	9.66 ab	11.69 bcd	16.94 de
	2N122 (MS)	11.69 abc	13.86 d	17.78 ef
	ILB-B (MS)	13.16 bcd	14.56 d	23.31 g
Mean square error		0.36	0.46	0.29

Inoculation with race 4

		Developmental Stage		
		2.9	4.5	5.3
Population	2N40 (BK)	7.00 a[2]	8.19 a	15.19 ab
	2N3 (BK)	7.56 a	15.19 bc	16.66 ab
	2N34 (BK)	7.56 a	12.81 ab	11.06 a
	2N430 (BK)	7.00 a	16.66 bcd	15.89 ab
	2N52 (BK)	7.00 a	14.00 b	15.61 ab
	2N319 (MS)	8.05 a	16.31 bc	21.42 bc
	2N29 (MS)	7.00 a	22.19 de	30.17 d
	2N43 (MS)	7.00 a	19.81 cd	27.16 cd
	2N122 (MS)	7.56 a	12.81 ab	32.20 d
	ILB-B (MS)	7.00 a	26.25 e	30.17 d
Mean square error		0.08	0.70	0.92

[1]The three stages of development: 2.9, 4.5, and 5.3, refer to plants 20, 35, and 45 days from germination, respectively, and are based on Liew and Gaunt's (1982) developmental key for beans.
[1]Data are means for 48 observations.
Comparisons among means were made using square root transformed data. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

this component ranged from 7.00 to 8.05 days. At stage 4.5, the rust-susceptible population 2N40 had the shortest mean LP (8.19 days), although it was statistically indistinguishable from the bulk population 2N34 (12.81 days), and from the mass-selected population 2N122 (12.81 days). The mass-selected population ILB-B had the longest mean LP (26.25 days), and it differed significantly from all other populations with the exception of population 2N29 (22.19 days). At developmental stage 5.3, no significant differences in mean LP were observed among the bulk populations. The mass-selected population 2N319 was found to differ significantly from only one of the bulk populations, 2N34, in addition to three of the mass-selected populations (2N29, 2N122, and ILB-B). There were no additional significant differences among the mass-selected populations.

The C.V. associated with this component was 34.37 % (Appendix AH). All interactions were significant, including the interaction between population and race, as well as the three-way interaction between population, race, and stage.

12.1.6 Latent period (LP_{50})

When the data were combined over developmental stages and rust races (Table 50), differences in LP_{50} between the bulk and mass-selected populations were pronounced, with the exception of the mass-selected population 2N319. This population (with a mean value for LP_{50} of 17.78 days) was statistically indistinguishable from the rust-susceptible populations 2N40 and 2N3 with mean LP_{50} values of 15.47 and 16.59 days,

respectively, and from the mass-selected populations 2N43 and 2N122 with mean values for this component of 19.32 and 19.39 days, respectively. The mass- selected populations 2N122 and ILB-B had the largest LP_{50} values (20.72 days), and these were significantly different from the bulk populations and from the mass-selected population 2N319.

The results for LP_{50} did not differ appreciably from those for LP, suggesting that the rate of development of subsequent uredinia paralleled that for the development of the initial uredinium. This was especially true for the mass-selected populations. The LP_{50} values, like the LP values, were smaller for the bulk populations than for the mass-selected populations.

Comparisons among plants inoculated at the three different developmental stages were significant. Plants inoculated at developmental stage 2.9 had the shortest mean LP_{50} (14.98 days), whereas those inoculated at stage 5.3 had the longest (19.88 days).

Comparisons between races for mean LP_{50} values were significant. Plants inoculated with urediniospores of race 4 had a larger mean value for this component (17.99 days) than those plants inoculated with urediniospores of race 3 (16.10 days).

When the data were analyzed as race-developmental stage combinations, differences among the populations for LP_{50} (Table 30) were less distinct than with the combined data. At developmental stage 2.9, when plants were inoculated with urediniospores of race 3, the rust-susceptible population 2N40 had the largest mean value for this component (22.47 days). It differed significantly from only two populations, the bulk populations 2N430 and 2N52 with mean values for LP_{50} of 16.31 and 16.87

days, respectively. No other comparisons among the populations in this race-developmental stage combination were significant. At developmental stage 4.5, the mass-selected population ILB-B had the largest mean value for this component (23.59 days). This population was significantly different from the bulk populations as well as from the mass-selected populations 2N319 and 2N43. The bulk population 2N430 had the smallest mean LP_{50} value (7.21), and while it was statistically indistinguishable from the bulk populations and from the mass-selected population 2N319, it differed significantly from the other mass-selected populations. At developmental stage 5.3, differences between the bulk and mass- selected populations were not distinct. The mass-selected population 2N29 had the largest value for this component (21.56 days), and the mass-selected population 2N122 the smallest (13.44 days).

When plants at developmental stage 2.9 were inoculated with urediniospores of race 4 the bulk population 2N52 had the smallest mean value for LP_{50} (7.63 days). This value was significantly smaller than the values for the bulk populations 2N3 and 2N430 (15.75 and 14.35, respectively), and for the mass-selected population 2N43 (14.77 days). No other significant differences were observed for this race-developmental stage combination. At stage 4.5, more significant differences were observed among the populations than at the earlier stage. The mass-selected population ILB-B had the largest mean value for LP_{50} (30.31 days) and it differed significantly from the other populations. At developmental stage 5.3, the bulk population 2N34 had the smallest value for this component (13.79), although it was not statistically distinguishable from the other bulk populations except 2N52 (18.62 days). The latter population which was indistinguishable from the mass-selected

TABLE 30. LP_{50} of ten faba bean populations, inoculated with two rust races at three developmental stages.

Inoculation with race 3

		Developmental Stage[1]		
		2.9	4.5	5.3
Population	2N40 (BK)	22.47 c[2]	13.16 abcd	16.80 b
	2N3 (BK)	21.56 ab	9.45 ab	14.28 a
	2N34 (BK)	19.11 ab	9.94 ab	13.93 a
	2N430 (BK)	16.31 a	7.21 a	18.62 bc
	2N52 (BK)	16.87 a	9.66 abc	15.96 abc
	2N319 (MS)	21.35 ab	11.76 abc	17.57 abc
	2N29 (MS)	17.29 ab	18.62 de	21.56 c
	2N43 (MS)	22.12 ab	15.33 bcd	14.56 a
	2N122 (MS)	17.50 ab	17.36 cde	13.44 a
	ILB-B (MS)	15.75 ab	23.59 e	20.37 bc
Mean square error		0.54	0.71	0.35

Inoculation with race 4

		Developmental Stage		
		2.9	4.5	5.3
Population	2N40 (BK)	10.99 ab[2]	14.28 a	16.94 a
	2N3 (BK)	15.75 b	20.58 bcd	17.92 a
	2N34 (BK)	13.30 ab	14.00 a	13.79 a
	2N430 (BK)	14.35 b	19.11 abcd	16.59 a
	2N52 (BK)	7.63 a	15.12 ab	18.62 b
	2N319 (MS)	14.00 ab	17.78 abc	24.92 bc
	2N29 (MS)	9.45 ab	23.24 d	28.00 c
	2N43 (MS)	14.77 b	22.12 cd	28.84 c
	2N122 (MS)	13.72 ab	21.42 bcd	30.03 c
	ILB-B (MS)	9.80 ab	30.31 e	26.67 c
Mean square error		0.93	0.47	0.87

[1]The three stages of development: 2.9, 4.5, and 5.3 refer to plants 20, 35, and 45 days from germination, respectively, and are based on Liew and Gaunt's (1982) developmental key for beans.
[2]Data are means for 48 observations.
Comparisons among means were made using square root transformed data. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

population 2N319 (24.92 days) was significantly different from all other populations. The mass-selected population 2N122 had the largest mean LP_{50} value (30.03 days), but it was indistinguishable from the other mass-selected populations.

In the race-developmental stage subsets of the data, larger LP_{50} values were observed with increasing maturity of populations inoculated with urediniospores of race 4. This trend was not exhibited by plants inoculated with urediniospores of race 3, possibly due to the unusually high LP_{50}'s of the bulk populations inoculated at developmental stage 2.9, especially the rust- susceptible populations 2N40 and 2N3. Conversely, the mass-selected population ILB-B, which was generally one of the most resistant populations in terms of latent period at developmental stages 4.5 and 5.3, was very susceptible when inoculated at the seedling stage. These fluctuations accounted for the positive stage x population and stage x race interactions (Appendix AI). The C.V. for LP_{50} was 33.39 % which was similar to the C.V. for LP (34.37 %).

12.1.7 LPSM

When the data were combined over developmental stages and rust races, significant differences for LPSM were observed among the populations (Table 31). The bulk population 2N34 had the smallest mean LPSM value (1.98). It differed significantly from the mass-selected populations, but was indistinguishable from the other bulk populations. Differences among the remaining bulk populations with LPSM values ranging from 2.00 for population 2N52 to 2.34 for the rust-susceptible population 2N3 were

not significant. The mass-selected population ILB-B had the highest value for this index (2.96) and it differed significantly from the bulk populations as well as from the mass-selected population 2N319. No other comparisons among the mass-selected populations were significant.

No significant differences were observed on the basis of LPSM among plants inoculated at either developmental stage 2.9 (2.15) or 4.5 (2.30). However, plants inoculated at developmental stage 5.3 had a significantly greater mean value for LPSM (2.81) than those plants inoculated at the two earlier stages.

Comparisons between the races for this index were significant. Plants inoculated with urediniospores of race 4 had a larger mean those plants inoculated with urediniospores of race 3 (2.28).

