EPIDEMIOLOGY AND MANAGEMENT OF BEAN RUST IN ETHIOPIA

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CONTENTS

Epidemiology and Management of Bean Rust in Ethiopia

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A survey of cropping practices and foliar diseases of common beans in Ethiopia

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Field surveys were conducted in three major bean growing areas of Ethiopia. Data collected included cropping systems and severities of bean diseases. We used correspondence analysis to characterize differences in disease severity between regions and seasons, and to determine associations between geographic areas and cropping systems, areas and diseases, and cropping systems and diseases. Chi-square analyses suggested a high probability of high plant density, high weediness, high bacterial blight and high anthracnose being associated with area 1 (Rift Valley). In area 2 (Sidamo) there was a high probability of high rust intensity, low plant density and low weediness. Area 3 (Keffa) was characterized by a high probability of angular and floury leaf spots. In area 1 (Rift Valley), low rust intensity was closely associated with year 1 (1990) and high rust intensity with year 4 (1993). Anthracnose and bacterial blight showed no clear association with years. Some linkages between cropping systems and disease severities were indicated. In areas 1 and 2, there was a high probability of low rust at early sowing and a high probability of bacterial blight at high weediness and high plant density situations. The probability of observing high rust severity at high weediness was low. This study suggests that specific needs of areas, with their own production situations, must be considered in the process of developing strategies for the improvement of production and crop protection in beans.

Keywords: correspondence analysis; rust; anthracnose; bacterial blight; angular leaf spot; floury leaf spot; sowing date; plant density; weediness

In Ethiopia, common bean (*Phaseolus vulgaris* L.) is grown in rotation with cereals (Imru, 1985). They are grown for the export market and as a food legume in parts of the country (IAR, 1991). Common beans are grown from sea level to about 2800 m (Schwartz and Galvez, 1980). Under Ethiopian conditions beans are well adapted to altitude ranges between 1200 m and 2000 m, and to rainfall conditions (Ohlander, 1980). Common bean is grown in most parts of Ethiopia, but production is concentrated mainly in the east (Hareghe highlands), the south and the south west (Sidamo), the west (Keffa and Wollega) and in the Rift Valley. This geographical range is associated with a wide range of bean cultivars and diseases (Bos, 1974; Habtu, 1987; O'Bannon, 1975; Westphal, 1974).

Common bean production was about 100,000 ha in 1990 (CSA, 1992a, b). Farm surveys conducted in the major bean production regions suggested an area at least twice the official figures (IAR, 1991). The national average for bean yield is low, c. 600–700 kg ha^{-1} and diseases are a major factor in reducing yields. Of the more than 80 fungal, bacterial, viral, and nematode diseases reported to occur on beans worldwide (Schwartz and Galvez, 1980; Allen, 1983), few were recorded in Ethiopia (Stewart and Dagnatchew, 1967). These older records gave little attention to geographic distribution and economic significance. Recently, an attempt was made to determine the occurrence and importance of diseases of beans at various research and/or experiment stations (Habtu, 1987). Disease epidemiology under farmers' conditions is nearly unknown.

Survey data can help to describe the geographical distribution of diseases, their relative importance and their epidemiology (James, 1969; King, 1972; Savary, 1987; Zadoks, 1961, 1966). Hence, a survey of bean diseases was initiated to investigate the intensity of bean diseases, their relative importance in several geographical areas, and their association with bean production practices (sowing data, growth condition, plant density, weediness, etc.) in Ethiopia.

Materials and methods

Sample regions

The surveys were conducted in three of the four major bean-growing areas of Ethiopia: the central Rift-valley (East and South Shoa), south and southwest (Sidamo), and west (Keffa). Areas visited and the survey route is

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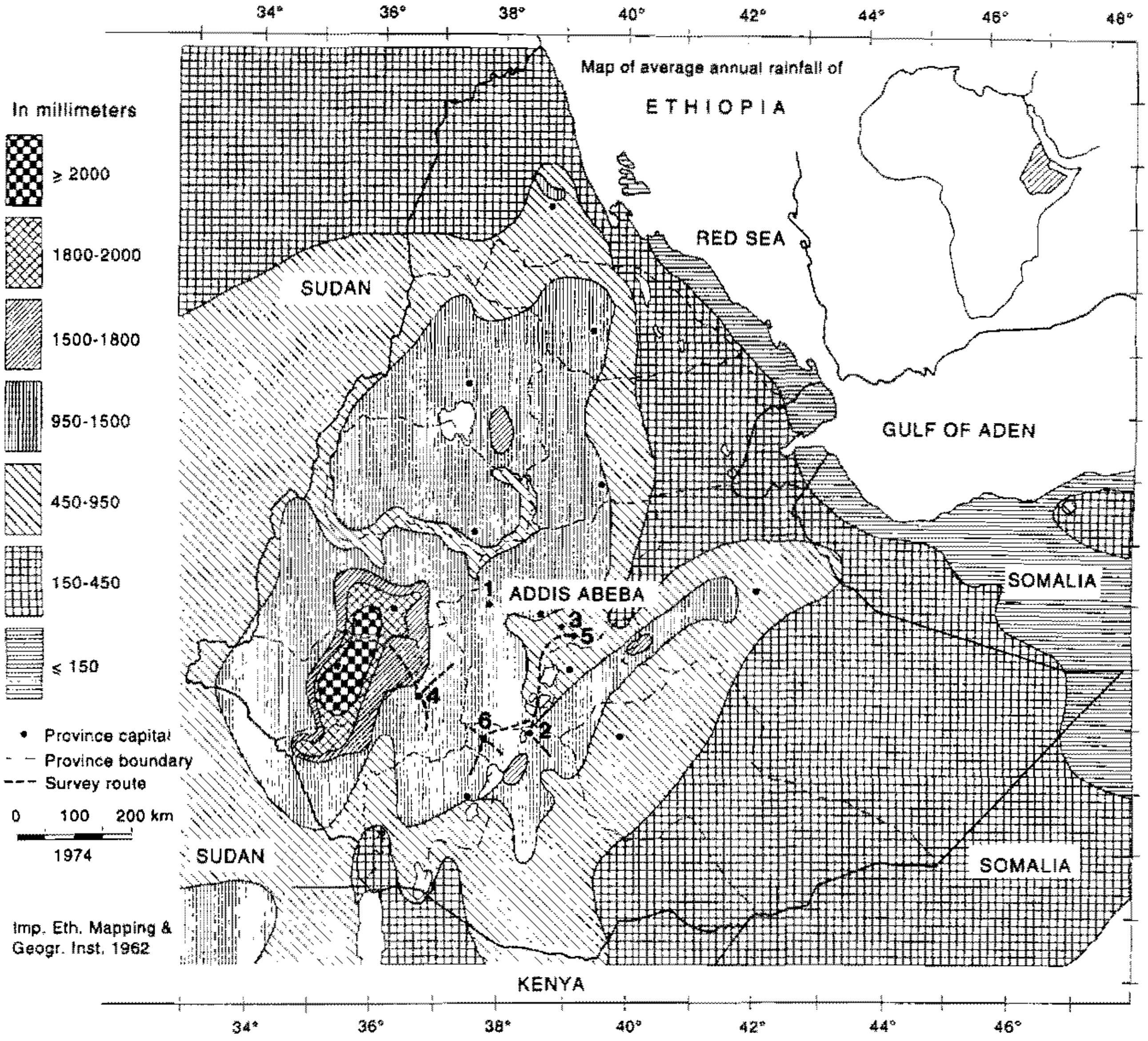

Figure 1. Map of Ethiopia showing average annual rainfall, representative locations and bean survey route. From Westphal (1974)

shown in *Figure 1*. Area 1, the central Rift-valley (AR1), represents the hot, dry and erratic rainfall climate where normally one bean crop is grown each year. Area 2, the south and south west (AR2), represents a major bean growing area where beans are planted at least twice a year either as an intercrop or a monocrop. Area 3, the west (AR3), is characterized by production of beans in intercropping systems with either maize or sorghum. Here beans are normally grown once in a year.

In the central Rift Valley, the survey was conducted for four consecutive years (1990–1993) and information was gathered from 129 fields. In Sidamo, the survey was conducted in 1990 and 1993 and data were collected from 80 fields. In Keffa, data were collected in 1990, 1992 and 1993 from 53 fields. In total, 262 fields were visited.

Sample fields

Fields were ordinarily selected at intervals of 5–10 km along the main roads. When necessary, the sample size (the number of observed fields per region) and the distance between sample units (the arbitrarily selected single plants) per field were adjusted to suit crop distribution and field size, respectively. All sample fields belonged to small, private farmers. Each field was visited once.

Sample units

Of each sample field, a general impression of the field was obtained as to size, shape and crop condition. Plants sampled were systematically selected by making a specified number of equally spaced paces following an inverted 'V' pattern. Having made the pre-set number of paces (according to the size of the field), the nearest plant to the right foot was sampled. For each field, 10 plants were sampled for disease assessment. A subsample of three trifoliolate leaves per plant was selected from the upper, middle and lower canopy layers of the main stem, yielding a total of 30 leaves per field. Means of canopy layers were determined per plant and then averaged per field for data analysis.

Crop and disease assessment

Each field was represented by a set of variables (*Table 1*) indicating field characteristics, crop developmental stage and disease severity for each of the following diseases, angular leaf spot (*Phaeoisariopsis griseola* (Sacc.) Ferraris), bean anthracnose (*Colletotrichum lindemuthianum* (Sacc. and Magn.) Bri. and Cav.), bean rust (*Uromyces appendiculatus* (Pers.) Ung. (*U. phaseoli* (Pers.) Wint.), common bacterial blight (*Xanthomonas campestris* pv. *phaseoli* (Erw. Smith) Dowson) and floury leaf spot (*Mycovellosiella phaseoli* (Drummond) Deighton). Disease severity was defined as the affected leaf area, including the lesion and associated chlorosis (i.e. the non-green area) as a percentage of total leaf area. Most data were collected around the pod filling stage (Fernandez *et al.*, 1986) at a time when diseases were conspicuous at all canopy layers.

Table 1. Categorization of variables used in correspondence analyses for a survey of cropping practices and bean diseases in three geographical regions of Ethiopia (I, central; II, south; and III, west)

Variable	Classes (boundaries)	Number of fields[1] I	II	III
Area (AR)	AR1 (central)	129	129	85
	AR2 (south)	80	80	80
	AR3 (west)	53	37	37
Total		262	246	202
Plant density (PD)	PD1 (1–20)[2]			86
	PD2 (21–40)			38
	PD3 (41 and above)			78
Total				202
Sowing date (SD)	SD1 (early)		48	
	SD2 (optimum)		130	
	SD3 (late)		68	
Total			246	
Weediness (WD)	WD1 (light)		103	101
	WD2 (moderate)		105	78
	WD3 (high)		38	23
Total			246	202
Diseases				
Angular (AL) leaf spot	AL0 (absent)	196		
	AL1 (present)	66		
Total		262		
Bacterial blight (BB)	BB1 (0–2)[3]	124	112	106
	BB2 (2–5)	50	46	37
	BB3 (5 and above)	88	88	59
Total		262	246	202
Bean (BA) anthracnose	BA1 (0–2)	140	129	105
	BA2 (2–5)	66	61	53
	BA3 (5 and above)	56	56	44
Total		262	246	202
Bean rust (BR)	BR1 (0–2)	106	95	71
	BR2 (2–5)	97	92	80
	BR3 (5 and above)	59	59	51
Total		262	246	202
Floury (FL) leaf spot	FL0 (absent)	224		
	FL1 (present)	48		
Total		262		

[1] Three analyses were performed due to imblance of sample fields. I, all sample fields were included in the analysis. II, data missing for sowing date and weediness in area 3 (AR3). III, data missing for plant density in area 1 (AR1)

[2] PD, number of plants m^{-2}. SD2, optimum sowing date as perceived by farmers, usually late June to early July for central, mid to late July for south and west, anything before is considered early and after late; WD1, weeded at least once and absence of visible weeds. WD2, weeds present but not in a strong competition with beans; WD3, bean field not weeded at all and weed infestation greater than 10 m^{-2}

[3] Disease severity (proportion of leaf area infected in %)

Data categorization

Categorization (here the allocation of severities, recorded on a continuous scale from 0 to 100, to a few distinct classes) is the transformation of quantitative data into coded, qualitative data. Class boundaries were chosen so that classes contained approximately equal totals (*Table 1*), 0–2%, 2–5% and >5% severity. Thus, bean rust severities were coded as BR1, BR2 and BR3. Three sowing dates (SD1–SD3), three weed intensities (WD1–WD3), three plant densities (PD1–PD3), three areas (AR1–AR3) and 4 years (Y1–Y4) were considered.

Contingency tables

All variables were encoded to build contingency tables (*Table 2*), to represent the bivariate distribution of fields according to two classifications (e.g. sowing date and bean rust severity). An entry in a cell of a contingency table represents the number of fields falling into that cell. The independence of the frequency distributions of two variables was tested by chi-square analysis (χ^2). Several contingency tables were combined into a single matrix, e.g. with disease severities as columns and other variables as rows.

Correspondence analysis

Because of the non-normal distribution of most variables and their low precision, a non-parametric method to analyse categorized information was used (Hill, 1974; Nutter *et al.*, 1991; Savary and Zadoks, 1992; Savary *et al.*, 1993). Correspondence analysis is a multivariate method that allows the pictorial representation of contingency tables in order to identify associations between two groups of variables. These two groups are the columns and the rows of *Table 2*. Disease severities in columns are variables to be explained while variables in the rows are explanatory variables. The variables were treated as either active (directly used in the analyses) or additional (projected in the graph but not used in the analyses).

Correspondence analysis was conducted for each bean growing area and across all three geographical areas to characterize associations between cropping systems and disease severities. The method generated graphs which plotted categorical variables to examine their relationships. The resulting graphs use a χ^2 distance to represent relationships among categorized variables (Benzécri, 1973; Greenacre, 1984; Savary *et al.*, 1993). The interpretation of the graphs is based on the strength of the association accounted for by the axes, the classes that contribute most to each of them, the proximity of points representing classes, and the

Table 2. Contingency tables for the analysis of data from four years (1990–1993) from a survey of three bean growing areas (central, south and west Ethiopia)

Area by disease

	BR1	BR2	BR3'	BA1	BA2	BA3	BB1	BB2	BB3	AL0	AL1	FL0	FL1
AR1	55	42	32	59	27	43	11	35	83	129	0	129	0
AR2	13	42	25	53	15	12	70	8	2	61	19	80	0
AR3	38	13	2	28	24	1	42	7	3	6	47	5	48

Year by disease'

	BR1	BR2	BR3	BA1	BA2	BA3	BB1	BB2	BB3
Y1	24	13	7	23	9	12	6	9	29
Y2	14	9	7	10	6	14	2	6	22
Y3	12	9	4	9	6	10	1	8	16
Y4	5	11	14	17	6	7	2	12	16

Cropping system by disease

	BR1	BR2	BR3	BA1	BA2	BA3	BB1	BB2	BB3
SD1	28	13	7	23	22	14	23	7	29
SD2	40	51	39	61	29	31	59	23	39
SD3	27	28	13	45	10	11	30	16	20

	BR1	BR2	BR3	BA1	BA2	BA3	BB1	BB2	BB3
WD1	36	42	25	66	30	19	81	19	15
WD2	37	38	30	47	24	23	25	19	50
WD3	22	12	4	16	7	14	6	8	23

	BR1	BR2	BR3	BA1	BA2	BA3	BB1	BB2	BB3
PD1	31	32	23	39	18	6	60	3	0
PD2	10	20	8	33	17	8	37	12	9
PD3	30	28	20	33	18	30	9	22	50

Area by cropping system

	PD1	PD2	PD3	WD1	WD2	WD3
AR1	0	8	77	22	46	17
AR2	52	28	0	57	19	4
AR3	34	2	1	22	13	2

For description of variables refer Table 1

Data from area 1 only

Table 3. Geographical distribution and disease severity (% measured as proportion of leaf area infected) of bean diseases in Ethiopia (1990–1993)

		Disease severity (%)					
Area	Year	BR	BA	BB	AL	FL	DT
Central	1990	2.3	3.4	6.1	0.0	0.0	0.9
	1991	3.0	6.6	8.0	0.0	0.0	3.1
	1992	2.2	4.3	6.4	0.0	0.0	3.5
	1993	5.1	3.9	5.4	0.0	0.0	2.0
	Mean	3.1	4.3	6.5	0.0	0.0	2.4
South	1990	5.8	0.9	0.8	1.3	0.0	1.5
	1993	3.1	2.2	1.0	0.1	0.0	2.2
	Mean	4.4	1.6	0.9	0.7	0.0	1.9
West	1990	1.3	2.2	0.1	2.5	1.4	–
	1992	2.0	2.4	3.3	4.6	3.2	0.5
	1993	2.9	3.7	3.1	10.3	8.2	0.0
	Mean	2.1	2.7	2.2	5.8	4.3	0.2

BR, bean rust; BA, anthracnose, BB common bacterial blight, AL, angular leaf spot, FL, floury leaf spot, DT, dead tissue

paths representing a succession of classes. Similarities in pattern or direction of paths indicate correspondences that can be tested further using the appropriate χ^2 tests (Savary *et al.*, 1993). Analyses of data were performed with the NDMS computer programme (Savary *et al.*, 1988).