When the data were analyzed as race-developmental stage combinations, all comparisons among plants inoculated with urediniospores of race 3, at developmental stage 2.9, were not significant (Table 32). Values for LPSM in this data subset ranged from 2.25 for the mass-selected population ILB-B to 3.21 for the rust-susceptible population 2N40. At stage 4.5, the bulk population 2N430 had the smallest LPSM value (1.03), and the mass-selected population ILB-B, the largest (3.37). Population 2N430 was statistically indistinguishable from the other bulk populations, and as well, from the mass-selected populations 2N319 and 2N43, with mean values of 1.62 and 2.19, respectively. Population ILB-B was significantly different from the bulk populations and from the mass-selected population 2N319. It was indistinguishable from the other mass-selected populations, however. At developmental stage 5.3, few comparisons among the populations were significant. The mass-selected

population 2N122 (with a mean LPSM value of 1.59) was statistically distinguishable from the mass-selected populations 2N29 and ILB-B, with values of 2.94 and 2.91, respectively. Only one other comparison was significant in this race-developmental stage combination; ILB-B differed significantly from the rust-susceptible population 2N3 (1.76).

Few significant differences were observed among the populations inoculated with urediniospores of race 4, at developmental stage 2.9. The bulk population 2N52 with the smallest mean LPSM value (1.09) differed significantly from the other populations which possessed values that ranged to 2.25 for the rust-susceptible population 2N3.

At developmental stage 4.5, the bulk population 2N34 had the smallest mean value for LPSM (1.99) and differed significantly from the other populations, with the exception of the mass-selected populations 2N29 and ILB-B, with mean values of 3.33 and 4.33, respectively. Population ILB-B, with the largest value for this index, was also statistically distinguishable from the rust- susceptible population 2N40 (2.04), the bulk population 2N52 (2.16), and the mass-selected population 2N319 (2.54).

At developmental stage 5.3, the bulk population 2N34, as at developmental stage 4.5, had the smallest mean value for LPSM (1.97), and while it was not statistically distinguishable from the other bulk populations, it differed significantly from the mass-selected populations. The mass-selected population 2N122 had the largest value (4.29), and it was found to be significantly greater than the values for the bulk, although not from the other mass-selected populations. The mass-selected populations 2N319 and ILB-B with mean values for LPSM of 3.56

TABLE 31. Effect of host population, developmental stage, and rust race on LPSM of ten faba bean populations grown under controlled environment conditions.

		LPSM
Population[1]	2N40 (BK)	2.21 abc[4]
	2N3 (BK)	2.34 abcd
	2N34 (BK)	1.98 a
	2N430 (BK)	2.17 abc
	2N52 (BK)	2.00 ab
	2N319 (MS)	2.53 bcde
	2N29 (MS)	2.93 ef
	2N43 (MS)	2.76 def
	2N122 (MS)	2.70 cdef
	ILB-B (MS)	2.96 f
Developmental Stage[2]	2.9	2.15 a
	4.5	2.30 a
	5.3	2.81 b
Race[3]	3	2.28 a
	4	2.57 b
Mean square error		1.61

[1]Data are means for 288 observations combined over developmental stages and races.
[2]Data are means for 960 observations combined over populations and races. The three stages of development: 2.9, 4.5, and 5.3, refer to plants 20, 35, and 45 days from germination, respectively, and are based on Liew and Gaunt's (1982) developmental key for beans.
[3]Data are means for 1440 observations combined over populations and developmental stages.
[4]Comparisons among means were made using square root transformed data. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

TABLE 32. LPSM of ten faba bean populations inoculated with two rust races at three developmental stages.

Inoculation with race 3

		Developmental Stage[1] 2.9	4.5	5.3
Population	2N40 (BK)	3.21 a[2]	1.88 abc	2.40 abc
	2N3 (BK)	3.16 a	1.31 ab	1.76 ab
	2N34 (BK)	2.73 a	1.42 abc	2.18 abc
	2N430 (BK)	2.33 a	1.03 a	2.66 abc
	2N52 (BK)	2.41 a	1.38 abc	2.28 abc
	2N319 (MS)	3.05 a	1.62 abc	2.51 abc
	2N29 (MS)	2.47 a	2.66 cd	2.94 bc
	2N43 (MS)	3.16 a	2.19 abcd	2.08 abc
	2N122 (MS)	2.50 a	2.48 bcd	1.59 a
	ILB-B (MS)	2.25 a	3.37 d	2.91 c
Mean square error		1.05	1.41	1.61

Inoculation with race 4

		Developmental Stage 2.9	4.5	5.3
Population	2N40 (BK)	1.57 a[2]	2.04 ab	2.42 ab
	2N3 (BK)	2.25 a	2.94 abc	2.56 abc
	2N34 (BK)	1.90 a	1.99 a	1.97 a
	2N430 (BK)	2.05 a	2.73 abc	2.37 ab
	2N52 (BK)	1.09 b	2.16 ab	2.66 abc
	2N319 (MS)	2.00 a	2.54 ab	3.56 bcd
	2N29 (MS)	1.35 a	3.33 ab	3.99 cd
	2N43 (MS)	2.11 a	3.16 abc	4.12 cd
	2N122 (MS)	1.96 a	3.06 abc	4.29 d
	ILB-B (MS)	1.40 a	4.33 c	3.81 bcd
Mean square error		1.40	1.80	2.56

[1]The three stages of development: 2.9, 4.5, and 5.3, refer to plants 20, 35, and 45 days from germination, respectively, and are based on Liew and Gaunt's (1982) developmental key for beans.
[2]Data are means for 48 observations.
Comparisons among means were made using square root transformed data. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

and 3.81, respectively, were indistinguishable from the bulk populations with the exception of 2N34, whereas populations 2N29 and 2N43 were, in addition, significantly different from the rust-susceptible population 2N40 and from the bulk population 2N430.

The C.V. for LPSM was 52.03 % (Appendix AJ). All interactions were significant with this component including the population x race interaction, and the triple interaction between population, race, and developmental stage.

LPSM proved to be useful in the evaluation of rate-reducing resistance in faba bean populations. The results with this component were similar to those observed with LP_{50}, and this was not unexpected since LP_{50} contributes, in part, to LPSM.

12.2 KENDALL'S TAU-B COEFFICIENTS OF CONCORDANCE

Kendall's coefficients of concordance for the pooled growth cabinet data are presented in Table 33 All comparisons among components were significant at the 1 or 5 % probability level except for those between FKN and the other components (except LP), between IT and the other components (except LP and ITR), and between ITR and LP_{50}. LP_{50} and LPSM were negatively associated with the other resistance components, but positively related to each other. All other associations among the components were positive.

The strongest association was observed for the comparison between LP_{50} and LPSM (0.751). This association was not unexpected since LP_{50}

TABLE 33. Kendall's tau-b coefficients of concordance for the components of slow-rusting for faba beans infected with rust in growth cabinet experiments.

	Components[1]						
Components	FKN	UDN	IT	ITR	LP	LP_{50}	LPSM
FKN	1.000	0.001	0.012	-0.040	-0.067*[2]	-0.048	-0.019
UDN		1.000	0.031	0.114**	-0.535**	-0.261**	-0.464**
IT			1.000	0.175**	-0.083**	-0.044	-0.045
ITR				1.000	-0.072*	-0.049	-0.071**
LP					1.000	0.573**	0.584**
LP_{50}						1.000	0.751**
LPSM							1.000

[1]FKN = Number of flecks per square centimeter of leaflet area
UDN = Number of uredinia per square centimeter of leaflet area
IT = Infection type
ITR = Range of infection types
LP = Latent period (time after inoculation until sporulation on at least one uredinium per leaflet)
LP_{50} = Latent period (time after inoculation until sporulation on 50 % of uredinia)
LPSM = Standardized rust severity measure
[2]Asterisks (* and **) indicate statistical significance at p-value <0.05 and p-value<0.01, respectively.

contributes to LPSM. This was followed by good correspondence for comparisons between the other latent period measures i.e., LP and LPSM, and LP and LP_{50} (0.584 and 0.573, respectively), as well as between UDN and LP, and UDN and LPSM (-0.535 and -0.464, respectively). Parlevliet (1980) demonstrated a strong association between infection frequency and latent period for the barley - yellow rust system. Recently, in further investigations of this system, he has observed that these components are governed by the same genes, and are pleiotropically associated (Parlevliet, 1986). Results from this study for the components UDN and latent period tend to support his findings.

There was a poor relationship between FKN and the other resistance components. The coefficient of concordance varied from -0.067 for the comparison between FKN and LP, to 0.001 for FKN and UDN. In addition, correspondence between UDN and IT, and between UDN and ITR was poor, as was the degree of association between IT and the components measuring latent period. The consistently poor correspondence between FKN and the other resistance components would tend to suggest that, at least under the conditions of these experiments, FKN is a poor indicator of the levels of rate-reducing resistance in faba bean populations. Similarly, IT and ITR appear to be inappropriate as measures of resistance. These results are in disagreement with Ohm and Shaner (1976), Shaner, Ohm, and Finney (1978), Wahl et al., (1980), as well as others who have reported that in greenhouse studies, infection type is an effective component of rate-reducing resistance. However, as mentioned previously, Habgood (1977) and Jeger et al., (1983) as well as others (Marshall, 1972 and Williams and Owen, 1975), found that infection type (lesion size) was not a good measure of rate-reducing resistance. Milus and Line (1980)

in their investigation of winter wheat infected with P. recondita reported that race-cultivar combinations that demonstrated a range of infection types were more resistant as determined by one or more other components. Results from this study are not in agreement with these authors.