Results

A summary of the disease survey data over a 4 year period (*Table 3*) indicates variation in disease severity with years and geographical areas. Bean rust (BR), anthracnose (BA) and bacterial blight (BB) were more widely distributed than angular leaf spot (AL) or floury leaf spot (FL) which were not found in some regions. In farmers' fields, disease severity was general and mean severity did not exceed 7%.

Analysis of the data with correspondence analysis suggests associations of years, areas and cropping practices with bean diseases. The axes generated by correspondence analyses accounted for >90% of the

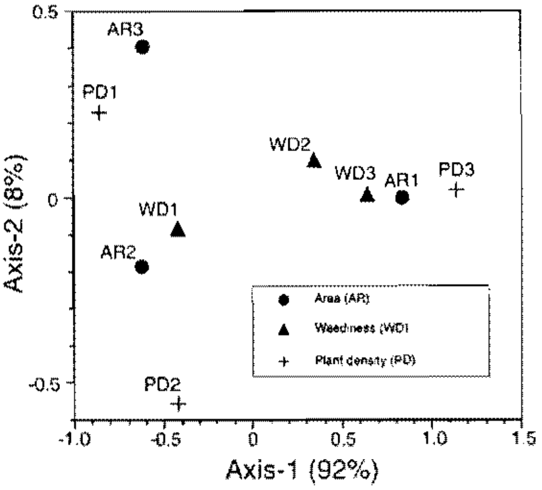

Figure 2. Ordination of six variables by correspondence analysis. The variables, all active, are area (AR1..AR3), plant density (PD1..PD3), and weediness (WD1..WD3), n = 202. The graph is largely dominated by axis 1 (horizontal, λ = 0.92). Axis 2 (vertical, λ = 0.08) nicely separates areas but has little explanatory value

total inertia (technical term of correspondence analysis approximately equivalent to variance). These axes were used to draw graphs and interpret results.

Area and cultural practices

Figure 2 is produced with area, plant density and weediness as active variables. Most inertia is explained by axis 1, roughly representing increases in plant density and weediness. The graph shows clear associations between area 1 (Rift Valley), high plant density and medium to high weediness. Area 2 (Sidamo) is associated with low weediness and low to medium plant densities, area 3 (Keffa) with low plant densities.

These associations are confirmed by χ^2 tests on two-dimensional contingency tables. High plant density has a high probability in area 1, medium plant density in area 2, and low plant density in areas 2 and 3, ($n = 202$, $\chi^2 = 188$, df = 4, $P << 0.001$). Low weediness has a low probability in area 1 (Rift Valley) and a high probability in area 2 (Sidamo). Area 1 has a high probability of medium and high weediness ($n = 246$, $\chi^2 = 37$, df = 4, $P << 0.001$). Plant density and weediness were also strongly associated ($n = 202$, $\chi^2 = 34$, df = 4, $P << 0.001$).

Year effects

The correspondence analysis of year effects on the major diseases, rust, anthracnose and bacterial blight is shown in *Figure 3*, in which all variables mentioned are active. The two axes represent 94% of total inertia. The horizontal axis is largely determined by rust and bacterial blight. The paths of rust and anthracnose cross at nearly right angles, indicating independence. The path from medium to high bacterial blight runs opposite to that of rust. Year 4 (1993) is associated with high and year 1 (1990) with low bean rust ($n = 129$, $\chi^2 = 15$, df = 6, $P = 0.02$). Years 2 and 3 (1991, 1992) were intermediate between years 1 and 4. No significant associations were found between years and anthracnose, though *Figure 3* seems to suggest an association between years 2 and 3 and high anthracnose.

Cultural practices and diseases

In *Figure 4*, the first axis largely represents the trajectories of bacterial blight, weediness and anthracnose. The second axis largely represents the lower part of the plant density trajectory and

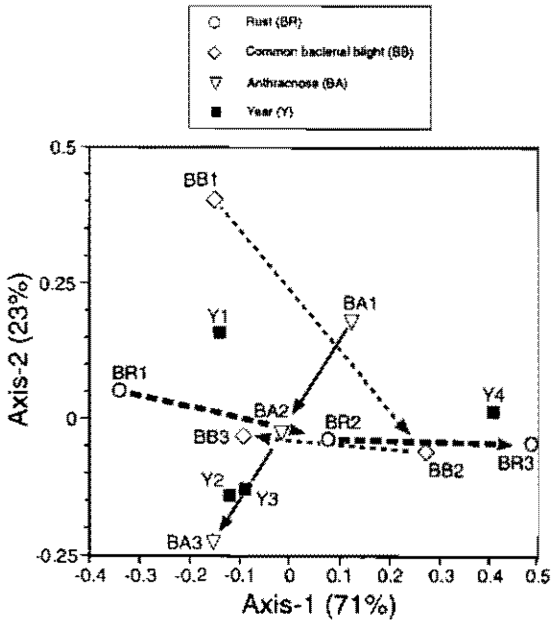

Figure 3. Ordination of four variables by correspondence analysis. The active variables are years (Y1..Y4), and three major bean diseases, rust (BR1..BR3), anthracnose (BA1..BA3) and bacterial blight (BB1..BB3). Total number of fields, n = 129

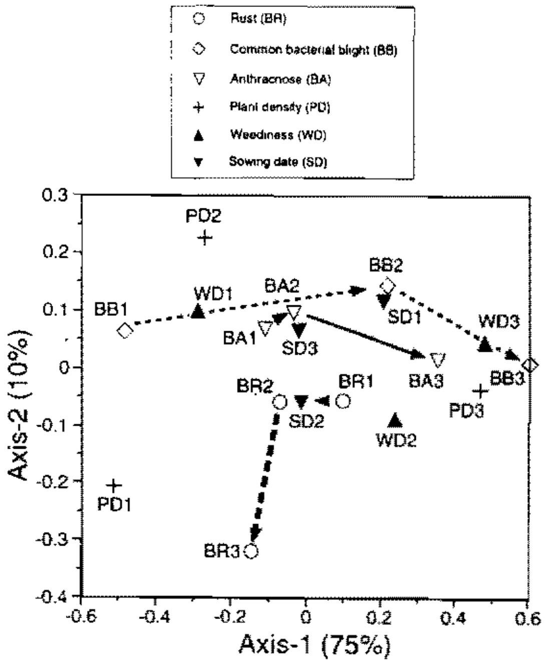

Figure 4. Ordination of six variables by correspondence analysis. The three major diseases (rust, anthracnose and bacterial blight) are related to three variables representing cultural practices (sowing date, weediness, plant density). All six variables are active. Total number of fields, n = 202

the upper part of the rust trajectory, which run in opposite directions. The third axis ($\lambda = 0.01$) is largely dominated by the sowing date trajectory, paralleled by the lower parts of the rust and anthracnose trajectories, the latter running in opposite directions.

In *Figure 4*, the rust and plant density trajectories run nearly parallel. Early sowing is associated with high values of weediness, bacterial blight and anthracnose. Low plant density (PD1) may be associated with high severities of rust. Early sowing is associated with low rust severities and intermediate sowing dates with intermediated to high rust values and low weediness (*Figure 4*). A low plant density is strongly associated with low weediness and low bacterial blight. High weediness and high plant densities are associated with high severities of bacterial blight and anthracnose.

Sowing date had a clear effect on disease severity. Early sowing was associated with low bean rust whereas normal sowing date was associated with high rust severity (*Figure 4*). Normal and late sowing were associated with intermediate and fewer high bean rust intensities ($n = 246$, $\chi^2 = 13$, df $= 4$, $P = 0.011$). Early sowing was associated to some degree with intermediate anthracnose levels. Late sowing showed the inverse pattern. Normal sowing was rather neutral with some excess of high anthracnose levels ($n = 246$, $\chi^2 = 13$, df $= 4$, $P = 0.11$). Bacterial blight showed no significant associations with sowing date.