It is apparent from this investigation that the resistance components were not equally effective in differentiating among the faba bean populations for levels of rate-reducing resistance. UDN was the most efficient followed by the components LP and LP_{50}. LPSM, a standardized disease index combining latent period and pustule density information, was also effective.

In addition, the components did not contribute equally to the overall resistance of the populations. Population ILB(332x133)B had the lowest values for UDN, LP, and LP_{50}, but had, in addition, the largest IT. This was also true, but to a lesser extent, for the populations 2N29 and 2N43. The mass-selected population 2N122, with a larger value for UDN, and a shorter LP and LP_{50} than ILB(332x133)B, had in addition, a small IT. Of the intermediate rusters, the mass-selected population 2N319 was low for FKN, intermediate for UDN, IT, and latent period, and had the narrowest range of infection types. On the other hand, the bulk population 2N430 had intermediate values for all of the components.

When the components of rate-reducing resistance were evaluated for faba beans grown under controlled environment conditions, a distinction between the mass-selected and bulk populations was apparent with the components UDN, LP, LP_{50}, and to a lesser extent with ITR, IT, and FKN. In general the mass-selected populations possessed greater rate-reducing

ability than did the bulk populations. The best slow-rusters, on the basis of all components, were the mass-selected populations 2N122, 2N43, 2N29, and ILB(332x133)B. The mass-selected population 2N319, and the bulk population 2N430 were intermediate, and the bulk populations 2N3, 2N34, and 2N52, were low in their rate-reducing abilities.

12.3 COMPARISONS BETWEEN FIELD AND GROWTH CABINET RESULTS

Growth cabinet studies indicated that differences in the slow-rusting ability of faba bean populations could be identified, and that they were most pronounced in plants inoculated at developmental stage 5.3, the latest stage examined in this study. These differences, however, did not correlate well with the field results, (Table 34), despite their significance (p-value<0.01 or p-value<0.05). The observed significance may be explained, in part, by the dependence of Kendall's tau-b coefficients of concordance on n, the number of observations (Neter et al., (1985), which for these comparisons was large. Mortensen and Green (1978) and Neervoort and Parlevliet (1978) have noted that growth cabinet and greenhouse investigations, respectively, often correspond poorly with the field situation. On the other hand, Bonman et al., (1986) have observed a close correspondence between field and greenhouse results in their investigation of the partial resistance of rice cultivars to blast. Johnson and Wilcoxson (1978;1979) have also reported good correlation between field and greenhouse studies for leaf rust of barley.

The largest coefficients of concordance were observed for comparisons between growth cabinet UDN and the field components. The strongest association was observed for growth cabinet UDN and field LPSM (-0.545).

Mortensen and Green (1978) determined that the assessment of receptivity in growth cabinets correlated better with field results than did measurements of spore productivity. Similarly, Johnson (1986) reported that the number of P. asparagi uredinia measured on asparagus shoots in the greenhouse was positively correlated with field assessment of AUDPC. However, Ricker et al., (1985) found that the number of lesions of C. arachidicola on peanut genotypes was an unreliable measure of resistance.

High values for coefficients were also observed for growth cabinet UDN and field values for FRS (0.409), AUDPC (0.400), AIR (0.395), and LP_{50} (-0.370). The components ITR and LP when measured on cabinet-grown plants were also associated with the field components, especially LP_{50} and LPSM (-0.332 and -0.408, respectively, for cabinet-ITR, and 0.287 and 0.374, respectively, for cabinet-LP), and to a lesser extent, with FRS (0.317 and -0.262, respectively). Parlevliet (1979) and others (Shaner, 1980; Subrahamanyam et al., 1983; Asher and Thomas, 1984) have reported a close association between greenhouse measurements of latent period and field results. ITR, which as a component of resistance has not been evaluated for many host-pathogen systems, was found by Milus and Line (1980) to be closely associated with other components of resistance evaluated in growth cabinet studies. ITR has not previously been compared with resistance components measured in field studies.

Growth cabinet assessment of the components FKN, LP_{50}, and IT was found not to correlate well with the field results. FKN has not previously been evaluated as a component of resistance. In this study, there was much variability in the number of flecks produced on the leaves of faba bean populations, and consequently, FKN proved unreliable in distinguishing among the populations.

TABLE 34. Kendall's tau-b coefficients of concordance for the relationship between field and growth cabinet studies of the various components of slow-rusting in faba beans.

	Components (field)[1]									
Components (cab.)	FKN	UDN	IT	ITR	LP_{50}	LPSM	RS	FRS	AUDPC	AIR
FKN	-0.002	-0.015	-0.101**[2]	0.126**	0.003	0.075**	-0.050**	-0.104**	-0.131**	-0.005
UDN	0.212**	0.210**	0.144**	0.227**	-0.370**	-0.545**	0.188**	0.409**	0.400**	0.395**
IT	-0.132**	-0.080**	-0.031*	-0.083**	0.019**	0.338	-0.081**	-0.067**	-0.126**	-0.240**
ITR	0.133**	0.094**	0.021	0.111**	-0.332**	-0.408**	0.063**	0.317**	0.125	0.193*
LP	-0.162**	-0.152**	-0.075**	-0.155**	0.287**	0.374**	-0.105**	-0.262**	-0.218**	-0.211*
LP_{50}	-0.091**	-0.074**	-0.008	-0.059**	0.152**	0.178**	-0.048**	-0.204**	-0.068**	-0.106**
LPSM	-0.161**	-0.131**	-0.062**	-0.127**	0.258**	0.360**	-0.102**	-0.281**	-0.212**	-0.224**

[1]FKN = Number of flecks per square centimeter of leaflet area
UDN = Number of uredinia per square centimeter of leaflet area
IT = Infection type
ITR = Range of infection types
LP = Latent period (time after inoculation until sporulation on at least one uredium per leaflet)
LP_{50} = Latent period (time after inoculation until sporulation on 50 % of uredinia)
LPSM = Standardized rust severity measure
RS = Mean rust severity
FRS = Final rust severity
AUDPC= Area under the disease progress curve
AIR = Apparent infection rate
[2]Asterisks (* and **) indicate statistical significance at p-value <0.05 and p-value<0.01, respectively.

LP_{50}, although effective in distinguishing among the faba bean populations in field experiments (Manuscript I), was not as effective in the growth cabinet studies. The reason for the good correspondence between LP, but not LP_{50}, and the field results, is unknown. Perhaps, the epidemic was of insufficient intensity in the growth cabinet experiments thus masking differences among the populations. IT, also did not correlate well with the field results. This component was highly variable possibly due to the heterogeneity of the faba bean populations under study.

When correlations between growth cabinet and field experiments were computed using only those plants inoculated at developmental stage 2.9 (Table 35), the coefficients were much smaller than for the data combined over developmental stages (Table 34). In addition, the number of insignificant coefficients were greater. Many of these involved the field components IT and ITR, as well as the parameters measuring disease intensity, especially RS and FRS. Additionally, comparisons between the growth cabinet components UDN and LP, and the field components were often insignificant. Mortensen and Green (1978) have reported similarly poor correlations between seedlings and field data, as has Johnson (1986).

The largest coefficients for the comparisons between the growth cabinet and field data at developmental stage 2.9, were associated with the growth cabinet component ITR and field measurements of FKN, UDN, LP_{50}, LPSM, FRS, AUDPC, and AIR. The best of these were with AIR (-0.257) and LPSM (0.224). There was poor correspondence between growth cabinet UDN and the field studies. This is in contrast to the results observed when the data were combined over developmental stages.

Similarly, comparisons between growth cabinet LP and the field results yielded very small coefficients of concordance especially with infection type and the disease intensity indicators.

At developmental stage 4.5, comparisons between growth cabinet and field experiments (Table 36) gave coefficients that were smaller than those observed for the data combined over developmental stages (Table 34); however, they were larger than those for plants inoculated at developmental stages 2.9 (Table 35) or 5.3 (Table 37). The relatively good correspondence between the growth cabinet adult plant results and the field data, especially for those plants inoculated at developmental stage 4.5 may be due to the fact that plants at this stage were the most susceptible in the field, and nearly so in the growth cabinet investigations. It may be as suggested by Johnson and Wilcoxson (1979), that high levels of infection are necessary to obtain good differentiation among host genotypes.

The largest coefficients for the comparisons between growth cabinet and field studies for plants inoculated at developmental stage 4.5, involved the growth cabinet components IT and ITR. Of these, the best association was observed for the comparison between growth cabinet ITR and field UDN (-0.348). Additionally, good correspondence occurred for the comparisons between growth cabinet IT and the field disease intensity indicators, especially AUDPC (0.310). The associations between growth cabinet LP_{50} and the field data were particularly poor.

At developmental stage 5.3, the magnitude of the coefficients of concordance for comparisons between growth cabinet and field-grown plants (Table 37) were smaller than for either plants inoculated at

TABLE 35. Kendall's tau-b coefficients of concordance for the relationships between field and growth cabinet studies of the components of slow-rusting in faba beans inoculated at developmental stage 2.9.