High weediness was associated with a higher probability of low bean rust levels whereas low and medium weediness were associated with medium and high rust levels, respectively ($n = 246$, $\chi^2 = 9$, df $= 4$, $P = 0.07$). Low weediness was highly associated with low bacterial blight, whereas medium and high weediness were strongly associated with high bacterial blight ($n = 246$, $\chi^2 = 62$, df $= 4$, $P << 0.001$). Intermediate bacterial blight was neutral as to weediness. The association between weediness and anthracnose was not significant.

High plant densities were associated with high levels of anthracnose, low plant density with low levels of anthracnose ($n = 202$, $\chi^2 = 19$, df $= 4$, $P << 0.001$). Similarly, high plant density was strongly associated with high bacterial blight ($n = 202$, $\chi^2 = 111$, df $= 4$, $P << 0.001$). No significant association was found between plant density and bean rust severities, despite strong graphical association of high levels of rust with low plant densities.

Geographical areas and diseases

The two axes generated by correspondence analysis accounted for nearly 100% of total inertia. Area 1 (Rift Valley) was closely associated with high and intermediate levels of bacterial blight and a high level of anthracnose (*Figure 5*). Area 2 (Sidamo) was closely associated with a low level of anthracnose and bacterial blight and intermediate to high level of rust. Area 3 (Keffa) was associated with a high presence of angular and floury leaf spot, low level of rust and intermediate level of anthracnose.

Whereas the three bean rust severity categories were rather evenly distributed over area 1 (Rift Valley), low bean rust severity had a very high probability in area 3 (Keffa) and a very low one in area 2 (Sidamo). Medium to high bean rust severities had a high probability in area 2 (Sidamo) and a low one in area 3 (Keffa). The linkages were highly significant ($n = 262$, $\chi^2 = 44$, df $= 4$, $P << 0.001$).

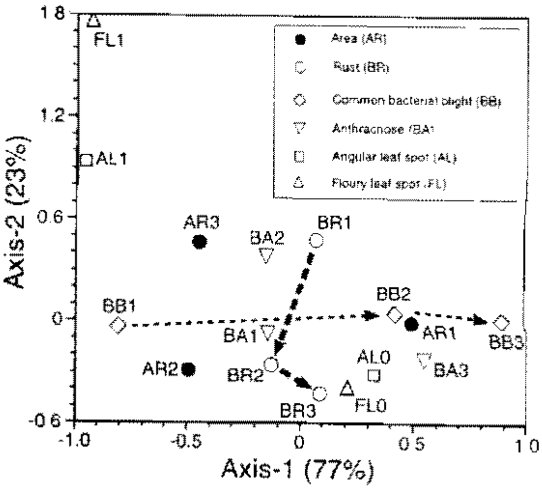

Figure 5. Ordination of six variables by correspondence analysis. The three areas (Rift Valley, Sidamo and Keffa) are related to five bean diseases (rust, anthracnose, bacterial blight, angular leaf spot and floury leaf spot). Areas, rust, anthracnose and bacterial blight were the active variables whereas angular and floury leaf spot were *additional variables*. Total number of fields, $n = 262$

High levels of anthracnose were over-represented in area 1 (Rift Valley), low anthracnose severities in area 2 (Sidamo), and intermediate severities in area 3 (Keffa). The association was significant ($n = 262$, $\chi^2 = 34$, df $= 4$, $P << 0.001$).

Low levels of bacterial blight were strongly under-represented in area 1 whereas medium and high values were under-represented in areas 2 and 3. High severities of bacterial blight were strongly over-represented in area 1 and under-represented in area 2 ($n = 262$, $\chi^2 = 161$, df $= 4$, $P << 0.001$).

Angular leaf spot showed a very high probability of low values in area 1 (Rift Valley) and of high values in area 3 (Keffa), whereas area 2 (Sidamo) was about average ($n = 262$, $\chi^2 = 157$, df $= 2$, $P << 0.001$).

High levels of floury leaf spot were strongly over-represented in area 3 (Keffa) and under-represented in area 2 (Sidamo) and especially in area 1 (Rift Valley) ($n = 262$, $\chi^2 = 232$, df $= 2$, $P = << 0.001$).

Discussion

Information on the geographical distribution of plant diseases is useful to understand the occurrence of disease in a new area and to set priorities for disease management. The understanding can be increased (Weltzien, 1972) by distinguishing degrees of intensity of the disease within the area of its occurrence, distinguishing subareas with high severity and marginal occurrence, and as an aid to explaining the associations between cropping systems and disease intensities. Habtu (1987) considered the presence or absence of diseases within a given area of Ethiopia, describing disease severities at experiment stations. The present study revealed the wide prevalence of some bean diseases, the limited occurrence of others and the association of disease intensities with cropping systems.

Cropping practices

The prevalence and severity of bean diseases vary with cropping practices. A general trend concerning the association of cropping practices and disease severities was found using correspondence analysis. In areas 1 and 2, low rust was associated with both early sowing and high weediness while high levels of rust were associated with intermediate sowing dates. The low severity of rust at early sowing dates may be due to several factors. First, early sowing dates might have led to the escape of crops from rust inoculum arriving late. Second, early in the cropping season, temperatures near the canopy may be still high and rainfull low resulting in long periods with little leaf wetness. Leaf wetness is an important factor for rust infection (Harter *et al.*, 1935; Imhoff *et al.*, 1981).

High severities of anthracnose and bacterial blight were associated with intermediate sowing dates. Early sowing and moderate weed density both favoured anthracnose and bacterial blight. In area 2, anthracnose and bacterial blight were nearly negligible during the survey period. Here the bean production practice is characterized by light weeding, low plant density, good crop rotation, and possibly by the use of healthy seeds. The difference in weeding and plant density between areas 1 and 2 (*Figure 2*) was obvious.

Area and year

The roles of the environment and of human action in the development of plant diseases are depicted by the disease tetrahedron (Zadoks and Schein, 1979). The prevalence and severity of bean diseases in Ethiopia varied considerably with the environment, both by area and year. Within an area, disease severities were influenced by cropping practices. Beans produced under cool conditions at intermediate to high altitudes are often affected by rust, anthracnose and angular leaf spot, under hot and dry conditions by bean common mosaic virus, common bacterial blight and root rots, and under hot and moist climates by web blight (Allen, 1983).

The central Rift Valley, area 1, is characterized by high temperature and high variation in rainfall amount and intensity. Under such conditions, the common bean diseases are bean common mosaic virus and common bacterial blight. In our study, common bacterial blight was most severe, but rust and anthracnose were also observed. In area 1, angular and floury leaf spots were practically absent. The south, area 2, is cooler than the central Rift Valley, and has dependable rains. Here, rust was severe and, surprisingly, anthracnose was insignificant. In the south, beans were carefully weeded, plant densities were rather low, perhaps adversely influencing the microenvironment required for the development of anthracnose. In the west, area 3, the situation was rather clear. Many diseases were present but the important ones were angular and floury leaf spots. The west is characterized by a humid climate, high temperature and high rainfall.

Though such is the general trend, disease severity was affected by seasonal variation, primarily rainfall and temperature (Savary, 1987). In area 1, when temperatures were high and moisture was limiting, common bacterial blight became dominant (*Table 4*, year 3). When there was a dependable rainfall resulting in a cooler temperature (year 2) anthracnose became the principal disease. Anthracnose became even more important when farmers used infected seed from their last harvest. A high anthracnose season, as in 1991, resulted in crop damage. In areas 2 and 3, the association of disease intensities with seasons is not very clear possibly due to the low variation of rainfall and temperatures between seasons in these two areas. It is difficult to find rainfall and temperature data to accurately describe these areas. *Table 4* provides a general picture where data is provided for Nazareth (area 1), Awassa (area 2) and Jima (area 3).

Obviously, not all bean diseases occur everywhere, at the same intensity. Their prevalence and severity depend on area and season. Generally speaking, rust, common bacterial blight and anthracnose had a wider distribution in Ethiopia than angular and floury leaf spot. Worldwide (Schwartz and Galvez, 1980) rust, anthracnose and angular leaf spot are reported to have wide distributions. Our results suggest priorities for strategies of control of angular and floury leaf spot in the west and rust in the south. In the central Rift Valley, where rust, common bacterial blight and anthracnose occur simultaneously, at different degrees, any control strategy designed to reduce the impacts of diseases must concurrently deal with these three diseases.