	Components (field)[1]									
Components (cab.)	FKN	UDN	IT	ITR	LP_{50}	LPSM	RS	FRS	AUDPC	AIR
FKN	0.123**[2]	0.126**	0.041*	0.044**	-0.167**	-0.204**	-0.016	0.051**	0.074**	0.226
UDN	-0.025	-0.051**	-0.029	-0.013	-0.030*	0.013	-0.005	0.026	-0.000	0.012
IT	-0.070**	-0.062**	-0.018	-0.030	0.135**	0.155**	0.044**	-0.033*	-0.064**	-0.181**
ITR	0.128**	0.127**	-0.017	-0.036*	0.197**	0.224**	0.014	-0.055**	-0.075**	-0.257*
LP	0.054**	0.055**	0.004	0.029	-0.071**	-0.091**	0.005	0.019	0.025	0.100*
LP_{50}	0.091**	0.088**	0.035*	0.042*	-0.102**	-0.134**	0.016	0.028	0.059**	0.143**
LPSM	0.024	0.076**	0.038*	0.023	-0.027*	-0.073**	0.035*	-0.021	0.005**	0.058**

[1]FKN = Number of flecks per square centimeter of leaflet area
UDN = Number of uredinia per square centimeter of leaflet area
IT = Infection type
ITR = Range of infection types
LP = Latent period (time after inoculation until sporulation on at least one uredium per leaflet)
LP_{50} = Latent period (time after inoculation until sporulation on 50 % of uredinia)
LPSM = Standardized rust severity measure
RS = Mean rust severity
FRS = Final rust severity
AUDPC= Area under the disease progress curve
AIR = Apparent infection rate
[2]Asterisks (* and **) indicate statistical significance at p-value <0.05 and p-value<0.01, respectively.

TABLE 36. Kendall's tau-b coefficients of concordance for the relationships between field and growth cabinet studies of the components of slow-rusting in faba beans inoculated at developmental stage 4.5.

	Components (field)[1]									
Components (cab.)	FKN	UDN	IT	ITR	LP_{50}	LPSM	RS	FRS	AUDPC	AIR
FKN	0.093**[2]	-0.036*	0.026	0.044*	-0.092**	-0.186**	0.088**	0.214**	0.225**	0.205**
UDN	0.020	0.018	0.031	0.038	-0.050**	0.090**	0.062**	0.195**	0.221**	0.117**
IT	0.118**	-0.023	0.061**	0.087**	-0.106**	-0.206**	0.129**	0.290**	0.310**	0.239**
ITR	0.257**	-0.348**	0.229	0.024	0.095	0.095	-0.134*	0.061	0.008	-0.095
LP	-0.036*	-0.010	-0.048*	-0.043*	0.075**	0.142**	-0.102**	-0.226**	-0.263**	-0.172*
LP_{50}	0.024	-0.025	-0.005	0.014	0.021	0.035**	-0.026	-0.089**	-0.116**	-0.050**
LPSM	0.012	-0.037*	-0.033**	-0.017	0.050**	0.091**	-0.076**	-0.197**	-0.236**	-0.117**

[1]FKN = Number of flecks per square centimeter of leaflet area
UDN = Number of uredinia per square centimeter of leaflet area
IT = Infection type
ITR = Range of infection types
LP = Latent period (time after inoculation until sporulation on at least one uredium per leaflet)
LP_{50} = Latent period (time after inoculation until sporulation on 50 % of uredinia)
LPSM = Standardized rust severity measure
RS = Mean rust severity
FRS = Final rust severity
AUDPC= Area under the disease progress curve
AIR = Apparent infection rate
[2]Asterisks (* and **) indicate statistical significance at p-value <0.05 and p-value<0.01, respectively.

developmental stage 4.5 (Table 36) or for data combined over developmental stages (Table 34). Many of the comparisons between growth cabinet and field results at developmental stage 5.3 were insignificant. The majority of these involved the field components UDN, ITR, and RS, as well as the growth cabinet component ITR. The best associations occurred between the growth cabinet component IT and the field components, especially LPSM and the disease intensity indicators. Additionally, the correspondence between growth cabinet LP and the field parameters RS and FRS, was good. However, there was poor association between cabinet LP_{50} and the disease intensity indicators.

In general comparisons among the resistance parameters measured in field and growth cabinet studies yielded results that were dependent upon the developmental stage of the plants at the time of inoculation. The best associations were observed at developmental stage 4.5 followed by stage 5.3. Poor associations occurred at the earliest developmental stage (2.9). These results suggest that selection for rate-reducing resistance in growth cabinet grown faba bean populations necessitates use of mature plants at approximately the same growth stage. Growth cabinet assessments of UDN, ITR, and LP were most strongly related to the field results whereas measurements of FKN, LP_{50}, and IT corresponded poorly with the field situation.

TABLE 37. Kendall's tau-b coefficients of concordance for the relationships between field and growth cabinet studies of the components of slow-rusting in faba beans inoculated at developmental stage 5.3.

	Components (field)[1]									
Components	FKN (cab.)	UDN	IT	ITR	LP_{50}	LPSM	RS	FRS	AUDPC	AIR
FKN	0.078**[2]	0.036	-0.048*	-0.018	-0.085**	-0.112**	0.067**	0.124**	0.050*	0.072**
UDN	-0.079**	-0.020	0.029	0.022	0.073**	0.098**	-0.045**	-0.147**	-0.161**	-0.112**
IT	0.026	0.116	0.147	0.150*	-0.240**	-0.271**	0.091	0.218**	0.195**	0.240**
ITR	0.241**	-0.120	-0.117	-0.067	-0.028	-0.013	-0.050	0.060	0.038	0.028
LP	0.078**	0.043*	-0.048*	-0.035	-0.131**	-0.172**	0.108**	0.233**	0.169**	0.152*
LP_{50}	-0.082**	0.015	0.058**	0.041*	0.032*	0.039*	-0.015	-0.039	0.000	-0.014
LPSM	-0.090**	0.016	0.067**	0.048*	0.041**	0.051**	-0.026	-0.054**	0.008	-0.015

[1]FKN = Number of flecks per square centimeter of leaflet area
UDN = Number of uredinia per square centimeter of leaflet area
IT = Infection type
ITR = Range of infection types
LP = Latent period (time after inoculation until sporulation on at least one uredium per leaflet)
LP_{50} = Latent period (time after inoculation until sporulation on 50 % of uredinia)
LPSM = Standardized rust severity measure
RS = Mean rust severity
FRS = Final rust severity
AUDPC= Area under the disease progress curve
AIR = Apparent infection rate
[2]Asterisks (* and **) indicate statistical significance at p-value <0.05 and p-value<0.01, respectively.

GENERAL DISCUSSION

The results from this investigation indicate that faba bean populations, which in three to four years of preliminary field evaluations, had low area under the disease progress curve (AUDPC) and final rust severity (FRS) scores (Conner and Bernier, 1982d; Rashid and Bernier, 1986), were distinguishable on the basis of the following resistance components: number of flecks per square centimeter of leaflet area (FKN), number of uredinia per square centimeter of leaflet area (UDN), infection type (IT), range of infection types (ITR), latent period (LP and LP_{50}), and the disese index, LPSM. In both field and growth cabinet studies, the populations were readily divisible into those that were derived by mass-selection, and those that were bulk populations. The mass-selected populations had, in general, more rate-reducing ability than did the bulk populations. This suggests that mass-selection is an appropriate selection technique for screening faba beans for rate-reducing resistance.

Not all of the components were equally effective in characterizing the resistance of the faba bean populations. FKN was effective in the field when measured at 7 days after inoculation (d.p.i.). However, it was not efficient when evaluated at 14 d.p.i., nor when assessed in controlled environment conditions. Additionally, there was poor correspondence between FKN and the following field performance indicators: mean and final rust severity (RS and FRS, respectively), individual

weekly assessments of rust severity (RS1 - RS4), apparent infection rate (AIR), and AUDPC. This lack of association points to the ineffectiveness of FKN in a resistance screening program despite the successful use of the related component, incubation period, measured as the time from inoculation to the first appearance of symptoms (`flecks'), or as the time from inoculation to the time when 50 % of the lesions (pustules) are visible (Jeger et al., 1983; Subrahmanyam et al., 1983; Nutter and Pederson, 1985), in disease resistance screening.

Infection type, while effective in differentiating among the faba bean populations in the field was, like FKN, ineffectual in the growth cabinet studies. Shaner and Finney (1980) have reported that interactions between this component and infection frequency may hamper its usefulness; such interactions may have been consequential in this study. An examination of fleck and uredinia numbers indicated that infection frequencies were higher in the field than in the growth cabinets. This may be why the mean IT values were greater in the growth cabinets than in the field. It is therefore possible that inoculum densities in the growth cabinet experiments were too low to allow for the full expression of the resistance, thereby masking differences between the populations. Another factor contributing to IT's lack of effectiveness in the growth cabinet studies might be temperature. Milus and Line (1980) found that differences in infection type were more evident in wheat incubated at 10 - 30°C than at 2 - 18°C. The faba beans in these growth cabinet studies were incubated at 15 - 20°C, whereas plants in the field were subjected to a greater range of temperatures (Appendix B).

The component ITR was superior to IT in both the field and growth cabinet studies. There was a strong relationship between growth cabinet

assessment of ITR and the field results. In general the better slow-rusters had the narrower range of infection types. In this study, all of the populations displayed a range of infection types. Conversely, Milus and Line (1980) reported that in their investigation, only the best slow-rusting wheats expressed this character. They suggested that ITR might be useful for selecting wheat lines with few uredinia, long latent periods, and few spores per uredinium. The use of ITR for screening faba beans for rate-reducing resistance might be somewhat more laborious than for cereals due to the necessity of establishing values for this component rather than simply acknowledging the presence or absence of a range.