Research implications

The variation among environments, crops and cropping regimens brings about concomitant variation in diseases and their intensities (Boudreau and Mundt, 1992; Zadoks and Schein, 1979). Management of diseases requires an understanding of these interrelated and interacting factors leading to epidemics.

The present study provided some clues to the understanding of the geographical distribution of bean diseases, the association of disease intensities with areas, seasonal variations of disease intensities and the interactions between cropping systems and disease intensities. Understanding the system will help to eventually achieve an economically sound and efficient

Table 4. Weather data from some representative locations sampled for bean diseases in Ethiopia between 1990 and 1993

Weather variables	Location	Years			
		1990	1991[a]	1992	1993
Rainfall[b]	Nazareth	451.8	548.3	555.0	584.6
	Awassa	370.2	509.6	419.1	455.7
	Jima	1208.9	752.3	1156.1	1119.6
Min. temp.[c]	Nazareth	15.9	15.1	14.8	15.4
	Awassa	13.3	13.4	13.8	13.6
	Jima	12.4	12.9	12.4	12.6
Max. temp	Nazareth	27.7	27.9	30.7	27.0
	Awassa	26.3	25.9	25.8	25.2
	Jima	24.7	25.4	24.7	24.6

[a] In 1991, data were available for only 4 months

[b] Rainfall (mm) data total of 5 months (May–September)

[c] Temperature (°C) data averaged over 5 months

crop and bean diseases management strategy. The Ethiopian National Bean Improvement programme is trying to better focus its breeding activities by regionalization, recognizing four major bean growing areas with different ecologies (differences in altitude, rainfall, temperature, soil, production system, production constraints and objectives). The present findings confirm that the regionalization of the breeding programme is well justified. To address the specific needs of the different regions, the programme should, perhaps, integrate breeding and crop protection activities, in order to develop an overall strategy for the management of common beans.

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Crop Growth, Disease and Yield Components of Rusted *Phaseolus* Beans in Ethiopia

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Abstract

Crop growth and disease epidemics in sprayed and non-sprayed bean plots, artificially infected with rust (*Uromyces appendiculatus*) 3 weeks after emergence, were assessed weekly in two cultivars, at two locations for two seasons. Disease intensity was regulated by the application of a fungicide at 5 spray frequencies. Fungicide application influenced leaf area index (LAI) and reduced rust intensity. The fungicide had no significant effect on other diseases and dead leaf area. Fungicide application increased seed yield (SY) by increased numbers of pods per plant (PP). Rust severity was strongly correlated with pustule density but the overall relationships among rust assessment parameters depended on cultivar and location. Seed yield and pods per plant were highly correlated with LAI. The relationships between LAI and seeds per pod or seed weight depended on cultivar and location. Overall rust assessment parameters (rust severity and pustule density) showed close, negative relationships with seed yield, seed weight and pods per plant but not with seeds per pod. The relationships obtained in the partially resistant line 6-R-395 were less definite than those in the susceptible line Mexican 142. The yield parameters seed yield and pods per plant showed strong positive relationships.

Zusammenfassung

Wachstum, Krankheiten und Ertragskomponenten rostbefallener *Phaseolus*-Bohnen in Äthiopien

In behandelten und unbehandelten Bohnenparzellen, die 3 Wochen nach dem Auflaufen mit dem Rostpilz *Uromyces appendiculatus* inokuliert worden waren, wurden Pflanzenwachstum und Krankheitsepidemien in 2 Vegetationsperioden bei 2 Sorten an 2 Standorten einmal wöchentlich bonitiert. Die Krankheitsstärke wurde ein Fungizid reguliert, das in fünf verschiedenen Häufigkeitsstufen angewendet wurde. Die Fungizidbehandlung beeinflußte den Blattflächenindex (LAI) und reduzierte den Rostbefall. Das Fungizid zeigte keine signifikante Wirkung auf andere Krankheiten und die Größe der abgestorbenen Blattfläche. Es erhöhte den Samenertrag (SY) durch eine Steigerung der Anzahl Hülsen Pflanze (PP). Die Roststärke war mit der Pusteldichte eng korreliert, doch die Beziehungen zwischen den bei der Rostbonitur berücksichtigten Parametern hingen von Sorte und Standort ab. Samenertrag und Anzahl Hülsen/Pflanze korrelierten eng mit dem Blattflächenindex. Auch die Beziehungen zwischen LAI und Anzahl Samen/Hülse oder Samengewicht waren von Sorte und Standort abhängig. Die bei der Rostbonitur berücksichtigten Parameter Krankheitsstärke und Pusteldichte zeigten enge, negative Beziehungen zu Samenertrag, Samengewicht und Anzahl Hülsen/Pflanze, aber nicht zur Anzahl Samen/Hülse. Bei der teilresistenten Linie 6-R-395 waren die Korrelationen weniger deutlich als bei der anfälligen Linie Mexican 142. Die Ertragsparameter Samenertrag und Anzahl Hülsen Pflanze zeigten starke, positive Korrelationen.

Introduction

Rust caused by *Uromyces appendiculatus* Pers. (Unger) is a wide-spread and important disease of beans (*Phaseolus vulgaris* L.) in eastern and southern Africa. In Ethiopia, severe outbreaks of bean rust were reported from the south and southwestern parts (IAR, 1974). A severe outbreak of bean rust resulted in nearly 100% yield loss in the popular and widely grown, but susceptible cultivar, Mexican 142. Howland and McCartney (1966) and Singh and Musiyimi (1981) suggested that a severe infection of rust may cause a 10–37% yield loss in East Africa.

These findings were mostly based on visual observation. Few quantitative data exist that show the impact of rust on crop growth, yield and yield components. Analysis of crop growth and yield components affected by rust should help to understand the relationship between the production situation (De Wit, 1982), disease and yield (Savary and Zadoks, 1992a,b). The tolerance of a crop to injury varies during the growing season (Zadoks, 1985), and so analysis of crop growth, disease development, yield components and their interrelationships at various constraint levels will help to understand the productivity of bean crops in Ethiopia.

Management of crop loss (Zadoks and Schein, 1979; Mackenzie, 1983) requires a good understanding of the relationship between crop growth and disease development. Savary and Zadoks (1992a,b) established relationships between production situations, injury and damage in a groundnut multiple pathosystem. In beans, no such relationships were studied. Experimental manipulation of epidemics is one way to influence crop growth, disease development and yield. This study reports on such experiments, addressing 1) the effect of different epidemics on leaf area index and yield components; 2) relationship between different parameters for rust assessment; 3) relationship between yield components; 4) relationship between leaf area index, rust development and yield components.

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Table 1
Descriptions of bean growth stages as used in this study, after Fernandez et al. (1986), with slight modifications

- V4 = Third trifoliolate leaf
- R5 = Pre-flowering, first floral bud
- R6 = Flowering
- R7 = Pod formation
  - R7A —1st week of pod formation
  - R7B—2nd week of pod formation
- R8 = Pod filling
  - R81 —1st week of pod filling
  - R82—2nd week of pod filling
  - R83—3rd week of pod filling
- R9 = Maturity (discoloration and drying of pods)

Materials and methods

Experimental design

Field experiments were performed in 1990 and 1991, in experimental fields of the Institute of Agricultural Research at Debre Zeit (1850 masl and ca. 900 mm annual rainfall) and the Plant Protection Research Centre at Ambo (2150 masl and ca. 960 mm annual rainfall).

The experiments were conducted as randomized complete block designs with six replications, in a split plot arrangement. Two cultivars, Mexican 142, susceptible (SUS), and 6-R-395, partially resistant (RES), formed the main plots and five spray treatments the sub-plots. Seeds were sown in mid-June at Ambo and early July at Debre Zeit. The experimental data at Debre Zeit in 1991 for RES were excluded from the analysis due to a severe infection by Bean Common Mosaic Virus (BCMV).

Standard agronomic practices were followed and no fertilizers were applied. The experimental sub-plots measured 4*4 m^2. One seed per hole was sown at 40 cm distance between the rows and 10 cm distance within a row. Each plot was surrounded by 3.2 m guard rows of wheat to reduce interplot interference.

Inoculation

Three weeks after emergence, each of the experimental plots was inoculated by spraying a urediniospore suspension (about 5 g urediniospore per 20 l of H_2O) containing a mixture of local isolates of bean rust collected from the respective locations.

Spray treatments

Fungicide spraying began 1-week after inoculation. To produce epidemics of varying intensity in each cultivar, plantvax 20% (oxycarboxin, a systemic fungicide at the rate of 0.1%) was applied at intervals of 5 (treatment 4), 10 (treatment 3), 15 (treatment 2) and 20 days (treatment 1). A check (treatment 0) was left unsprayed to allow maximum development of bean rust.

Crop assessment

Growth stages were determined at the dates of disease assessment following Fernandez et al. (1986) with slight modifications (Table 1). At the first and last disease assessment dates, the number of plants in the middle four rows of each plot was counted. Counts were converted to plant density (theoretically 25 plants m^{-2}). The leaf area of each plant selected for disease assessment was calculated using a pictorial key. The leaf area index (LAI) was determined at weekly intervals.

Disease assessment

From about 10 days after inoculation, assessment of incidence (number of infected leaves per plant), severity (percent leaf area infected), pustule density (number of pustules per leaf), and pustule size (1 = no visible symptoms; 2 = necrotic spots without sporulation; 3 = diameter of sporulating pustule < 300 μm, 4 = 300–500 μm; 5 = 500–800 μm; 6 = > 800 μm) were estimated (Stavely et al., 1983) at weekly intervals. Observations were made on 12 randomly selected and marked plants per plot, avoiding plot borders. Well-developed green leaves randomly selected and representing the upper, middle and lower canopy layers were used for disease assessment. These tagged plants (non-destructive sampling) were used on each observation day.

Other diseases such as common bacterial blight (*Xanthomonas campestris* pv. *phaseoli* (Erw. Smith) Dowson) at Debre Zeit and anthracnose (*Colletotrichum lindemuthianum* (Sacc. and Magn.) Bri. and Cav. at Ambo, yellowing and dead tissue (mainly insect damage and slight necrosis) were assessed separately. At Ambo, seeds were treated with benomyl (Habtu and Awgechew, 1984) prior to planting because of the high incidence of anthracnose.

Yield assessment

At the end of the growing season, seed yield (SY) in g m^{-2}, seed weight (SW) in mg $seed^{-1}$, number of pods $plant^{-1}$ (PP), and number of seeds pod^{-1} (SP) of the four central rows were assessed. SY and SW were determined at 12% moisture after sun-drying threshed seeds for 5 days. PP and SP were counted at harvest.

Computation

Cross-sectional analyses (Zadoks, 1978) were conducted to check the effects of treatments on LAI, disease intensity (rust incidence (IN), rust severity (RS), pustule density (PD), pustule size (PS), severity of other diseases (OD) and dead tissue (DT)) per canopy layer and per growth stage. The analyses tested for the effects of cultivar, treatment and interactions of cultivars by treatments (C*T). Coefficients of correlation of rust intensity parameters (IN, RS, PD, and PS) were calculated to determine mutual relationships. Statistical analyses were performed using MSTAT (Freed et al., 1986). All tests for significance were performed at $P \leqslant 0.05$.

Results

Production situation

The production situation is characteristic of low input agriculture, without N, P or water added (De Wit, 1982). Ambo has more rainy days, more cloud cover, less radiation, cooler nights and higher rust pressure than Debre Zeit. Yield capacity is reflected by the average maximum yield (yield of the rust free plot) of 1860 kg ha^{-1} for SUS at Debre Zeit and by the maximum yield of 2180 kg ha^{-1} for RES at Ambo.

Effects of spray treatments

Leaf area index

Differences in LAI between spray treatments were significant from flowering (R6) onwards (Table 2), in 1990, and at all growth stages in 1992 (Table 3). In SUS, LAI reached a maximum of 2.25 at Ambo 1990, and 2.81 at Debre Zeit 1991, both in treatment 4. For treatment 4 LAI reached its maximum at R7A, at R6 for the other treatments, then declined. The decline was most prominent for treatment 0. RES also showed significant differences between spray treatments, but the differences were not large. Differences between cultivars were significant at V4 and at ≥R7B. At two growth stages (R8 and R9) the interaction between cultivar and treatment (C*T) was significant. In Debre Zeit 1991 the block effect, significant at all growth stages, reflected the waterlogging (common at Debre Zeit) that affected some treatments.

Incidence

In SUS at Ambo 1990, rust incidence reached its highest level (80%) in treatment 0. Differences between treatments were significant at all stages of crop development (Table 2). In RES rust incidence never exceeded 25%. The trend in RES was similar to that in SUs except for the magnitude of the differences

Table 2
Cross-sectional analysis of effects of treatments on LAI, incidence, severity, density, and pustule size, Ambo, 1990

		Variance ratio values at GS =								
Variables	Source of variation	V4	R5	R6	R7A	R7B	R81	R82	R83	R9
LAI	Cultivars	14.0	ns	ns	ns	6.4	8.1	19.4	9.4	25.9
	Treatments	2.6	ns	5.0	19.4	16.0	19.0	21.8	23.3	19.7
	C*T	4.1	ns	ns	ns	ns	3.4	4.0	4.7	2.7
Incidence	Cultivars	23.7	35.3	156.7	67.1	82.7	98.7	198.0	68.4	10.1
	Treatments	38.4	31.2	137.1	74.3	77.5	104.6	64.3	20.3	6.6
	C*T	13.9	9.5	62.2	36.0	44.2	43.5	18.3	8.8	3.1
Severity-UC[b]	Cultivars	ns	8.0	117.3	15.7	19.7	20.0	13.9	—	—
	Treatments	ns	5.8	65.1	57.2	21.5	16.6	12.7	—	—
	C*T	ns	ns	16.2	14.1	6.6	7.9	6.7	—	—
-MC	Cultivars	ns	8.2	ns	19.5	10.6	—	—	—	—
	Treatments	17.4	16.0	11.6	16.5	7.4	—	—	—	—
	C*T	ns	ns	ns	3.9	ns	—	—	—	—
-LC	Cultivars	ns	ns	ns	—	—	—	—	—	—
	Treatments	6.0	4.0	4.9	—	—	—	—	—	—
	C*T	ns	ns	5.3	—	—	—	—	—	—
Density-UC	Cultivars	ns	ns	18.7	28.1	21.0	10.0	ns	—	—
	Treatments	ns	6.0	36.6	36.1	29.3	18.6	16.0	—	—
	C*T	ns	ns	9.4	9.8	10.1	6.0	5.0	—	—
-MC	Cultivars	ns	ns	10.3	9.2	9.6	—	—	—	—
	Treatments	20.5	17.2	16.0	10.7	7.1	—	—	—	—
	C*T	ns	ns	3.7	3.1	4.5	—	—	—	—
-LC	Cultivars	ns	ns	ns	—	—	—	—	—	—
	Treatments	13.8	2.7	5.7	—	—	—	—	—	—
	C*T	ns	ns	3.1	—	—	—	—	—	—
Size-UC	Cultivars	ns	ns	ns	ns	ns	ns	ns	—	—
	Treatments	ns	ns	14.2	39.8	17.3	13.9	13.8	16.4	—
	C*T	ns	3.4	4.4	ns	ns	ns	5.3	—	—
-MC	Cultivars	ns	ns	ns	ns	ns	—	—	—	—
	Treatments	20.0	38.1	39.7	13.0	8.2	—	—	—	—
	C*T	ns	ns	3.5	ns	ns	—	—	—	—
-LC	Cultivars	ns	ns	ns	—	—	—	—	—	—
	Treatments	ns	5.0	11.4	—	—	—	—	—	—
	C*T	3.2	ns	2.7	—	—	—	—	—	—

[a] ns = not significant, — = not determined, all others significant at $P \leqslant 0.05$
[b] UC = Upper canopy layer; MC = middle canopy layer; LC = lower canopy layer.

between treatments. In Debre Zeit 1991, differences between treatments of SUS were not quite as large as in Ambo 1990. Significant differences were obtained between R5 and R7A (Table 3).

At Ambo 1990, interaction effects between cultivar and treatment (C*T) were large and consistent. At Debre Zeit 1991 the block effect, significant in 4 out of 8 cases, was largest at the earlier growth stages.

Rust severity

Upper canopy layer

For SUS, rust severity reached a maximum of 55% at Ambo 1990, and of 15 at Debre Zeit 1991, at R7B in treatment 0. In Ambo, differences between treatments, significant from R5 onwards, were highest at R6 (Table 2). For RES, rust development reached a maximum of 15 in treatment 0 at Ambo, and significant differences between the control and sprayed treatments were obtained at R7 and R8. At Ambo there was no block effect but a significant C*T interaction was found from R6 onwards. At Debre Zeit (SUS), differences between treatments were significant at R7B and R81 (Table 3). Block effects were consistently significant.