The component UDN and the measures of latent period (LP and LP_{50}) were useful in distinguishing among the populations in both the field and growth cabinet studies. In addition, there was good correspondence between growth cabinet evaluations of these components and field performance. UDN is considered to be a component that is difficult to assess due to problems in obtaining uniform inoculation of the host (Parlevliet and Kuiper, 1977a; Johnson and Wilcoxson, 1979; Shaner and Finney, 1980; Zummo, 1988). The inoculation procedures used in this study (Materials and Methods, Manuscripts I and II), allowed for the adequate assessment of UDN. In the field, good levels of infection were achieved by using small plots which, when covered with polyethylene sheeting following inoculation, maintained leaf wetness overnight (Rashid and Bernier, 1984). Growth cabinet assessment of LP was closely associated with the field results. This was not unexpected since numerous researchers have advocated the use of latent period as an appropriate measure of rate-reducing resistance. LP_{50} was superior to

LP in the field experiments, but inferior in the growth cabinet studies. This may have been due to the suboptimal humidity levels in the growth cabinets, as this may have hindered subsequent development of the uredinia (Rowell, 1984).

LPSM, a standardized disease index developed by combining LP_{50} and uredinial density information, was effective in both the field and growth cabinet studies. The strongest associations among the resistance parameters were found between the growth cabinet components, especially UDN, ITR, LP, and LPSM, and field measurement of LPSM. This index was proposed for the following reasons: (1) it was observed that two populations could be quite similar in terms of latent period, but differ substantially in the number of erupted uredinia, (2) due to the partially outcrossing nature and heterogeneity of faba beans, it was felt that use of any one component was inadequate to assess resistance levels and this was verified by principal component analysis; LPSM, however, combined information from two of the most reliable and least variable parameters (Parlevliet et al., 1985; Ricker et al., 1985), and (3) as a standardized index, LPSM could be used, without transformation, in many statistical analyses unlike many of the other components.

The rate-reducing ability of the faba bean populations was similar in both the field and growth cabinet studies. The best slow-rusters were the mass-selected populations 2N43, 2N122, and ILB(332x133)B (the latter population was not evaluated in the field due to a shortage of seed). These populations had few flecks and uredinia, long latent periods, a small IT (with the exception of ILB(332x133)B which had a very large IT), and a narrow ITR, in addition to reduced rust development in the field as determined by the population performance indicators. The mass-

selected population 2N319 and the bulk population 2N430 had intermediate levels of rate-reducing resistance with median values for all components. The other bulk populations were poor in their rate-reducing abilities.

In this study, population rankings were similar to those reported by Conner and Bernier (1982d) and Rashid and Bernier (1986), despite differences in the methodology employed in their studies. Conner and Bernier (1982d) and Rashid and Bernier (1986) used AUDPC and FRS to distinguish among the faba bean populations. Both AUDPC and FRS were assessed on populations inoculated by movement of rust from spreader rows. In this study, however, assessments were made on individual leaflets inoculated directly. Mean population AUDPC and FRS values, however, were comparable although coefficients of variation were greater in this study due to the heterogeneity of the individual plants within a population. It appears that assessments made on individual leaflets can provide reliable information if sufficiently large populations are used. Similarly, it appears that the faba bean populations evaluated in this study possess a broadly-based type of resistance. Consequently, it is possible that selection for one or two components in either the field or in growth cabinet studies might enhance resistance as measured by the others. The resulting underlying complexity might, in turn, confer durabilty.

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Appendix A

PROCEDURES FOR UREDINIOSPORE COLLECTION AND INOCULATION.

To ensure dependable production of pure inoculum, two-week-old plants of the susceptible faba bean 2N40 (P.I. 222128) were inoculated with single uredinial transfers of rust races 3 and 4. The plants were inoculated in a plexiglass chamber that had previously been washed with 70 % ethanol and then misted with water to prevent deposition of contaminating spores on the plants.

Urediniospores, suspended in light oil (Soltrol 170; Philips Petroleum Co., Special Products Division, Borger, TX 79007) were applied to leaf surfaces with a fine camel's hair brush. The oil was then allowed to dry and the plants were covered with polyvinyl sleeves prior to incubation under 100 % relative humidity. Following incubation for 24 h, the plants were moved to a greenhouse with supplemental fluorescent lighting. The sleeves were connected to a source of filtered air by rubber tubing to prevent cross-contamination and excessive build-up of moisture. Urediniospores were collected using a cyclone spore collector (Browder, 1971), and were stored at 5°C for one to two months, prior to use.

Appendix B

MEAN MAXIMUM AND MINIMUM TEMPERATURES, RELATIVE HUMIDITY, AND PRECIPITATION AT WINNIPEG, FOR JUNE - SEPTEMBER IN 1982 AND 1983.

Year - Month	Temperature(°C)				Relative Humidity(%)				Precipitation(mm)	
	Mean Maximum	Normal*	Mean Minimum	Normal	Mean Maximum	Normal	Mean Minimum	Normal		Normal
1982 - June	20.6	23.1	6.5	10.5	88	88	38	44	54.2	80.1
July	26.0	25.9	14.0	13.3	92	89	49	44	106.9	75.9
Aug	23.0	24.7	10.6	11.8	92	92	45	47	59.2	75.2
Sept	18.6	18.4	5.7	6.3	90	91	46	49	58.2	53.3
1983 - June	23.3	23.1	10.8	10.5	91	88	47	45	139.2	80.1
July	28.1	25.9	16.3	13.3	87	89	49	45	29.8	75.9
Aug	29.7	24.7	15.2	11.8	87	91	38	46	85.2	75.2
Sept	18.8	18.4	7.0	6.3	86	91	49	49	52.8	53.0

* indicates 30 year normals 1951-1980
Source - Environment Canada. Atmospheric Environment Service. Monthly Meterological Summary.

Appendix C

ANALYSIS OF VARIANCE IN THE NUMBER OF FLECKS PER SQUARE CENTIMETER OF LEAFLET AREA AT 7 DAYS AFTER INOCULATION.

Source	D.F.	Sum of Squares	Mean Square	F value
Model	95	110.29	1162	14.02
Year	1	0.16		1.93
Race	1	3.19		38.53*
Year X race	1	6.34		76.58*
Stage	2	10.64		64.25*
Year X stage	2	1.90		11.48*
Race X stage	2	2.69		16.27*
Year X race X stage	2	3.34		20.19*
Population	7	56.02		96.68*
Race X population	7	3.00		5.17*
Year X race X population	14	7.43		6.41*
Stage X population	14	4.75		4.10*
Year X race X stage X population	42	10.82		3.11*
Error	433	35.84	0.08	
Total	528	146.13		

R^2= 0.75
C.V.= 63.32%

* Significant at p-value<0.01.

Appendix D

ANALYSIS OF VARIANCE IN THE NUMBER OF FLECKS PER SQUARE CENTIMETER OF LEAFLET AREA AT 14 DAYS AFTER INOCULATION.

Source	D.F.	Sum of Squares	Mean Square	F value
Model	13	17.91	1.38	19.51
Year	1	1.13		16.01*
Race	1	0.00		0.01
Stage	2	7.29		51.60*
Year X stage	2	5.41		38.34*
Population	7	4.08		8.25*
Error	509	35.94	0.07	
Total	522	53.86		

R^2= 0.33
C.V.= 112.19%

* Significant at p-value<0.01.

Appendix E

ANALYSIS OF VARIANCE IN THE NUMBER OF UREDINIA PER SQUARE CENTIMETER OF LEAFLET AREA AT 7 DAYS AFTER INOCULATION.

Source	D.F.	Sum of Squares	Mean Square	F value
Model	81	78.32	0.97	25.44
Year	1	10.10		265.68*
Race	1	3.61		94.91*
Year X race	1	10.83		284.87*
Stage	2	2.18		28.69*
Year X stage	2	9.34		122.87*
Race X stage	2	5.57		73.32*
Year X race X stage	2	2.41		31.68*
Population	7	15.04		56.55*
Year X population	7	3.56		13.38*
Year X race X population	14	5.16		9.70*
Year X stage X population	28	5.03		4.73*
Race X stage X population	14	5.50		10.33*
Error	447	16.99	0.04	
Total	528	95.31		

R^2= 0.82
C.V.= 104.36%

* Significant at p-value<0.01.

Appendix F

ANALYSIS OF VARIANCE IN THE NUMBER OF UREDINIA PER SQUARE CENTIMETER OF LEAFLET AREA AT 14 DAYS AFTER INOCULATION.

Source	D.F.	Sum of Squares	Mean Square	F value
Model	25	190.76	7.63	44.73
Year	1	10.77		63.14*
Race	1	3.02		17.72*
Stage	2	0.91		2.66
Race X stage	2	7.85		23.01*
Year X race X stage	5	4.76		5.58*
Population	7	155.90		130.55*
Year X population	7	7.55		6.32*
Error	497	84.79	0.17	
Total	522	275.55		
			R^2= 0.69	
			C.V.= 47.08%	

* Significant at p-value<0.01.

Appendix G

ANALYSIS OF VARIANCE IN INFECTION TYPE AT 7 DAYS AFTER INOCULATION.

Source	D.F.	Sum of Squares	Mean Square	F value
Model	39	186.45	4.78	24.27
Year	1	6.83		34.67*
Race	1	32.58		165.38*
Stage	2	30.13		76.46*
Year X stage	2	15.04		38.18*
Race X stage	2	35.01		88.86*
Year X race X stage	3	3.97		6.72*
Population	7	46.35		33.61*
Year X population	7	7.73		5.60*
Year X race X population	14	8.80		3.19*
Error	511	100.68	0.20	
Total	550	287.13		

R^2= 0.65
C.V.= 42.74%

* Significant at p-value<0.01.

Appendix H

ANALYSIS OF VARIANCE IN INFECTION TYPE AT 14 DAYS AFTER INOCULATION.

Source	D.F.	Sum of Squares	Mean Square	F value
Model	18	40.51	2.25	9.86
Year	1	1.41		6.18
Race	1	1.65		7.23
Stage	2	1.21		2.64
Year X stage	2	5.35		11.72*
Year X race X stage	5	7.44		6.51*
Population	7	23.45		14.67*
Error	374	85.40	0.23	
Total	392	125.90		
			R^2= 0.32	
			C.V.= 31.17%	

* Significant at p-value<0.01.

Appendix I

ANALYSIS OF VARIANCE IN RANGE OF INFECTION TYPES AT 7 DAYS AFTER INOCULATION.

Source	D.F.	Sum of Squares	Mean Square	F value
Model	53	1498.18	28.27	20.44
Year	1	73.16		52.91*
Race	1	171.63		124.13*
Stage	2	291.61		105.45*
Year X stage	2	122.91		44.45*
Race X stage	2	120.74		143.66*
Year X race X stage	3	29.58		7.13*
Population	7	556.86		57.53*
Year X population	7	26.36		2.72
Year X race X population	14	47.94		2.48
Stage X population	14	57.39		2.96*
Year X stage X population	21	17.64		4.38*
Error	497	687.21	1.38	
Total	550	2185.39		

R^2= 0.68
C.V.= 48.10%

* Significant at p-value<0.01.

Appendix J

ANALYSIS OF VARIANCE IN RANGE OF INFECTION TYPES AT 14 DAYS AFTER INOCULATION.

Source	D.F.	Sum of Squares	Mean Square	F value
Model	60	761.28	12.69	6.35
Year	1	42.29		21.16*
Race	1	54.18		27.11*
Stage	2	14.21		3.55
Year X stage	2	35.23		8.81*
Race X stage	2	21.59		5.40
Year X race X stage	3	25.93		4.33
Population	7	388.97		27.81*
Year X population	7	52.08		3.72*
Race X stage X population	35	126.79		1.81
Stage X population	14	17.53		6.53*
Error	332	663.47	2.00	
Total	392	1424.75		

R^2= 0.53
C.V.= 34.25%

* Significant at p-value<0.01.

Appendix K

ANALYSIS OF VARIANCE IN LATENT PERIOD OF FIELD-GROWN FABA BEAN POPULATIONS.

Source	D.F.	Sum of Squares	Mean Square	F value
Model	67	183.15	2.73	16.33*
Year	1	33.21		198.37*
Race	1	0.01		0.02
Year X race	1	24.67		147.37*
Stage	2	2.81		8.40*
Year X stage	2	16.08		48.02*
Race X stage	2	27.79		83.01*
Year X race X stage	2	6.55		19.55*
Population	7	42.78		36.51*
Year X population	7	5.41		4.61*
Year X race X population	14	6.57		2.80*
Stage X population	14	9.48		4.05*
Year X stage X population	14	7.79		3.33*
Error	2103	352.05	0.17	
Total	2170	535.20		

R^2= 0.34
C.V.= 24.93%

* Significant at p-value<0.01.

Appendix L

ANALYSIS OF VARIANCE IN LP_{50} OF FIELD-GROWN FABA BEAN POPULATIONS.

Source	D.F.	Sum of Squares	Mean Square	F value
Model	74	371.68	5.02	26.21
Year	1	48.87		255.03*
Race	1	0.75		3.93
Year X race	1	45.40		236.92*
Stage	2	1.23		3.22
Year X stage	2	39.69		103.55*
Race X stage	2	73.92		192.61*
Year X race X stage	2	11.55		30.13*
Population	7	97.73		72.86*
Race X population	7	6.59		4.92*
Stage X population	14	17.53		6.53*
Year X stage X population	21	17.64		4.38*
Race X stage X population	14	10.88		4.05*
Error	2096	401.65	0.19	
Total	2170	773.33		

R^2= 0.48
C.V.= 21.26%

* Significant at p-value<0.01.

Appendix M

ANALYSIS OF VARIANCE IN RUST SEVERITY OF FIELD-GROWN FABA BEAN POPULATIONS.

Source	D.F.	Sum of Squares	Mean Square	F value
Model	95	108.03	1.14	12.58
Year	1	10.76		119.05*
Race	1	0.06		0.68
Year X race	1	4.76		52.70*
Stage	2	0.24		1.30
Year X stage	2	12.19		67.42*
Race X stage	2	0.90		4.96*
Year X race X stage	2	11.95		66.08*
Population	7	51.54		81.46*
Year X population	7	2.79		4.41*
Year X stage X population	28	5.77		2.28*
Year X race X stage X population	42	7.09		1.87*
Error	476	43.02	0.09	
Total	571	151.05		

R^2= 0.72
C.V.= 7.49%

* Significant at p-value<0.01.

Appendix N

ANALYSIS OF VARIANCE IN FINAL RUST SEVERITY OF FIELD-GROWN FABA BEAN POPULATIONS.

Source	D.F.	Sum of Squares	Mean Square	F value
Model	16	191.58	11.97	47.27
Year	1	34.95		137.98*
Race	1	0.98		3.87
Year X race	1	7.85		30.98*
Stage	2	1.72		3.40
Year X stage	2	3.90		7.70*
Race X stage	2	8.28		16.35*
Population	7	133.90		75.52*
Error	422	106.89	0.25	
Total	438	298.47		
			R^2= 0.64	
			C.V.= 17.46%	

* Significant at p-value<0.01.

Appendix O

EFFECT OF HOST POPULATION, DEVELOPMENTAL STAGE, RUST RACE, AND YEAR ON THE RUST SEVERITY OF EIGHT FIELD-GROWN FABA BEAN POPULATIONS AT ONE WEEK AFTER INOCULATION.

		Rust severity
Population[1]	2N40 (BK)	0.55 a[5]
	2N34 (BK)	0.07 b
	2N430 (BK)	0.05 b
	2N52 (BK)	0.08 b
	2N319 (MS)	0.01 b
	2N29 (MS)	0.01 b
	2N43 (MS)	0 b
	2N122 (MS)	0.01 b
Developmental Stage[2]	2.9	0.19 a
	4.5	0.04 b
	5.3	0.05 b
Race[3]	3	0.15 a
	4	0.04 b
Year[4]	1982	0.05 a
	1983	0.15 b
Mean square error		0.01

[1]Data are means for 432 observations combined over developmental stages, races, and years.
[2]Data are means for 1152 observations combined over populations, races, and years. The three stages of development: 2.9, 4.5, and 5.3, refer to plants 35, 50, and 65 days from planting, respectively, and are based on Liew and Gaunt's (1982) developmental key for beans.
[3]Data are means for 1728 observations combined over populations, developmental stages, and years.
[4]Data are means for 1728 observations combined over populations, developmental stages, and races.
[5]Comparisons among means were made using logit transformed data. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

Appendix P

ANALYSIS OF VARIANCE IN RUST SEVERITY AT ONE WEEK AFTER INOCULATION.

Source	D.F.	Sum of Squares	Mean Square	F value
Model	95	14.27	0.15	10.87
Year	1	0.24		17.56*
Race	1	0.27		19.37*
Year X race	1	0.50		35.95*
Stage	2	0.45		16.29*
Year X stage	2	0.64		23.31*
Race X stage	2	0.70		25.33*
Year X race X stage	2	1.09		39.48*
Population	7	2.62		27.11*
Year X population	7	0.37		3.88*
Race X population	7	0.28		2.90
Year X stage X population	7	0.95		9.85*
Stage X population	14	0.82		4.25*
Year X stage X population	14	1.11		5.75*
Race X stage X population	14	1.41		7.29*
Year X race X stage X population	14	2.80		14.49*
Error	458	6.33	0.01	
Total	553	20.60		

R^2= 0.69
C.V.= 2.58%

* Significant at p-value<0.01.

Appendix Q

EFFECT OF HOST POPULATION, DEVELOPMENTAL STAGE, RUST RACE, AND YEAR ON THE RUST SEVERITY OF EIGHT FIELD-GROWN FABA BEAN POPULATIONS AT TWO WEEKS AFTER INOCULATION.

		Rust severity
Population[1]	2N40 (BK)	3.77 a[5]
	2N34 (BK)	1.04 b
	2N430 (BK)	0.84 b
	2N52 (BK)	0.95 b
	2N319 (MS)	0.50 bc
	2N29 (MS)	0.24 c
	2N43 (MS)	0.21 c
	2N122 (MS)	0.19 c
Developmental Stage[2]	2.9	0.72 a
	4.5	1.01 b
	5.3	1.05 b
Race[3]	3	1.22 a
	4	0.70 b
Year[4]	1982	0.85 a
	1983	1.01 b
Mean square error		0.12

[1]Data are means for 432 observations combined over developmental stages, races, and years.
[2]Data are means for 1152 observations combined over populations, races, and years. The three stages of development: 2.9, 4.5, and 5.3, refer to plants 35, 50, and 65 days from planting, respectively, and are based on Liew and Gaunt's (1982) developmental key for beans.
[3]Data are means for 1728 observations combined over populations, developmental stages, and years.
[4]Data are means for 1728 observations combined over populations, developmental stages, and races.
[5]Comparisons among means were made using logit transformed data. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

Appendix R

ANALYSIS OF VARIANCE IN RUST SEVERITY AT TWO WEEKS AFTER INOCULATION.