Middle canopy layer

In SUS, rust severity reached a maximum of 50 at R7 for treatment 0. In RES the highest rust level (18) was found at R6. Differences between treatments in RES were significant from V4 to R7B. Significant differences between cultivars were observed at R5, R7A and R7B at Ambo. The only C*T interaction effect, observed at R7A, was highly significant. At Debre Zeit, treatment differences were significant at R6, R7B and R81. Block effects were more common in Debre Zeit than in Ambo.

Table 3
Cross-sectional analysis of effects of treatments on leaf area index, incidence, severity, density, and pustule size, Debre Zeit, 1991

Variables	Variance ratio values at GS =								
	V4	R5	R6	R7A	R7B	R81	R82	R83	R9
LAI	3.3[a]	5.7	11.1	16.8	20.8	15.0	10.6	11.9	3.4
Incidence	ns	9.2	11.0	7.2	ns	ns	—	—	—
Severity-UC[b]	—	—	ns	ns	7.6	6.5	—	—	—
-MC	—	ns	5.9	ns	17.9	27.0	—	—	—
-LC	4.0	8.2	ns	ns	—	—	—	—	—
Density-UC	—	—	ns	5.0	20.9	16.4	—	—	—
-MC	—	ns	8.1	8.5	12.6	18.8	—	—	—
-LC	5.2	6.1	11.9	ns	—	—	—	—	—
Size-UC	—	—	ns	5.7	31.9	8.9	—	—	—
-MC	—	ns	16.7	11.3	11.9	4.8	—	—	—
-LC	ns	6.4	8.1	ns	—	—	—	—	—

[a] ns = not significant; — = not determined; all other significant at $P \leqslant 0.05$
[b] UC = Upper canopy layer; MC = middle canopy layer; LC = lower canopy layer.

Lower canopy layer

Rust severity declined as the season progressed. For the control plots of SUS, rust severity decreased from 10 to 5. In Ambo, only three assessments were done on the lower canopy layer as leaves began to drop at R7A. Trends in SUS and RES were similar. Despite low disease values, differences between treatments remained significant. At R6 C*T interaction was significant (Table 2). In Debre Zeit significant differences between treatments were obtained at R5 and R6 (Table 3).

Pustule density

Upper canopy layer

Numbers of pustules reached a maximum of 230 pustules per leaf for treatment 0. In Ambo, differences between treatments were significant from R5 to R7. The trend remained the same for both cultivars, but in SUS density was highest and variation between treatments was greatest. In SUS at Debre Zeit, despite significant differences (R7, R8) between treatments, density was rather low, not exceeding 60 pustules per leaf.

Middle canopy layer

In SUS at Ambo, the pustule density did not exceed 150 in middle canopy layer. At V4, pustule density was already 30 per leaf for treatment 0. In RES pustule density was low throughout the season and differences among treatments were small but significant, beginning at V4. A significant C*T interaction was found at R6 and R7. In Debre Zeit, treatment effects remained significant after R6 with highest differences at R7B and R81.

Lower canopy layer

Rust was first observed in the lower canopy layer. As the crop developed, leaves with pustules were removed from the infection process by normal leaf drop and mean pustule density was reduced. For SUS and RES in Ambo, differences between treatments were significant with significant C*T interaction at R6. In Debre Zeit, the results were similar and differences between treatments were significant.

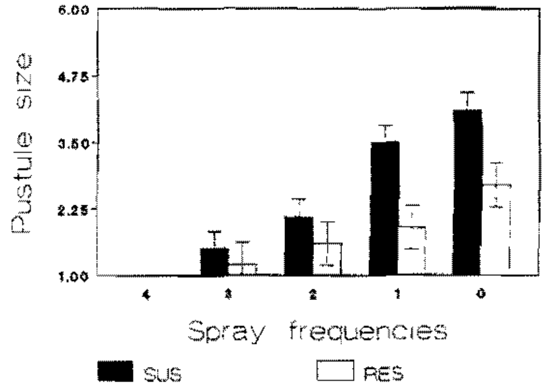

Fig. 1 Effect of spray treatments on pustule size, Ambo, 1990, at R7A. Data values are mean of upper, middle and bottom canopy layer. Black columns, SUS, white columns, RES. Each column is the mean of six replications

Pustule size

Upper canopy layer

In 1990 at Ambo differences in size of pustules among the treatments began to show at R5. Differences among treatments were strong at R6 to R8. The trend was similar for both cultivars. Differences between treatments were larger in SUS than in RES (Fig. 1). For SUS in Debre Zeit, differences between treatments were significant after R7.

Middle canopy layer

When bean crops were not sprayed with fungicides, pustule size continued to increase. Differences between treatments were significant after V4 in Ambo, 1990, and after R6 in Debre Zeit, 1991. In Ambo, a significant C*T interaction was found at R6.

Lower canopy layer

In most cases, the data were collected only three times due to fast defoliation. All spray treatments resulted in a reduced pustule size. As the crop developed, reduction of pustule size was continuous for all spray treatments. Treatment 0 resulted in a

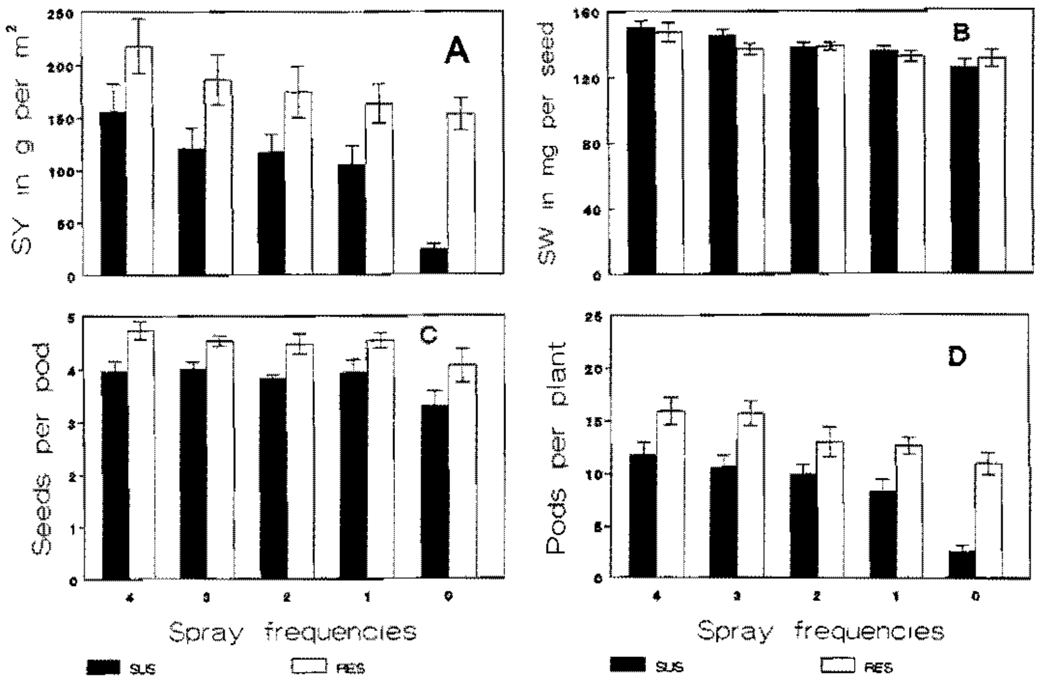

Fig. 2 Effect of spray treatments on yield parameters, Ambo, 1990. (A), seed yield (SY) in g per m^{-2}; (B), seed weight (SW) in mg seed^{-1}; (C), number of seeds pod^{-1} (SP); (D), number of pods plant^{-1} (PP). Black columns, SUS; white columns, RES; bars indicate SD. Each column is the mean of six replications

large pustule size, especially in SUS. In RES, differences between treatments were significant at R6.

Other diseases

Severity of other diseases, mainly common bacterial blight, anthracnose and ascochyta blight did not exceed 11% in any treatment. Differences between treatments were non-significant except at R6 and R7 in the upper canopy layer. The trends were similar for the two cultivars. Disease intensity increased from upper to lower canopy layers.