Source	D.F.	Sum of Squares	Mean Square	F value
Model	25	82.07	3.28	27.78
Year	1	1.10		9.32
Race	1	6.11		51.68*
Year X race	1	2.32		19.65*
Stage	2	4.26		18.02*
Race X stage	2	3.26		13.78*
Year X race X stage	4	1.93		4.09
Population	7	60.84		73.56*
Race X population	7	2.26		2.73
Error	493	58.25	0.12	
Total	518	140.32		

R^2= 0.58
C.V.= 8.17%

* Significant at p-value<0.01.

Appendix S

EFFECT OF HOST POPULATION, DEVELOPMENTAL STAGE, RUST RACE, AND YEAR ON THE RUST SEVERITY OF EIGHT FIELD-GROWN FABA BEAN POPULATIONS AT THREE WEEKS AFTER INOCULATION.

		Rust severity
Population[1]	2N40 (BK)	12.33 a[5]
	2N34 (BK)	3.62 b
	2N430 (BK)	2.62 bc
	2N52 (BK)	3.23 b
	2N319 (MS)	1.76 cd
	2N29 (MS)	1.37 d
	2N43 (MS)	1.36 cd
	2N122 (MS)	1.15 d
Developmental Stage[2]	2.9	3.84 a
	4.5	3.97 a
	5.3	2.29 b
Race[3]	3	3.53 a
	4	3.19 b
Year[4]	1982	4.18 a
	1983	2.42 b
Mean square error		0.19

[1]Data are means for 432 observations combined over developmental stages, races, and years.
[2]Data are means for 1152 observations combined over populations, races, and years. The three stages of development: 2.9, 4.5, and 5.3, refer to plants 35, 50, and 65 days from planting, respectively, and are based on Liew and Gaunt's (1982) developmental key for beans.
[3]Data are means for 1728 observations combined over populations, developmental stages, and years.
[4]Data are means for 1728 observations combined over populations, developmental stages, and races.
[5]Comparisons among means were made using logit transformed data. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

Appendix T

ANALYSIS OF VARIANCE IN RUST SEVERITY AT THREE WEEKS AFTER INOCULATION.

Source	D.F.	Sum of Squares	Mean Square	F value
Model	25	219.27	8.77	45.25
Year	1	11.90		61.37*
Race	1	2.42		12.49*
Year X race	1	3.54		18.26*
Stage	2	8.18		21.11*
Year X stage	2	12.31		31.74*
Race X stage	2	30.18		77.86*
Year X race X stage	2	7.90		20.37*
Population	7	136.50		100.60*
Year X population	7	6.34		4.67*
Error	407	78.89	0.19	
Total	432	298.16		

R^2= 0.73
C.V.= 12.45%

* Significant at p-value<0.01.

Appendix U

EFFECT OF HOST POPULATION, DEVELOPMENTAL STAGE, RUST RACE, AND YEAR ON THE RUST SEVERITY OF EIGHT FIELD-GROWN FABA BEAN POPULTIONS AT FOUR WEEKS AFTER INOCULATION.

		Rust severity
Population[1]	2N40 (BK)	20.94 a[5]
	2N34 (BK)	6.57 b
	2N430 (BK)	5.61 bc
	2N52 (BK)	6.63 b
	2N319 (MS)	3.94 cd
	2N29 (MS)	3.45 d
	2N43 (MS)	3.75 cd
	2N122 (MS)	3.01 d
Developmental Stage[2]	2.9	6.39 a
	4.5	7.15 b
	5.3	5.68 a
Race[3]	3	5.72 a
	4	6.79 a
Year[4]	1982	8.32 a
	1983	4.07 b
Mean square error		0.27

[1]Data are means for 432 observations combined over developmental stages, races, and years.
[2]Data are means for 1152 observations combined over populations, races, and years. The three stages of development: 2.9, 4.5, and 5.3, refer to plants 35, 50, and 65 days from planting, respectively, and are based on Liew and Gaunt's (1982) developmental key for beans.
[3]Data are means for 1728 observations combined over populations, developmental stages, and years.
[4]Data are means for 1728 observations combined over populations, developmental stages, and races.
[5]Comparisons among means were made using logit transformed data. Means followed by the same letter within a column are not significantly different (p-value<0.01) according to Scheffé's significant difference procedure.

Appendix V

ANALYSIS OF VARIANCE IN RUST SEVERITY AT FOUR WEEKS AFTER INOCULATION.

Source	D.F.	Sum of Squares	Mean Square	F value
Model	37	210.29	5.68	22.32
Year	1	49.91		196.03*
Race	1	0.00		0.00
Stage	2	0.61		1.19
Year X race	1	3.58		14.05*
Year X stage	2	7.09		13.92*
Race X stage	2	4.62		9.07*
Population	7	130.78		73.38*
Year X population	7	5.03		2.82
Year X race X population	14	8.67		2.43
Error	366	93.19	0.25	
Total	403	303.48		

R^2= 0.69
C.V.= 17.26%

* Significant at p-value<0.01.

Appendix W

ANALYSIS OF VARIANCE IN APPARENT INFECTION RATE OF FIELD-GROWN FABA BEAN POPULATIONS.

Source	D.F.	Sum of Squares	Mean Square	F value
Model	13	0.10	0.01	24.46*
Year	1	0.04		124.78*
Race	1	<0.01		0.09
Stage	2	<0.01		1.14
Population	7	0.05		23.32*
Year X Stage	2	0.01		13.81*
Error	82	0.02	<0.01	
Total	95	0.12		

R^2= 0.79
C.V.= 22.07%

* Significant at p-value<0.01.

Appendix X

ANALYSIS OF VARIANCE IN AUDPC VALUES OF FIELD-GROWN FABA BEAN POPULATIONS.

Source	D.F.	Sum of Squares	Mean Square	F value
Model	47	24611.82	523.66	25.42
Year	1	1085.11		52.68*
Race	1	78.99		3.84
Year X race	1	430.91		20.92*
Stage	2	192.85		4.68
Population	7	19532.41		135.47*
Year X population	7	1532.55		10.63*
Year X race X population	14	897.52		3.11*
Stage X population	14	861.48		2.99*
Error	356	7332.64	20.60	
Total	403	31944.46		

R^2= 0.77
C.V.= 64.15%

* Significant at p-value<0.01.

Appendix Y

ANALYSIS OF VARIANCE IN LPSM OF FIELD-GROWN FABA BEAN POPULATIONS.

Source	D.F.	Sum of Squares	Mean Square	F value
Model	67	365.46	5.45	28.12
Year	1	48.87		251.98*
Race	1	0.75		3.89
Year X race	1	45.40		234.09*
Stage	2	1.23		3.18
Year X stage	2	39.69		102.31*
Race X stage	2	73.82		190.30*
Year X race X stage	2	11.55		29.77*
Population	7	97.73		71.99*
Year X population	7	3.88		2.86
Race X population	7	6.42		4.73*
Year X race X population	7	4.29		3.16
Stage X population	14	17.12		6.31*
Year X stage X population	14	14.70		5.41*
Error	2103	407.87	0.19	
Total	2170	773.33		

R^2= 0.47
C.V.= 21.38%

* Significant at p-value<0.01.

Appendix Z

KENDALL'S TAU-B COEFFICIENTS OF CONCORDANCE FOR THE COMPONENTS OF RATE-REDUCING RESISTANCE FOR FIELD-GROWN FABA BEANS INOCULATED WITH RUST RACE 3 IN 1982.

	Components[1]									
Components	FKN	UDN	IT	ITR	LP_{50}	LPSM	RS	FRS	AUDPC	AIR
FKN	1.000	0.572**[2]	0.229	0.348**	-0.373*	-0.471**	0.362*	0.261	0.425**	0.378**
UDN		1.000	0.338*	0.500**	-0.530**	-0.638**	0.297*	0.283	0.417**	0.465**
IT			1.000	0.737**	-0.168	-0.381**	0.476**	0.461**	0.596**	0.623**
ITR				1.000	-0.336	-0.471**	0.420**	0.420**	0.599**	0.604**
LP_{50}					1.000	0.530**	-0.217	-0.231	-0.273	-0.322
LPSM						1.000	-0.486**	-0.457**	-0.476**	-0.582**
RS							1.000	0.609**	0.584**	0.713**
FRS								1.000	0.664**	0.691**
AUDPC									1.000	0.791**
AIR										1.000

[1]FKN = Number of flecks per square centimeter of leaflet area
UDN = Number of uredinia per square centimeter of leaflet area
IT = Infection type
ITR = Range of infection types
LP_{50} = Latent period (time after inoculation until sporulation on 50 % of uredinia)
LPSM = Standardized rust severity measure
RS = Mean rust severity
FRS = Final rust severity
AUDPC= Area under the disease progress curve
AIR = Apparent infection rate

[2]Asterisks (* and **) indicate statistical significance at p-value <0.05 and p-value<0.01, respectively.

Appendix AA

KENDALL'S TAU-B COEFFICIENTS OF CONCORDANCE FOR THE COMPONENTS OF RATE-REDUCING RESISTANCE FOR FIELD-GROWN FABA BEANS INOCULATED WITH RUST RACE 4 IN 1982.

	Components[1]									
Components	FKN	UDN	IT	ITR	LP_{50}	LPSM	RS	FRS	AUDPC	AIR
FKN	1.000	0.022	0.138	0.188	-0.068	-0.115	0.210	0.232	0.145	0.255
UDN		1.000	0.087	0.210	-0.267	-0.462**[2]	0.391**	0.471**	0.457**	0.387**
IT			1.000	0.543**	0.299*	0.028	0.275	0.312*	0.181	0.263
ITR				1.000	0.307*	-0.059	0.225	0.333*	0.203	0.190
LP_{50}					1.000	0.490**	-0.227	-0.139	-0.235	-0.284
LPSM						1.000	-0.431**	-0.352*	-0.360*	-0.433**
RS							1.000	0.659**	0.688**	0.672**
FRS								1.000	0.739**	0.766**
AUDPC									1.000	0.693**
AIR										1.000

[1]FKN = Number of flecks per square centimeter of leaflet area
UDN = Number of uredinia per square centimeter of leaflet area
IT = Infection type
ITR = Range of infection types
LP_{50} = Latent period (time after inoculation until sporulation on 50 % of uredinia)
LPSM = Standardized rust severity measure
RS = Mean rust severity
FRS = Final rust severity
AUDPC= Area under the disease progress curve
AIR = Apparent infection rate

[2]Asterisks (* and **) indicate statistical significance at p-value <0.05 and p-value<0.01, respectively.

Appendix AB

KENDALL'S TAU-B COEFFICIENTS OF CONCORDANCE FOR THE COMPONENTS OF RATE-REDUCING RESISTANCE FOR FIELD-GROWN FABA BEANS INOCULATED WITH RUST RACE 3 IN 1983.

	Components[1]									
Components	FKN	UDN	IT	ITR	LP_{50}	LPSM	RS	FRS	AUDPC	AIR
FKN	1.000	0.514**[2]	0.123	0.246	-0.362*	-0.377**	0.210	0.225	0.297*	0.281
UDN		1.000	0.464**	0.543**	-0.530**	-0.457**	0.319*	0.348*	0.377**	0.332
IT			1.000	0.775**	-0.230	-0.109	0.014	0.304*	0.159	0.018
ITR				1.000	-0.369*	-0.261	0.080	0.326*	0.283	0.091
LP_{50}					1.000	0.611**	-0.472**	-0.332*	-0.479**	-0.382**
LPSM						1.000	-0.225	-0.181	-0.268	-0.353
RS							1.000	0.435**	0.652**	0.550**
FRS								1.000	0.609**	0.317
AUDPC									1.000	0.470**
AIR										1.000

[1]FKN = Number of flecks per square centimeter of leaflet area
UDN = Number of uredinia per square centimeter of leaflet area
IT = Infection type
ITR = Range of infection types
LP_{50} = Latent period (time after inoculation until sporulation on 50 % of uredinia)
LPSM = Standardized rust severity measure
RS = Mean rust severity
FRS = Final rust severity
AUDPC= Area under the disease progress curve
AIR = Apparent infection rate

[2]Asterisks (* and **) indicate statistical significance at p-value <0.05 and p-value<0.01, respectively.

Appendix AC

KENDALL'S TAU-B COEFFICIENTS OF CONCORDANCE FOR THE COMPONENTS OF RATE-REDUCING RESISTANCE FOR FIELD-GROWN FABA BEANS INOCULATED WITH RUST RACE 4 IN 1983.

	Components[1]									
Components	FKN	UDN	IT	ITR	LP_{50}	LPSM	RS	FRS	AUDPC	AIR
FKN	1.000	0.667**[2]	0.439**	0.442**	-0.627**	-0.638**	0.420**	0.457**	0.529**	0.388**
UDN		1.000	0.410**	0.529**	-0.635**	-0.725**	0.507**	0.442**	0.514**	0.424**
IT			1.000	0.722**	-0.551**	-0.396**	0.642**	0.563**	0.621**	0.547**
ITR				1.000	-0.502**	-0.428**	0.746**	0.667**	0.710**	0.623**
LP_{50}					1.000	0.782**	-0.561**	-0.554**	-0.642**	-0.493**
LPSM						1.000	-0.435**	-0.457**	-0.558**	-0.352
RS							1.000	0.674**	0.717**	0.813**
FRS								1.000	0.841**	0.674**
AUDPC									1.000	0.674**
AIR										1.000

[1]FKN = Number of flecks per square centimeter of leaflet area
UDN = Number of uredinia per square centimeter of leaflet area
IT = Infection type
ITR = Range of infection types
LP_{50} = Latent period (time after inoculation until sporulation on 50 % of uredinia)
LPSM = Standardized rust severity measure
RS = Mean rust severity
FRS = Final rust severity
AUDPC= Area under the disease progress curve
AIR = Apparent infection rate

[2]Asterisks (* and **) indicate statistical significance at p-value <0.05 and p-value<0.01, respectively.

Appendix AD

ANALYSIS OF VARIANCE IN THE NUMBER OF FLECKS PER SQUARE CENTIMETER OF LEAFLET AREA FOR TEN FABA BEAN POPULATIONS GROWN UNDER CONTROLLED ENVIRONMENT CONDITIONS.

Source	D.F.	Sum of Squares	Mean Square	F value
Model	59	350.81	5.95	9.74*
Population	9	13.48		2.46*
Race	1	171.56		281.12*
Population X race	9	11.70		2.13
Stage	2	8.67		7.11*
Population X stage	18	53.16		4.84*
Race X stage	2	23.04		18.88*
Population X race X stage	18	69.20		6.30*
Error	1343	819.58	0.61	
Total	1402	1170.39		

R^2= 0.30
C.V.=116.00%

* Significant at p-value<0.01.

Appendix AE

ANALYSIS OF VARIANCE IN THE NUMBER OF UREDINIA PER SQUARE CENTIMETER OF LEAFLET AREA FOR TEN FABA BEAN POPULATIONS GROWN UNDER CONTROLLED ENVIRONMENT CONDITIONS.

Source	D.F.	Sum of Squares	Mean Square	F value
Model	59	2333.86	39.56	24.31
Population	9	1612.64		110.12*
Race	1	84.58		51.98*
Population X race	9	52.16		3.56*
Stage	2	108.13		33.23*
Population X stage	18	158.02		5.40*
Race X stage	2	150.63		46.29*
Population X race X stage	18	167.70		5.73*
Error	1343	2185.30	1.63	
Total	1402	4519.17		

R^2= 0.52
C.V.=70.72%

* Significant at p-value<0.01.

Appendix AF

ANALYSIS OF VARIANCE IN INFECTION TYPE FOR TEN FABA BEAN POPULATIONS GROWN UNDER CONTROLLED ENVIRONMENT CONDITIONS.

Source	D.F.	Sum of Squares	Mean Square	F value
Model	59	164.88	2.79	6.12*
Population	9	29.65		7.21*
Race	1	12.46		27.28*
Stage	2	14.82		16.22*
Population X stage	18	43.36		5.27*
Race X stage	2	14.32		15.67*
Population X race X stage	18	50.27		4.08*
Error	840	383.78	0.46	
Total	899	548.66		
			R^2= 0.30	
			C.V.=29.91%	

* Significant at p-value<0.01.

Appendix AG

ANALYSIS OF VARIANCE IN RANGE OF INFECTION TYPE FOR TEN FABA BEAN POPULATIONS GROWN UNDER CONTROLLED ENVIRONMENT CONDITIONS.

Source	D.F.	Sum of Squares	Mean Square	F value
Model	59	3396.32	57.56	12.16*
Population	9	507.15		11.91*
Race	1	1046.50		221.12*
Stage	2	273.61		28.91*
Population X stage	18	334.01		3.92*
Race X stage	2	528.37		55.82*
Population X race X stage	27	706.67		5.53*
Error	2726	12901.508	4.736	
Total	2785	16297.82		
			R^2= 0.21	
			C.V.=65.16%	

* Significant at p-value<0.01.

Appendix AH

ANALYSIS OF VARIANCE IN LATENT PERIOD FOR TEN FABA BEAN POPULATIONS GROWN UNDER CONTROLLED ENVIRONMENT CONDITIONS.

Source	D.F.	Sum of Squares	Mean Square	F value
Model	59	2364.24	40.07	85.37*
Population	9	437.40		103.54*
Race	1	75.40		160.64*
Population X race	9	73.61		17.43*
Stage	2	754.98		804.25*
Population X stage	18	442.47		52.37*
Race X stage	2	449.92		479.28*
Population X race X stage	18	130.44		15.44*
Error	2820	1323.62	0.47	
Total	2879	3687.86		

R^2= 0.64
C.V.=34.37%

* Significant at p-value<0.01.

Appendix AI

ANALYSIS OF VARIANCE IN LP_{50} FOR TEN FABA BEAN POPULATIONS GROWN UNDER CONTROLLED ENVIRONMENT CONDITIONS.

Source	D.F.	Sum of Squares	Mean Square	F value
Model	59	1465.72	24.84	37.18*
Population	9	298.16		49.58*
Race	1	34.13		51.07*
Population X race	9	85.02		14.14
Stage	2	198.71		148.69*
Population X stage	18	386.37		32.12*
Race X stage	2	347.28		259.86*
Population X race X stage	18	116.06		9.65*
Error	2290	1530.19	0.67	
Total	2349	2995.91		

R^2= 0.49
C.V.=33.39%

* Significant at p-value<0.01.

Appendix AJ

ANALYSIS OF VARIANCE IN LPSM FOR TEN FABA BEAN POPULATIONS GROWN UNDER CONTROLLED ENVIRONMENT CONDITIONS.

Source	D.F.	Sum of Squares	Mean Square	F value
Model	59	1493.80	25.32	15.72*
Population	9	281.39		19.41*
Race	1	40.39		25.08*
Population X race	9	100.54		6.94*
Stage	2	186.35		57.85*
Population X stage	18	394.80		13.62*
Race X stage	2	360.49		111.91*
Population X race X stage	18	129.84		4.48*
Error	2290	3688.27	1.61	
Total	2349	5182.07		

R^2= 0.29
C.V.=52.03%

* Significant at p-value<0.01.