Dead tissue

In almost all cases (except the middle canopy layer at R5 in Ambo and the upper canopy layer at R8 and the middle canopy layer at R7B in Debre Zeit) differences between treatments were non-significant ($P \leqslant 0.05$). In the upper canopy layer dead tissue did not exceed 10% while in the middle canopy layer it ranged between 10 and 15 for SUS and 12 to 24 for RES. In the lower canopy layer dead tissue values were up to 30.

Yield and yield components

Seed yield

In Ambo (Fig. 2A), seed yield varied from 24 g m^{-2} to 156 g m^{-2} in SUS and from 153 g m^{-2} to 218 g m^{-2} in RES. In Debre Zeit in SUS (Fig. 3A), values ranged from 106 g m^{-2} to 186 g m^{-2}. The range between the highest and lowest yield value was 132 g m^{-2} for SUS and 65 g m^{-2} for RES, suggesting an interaction effect of spray treatments and cultivars. Close examination of the graphs (Figs 2A, 3A) shows that the interaction effect is largely due to treatment 0 where no spray resulted in a significantly lower yield for SUS. When the disease pressure was low, as in Debre Zeit, the range in SUS was only 80 g m^{-2}. Differences between cultivars and treatments were significant. In Ambo, a significant C*T interaction was found (data not shown).

Seed weight

Spray treatments increased seed weight in both cultivars, but the effects were slight. Differences between treatments were significant. Seed weight ranged from 125 mg for treatment 0 to 150 mg for treatment 4 in SUS and from 130 mg to 147 mg in RES (Fig. 2B). The range of variation for SUS (25 mg) was larger than for RES (17 mg). In Debre Zeit, seed weight of SUS ranged between 124 mg and 136 mg (Fig. 3B).

Seeds per pod

Seeds per pod ranged between 3.3 for 4.0 for SUS and 4.1 to 4.7 for RES in Ambo, and 3.5 to 4.1 for SUS in Debre Zeit. In Ambo, there were significant differences between cultivars (Figs 2C, 3C). Differences among treatments in both Ambo and Debre Zeit were small except for the differences between sprayed and non-sprayed.

Pods per plant

In SUS, pods per plant ranged from 2.5 to 11.8 in Ambo and 11.8 to 20.0 in Debre Zeit (Fig. 2D). In RES, at Ambo, the range was between 10.9 and 15.9 (Fig. 3D). Differences between cultivars and treatments were large in Ambo. Significant C*T interactions were found, located mainly in the contrast between sprayed and unsprayed plots of SUS.

Correlations between parameters for rust assessment

Table 4 provides correlation coefficients (*r*) for the relationships between the various bean rust parameters. For SUS in Ambo, the *r* values increased as the crop developed, being low at V4 and R5 and high at R7 and R8. Highest correlations ($\geqslant 0.85$) were found between rust severity and pustule density at R7A-R81. For RES the relationships were relatively low and unrelated to plant development. The *r* values were highest at R5 for pustule density and incidence or rust severity.

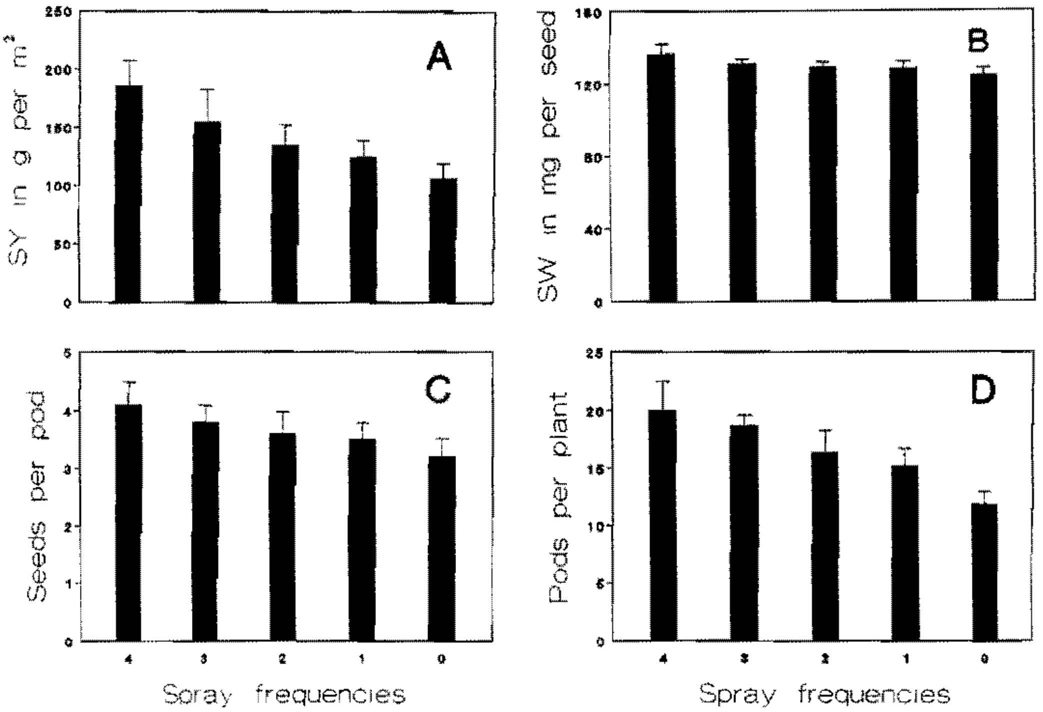

Fig. 3 Effect of spray treatments on yield parameters, Debre Zeit, 1991. (A) seed yield (SY) in g per m^{-1}; (B) seed weight (SW) in mg $seed^{-1}$; (C) number of seeds pod^{-1} (SP); (D) number of pods $plant^{-1}$ (PP). Black columns, SUS; RES failed because of virus attack; bars indicate SD. Each column is the mean of six replications

Table 4
Linear correlation coefficients *r* between rust parameters[a]

Growth Stage	Location	Year	Cul.	IN-RS[b]	IN-PD	IN-PS	RS-PD	RS-PS	PD-PS
V4	Ambo	1990	SUS	ns[c]	0.47	0.64	0.36	ns	0.51
R5				ns	0.39	0.70	0.69	0.47	0.59
R6				0.63	0.65	0.76	0.77	0.74	0.68
R7A				0.72	0.83	0.85	0.89	0.79	0.84
R7B				0.79	0.84	0.79	0.93	0.81	0.72
R81				0.76	0.82	0.76	0.88	0.82	0.75
V4			RES	ns	0.77	0.73	ns	0.46	0.63
R5				0.73	0.87	0.79	0.86	0.59	0.65
R6				ns	0.55	0.76	ns	0.55	0.63
R7A				0.56	0.42	0.68	ns	ns	ns
R7B				0.63	0.36	0.61	0.60	0.53	0.64
R81				ns	0.38	0.53	ns	ns	0.65
R5	DZ	1991	SUS	0.42	ns	0.45	0.63	0.56	0.52
R6				0.44	0.53	ns	0.59	0.38	ns
R7A				0.49	0.53	ns	0.81	0.37	ns
R7B				ns	ns	0.39	0.82	0.52	ns
R81				ns	ns	ns	0.63	ns	ns

[a] number of plots to test correlation = 30 (5 treatments by 6 replications).
[b] IN = rust incidence; RS = rust severity; PD = pustule density; PS = pustule size; Loc = location; Cul = cultivar
[c] ns = not significant; r values ≥ 0.36 significant at $P \leq 0.05$.

Table 5
Linear correlation coefficients between LAI and pods per plant (PP), seeds per pod (SP), seed weight (SW), and seed yield (SY)

	Ambo, 1990								Debre Zeit, 1991			
	SUS				RES				SUS			
Growth stage	PP[a]	SP	SW	SY	PP	SP	SW	SY	PP	SP	SW	SY
V4	0.41[b]	ns	ns	0.49	0.41	0.41	ns	0.51	ns	ns	ns	0.41
R5	0.41	ns	ns	0.50	0.72	ns	ns	0.83	ns	ns	ns	0.56
R6	0.54	ns	ns	0.50	0.69	0.47	ns	0.71	ns	ns	ns	0.52
R7A	0.75	ns	0.42	0.73	0.80	ns	0.43	0.82	0.55	ns	ns	0.70
R7B	0.86	ns	0.41	0.82	0.76	ns	0.53	0.61	0.45	ns	ns	0.73
R8-1	0.86	0.42	0.50	0.93	0.65	ns	ns	0.61	0.68	ns	0.36	0.65
R8-2	0.91	0.46	0.56	0.93	0.80	ns	ns	0.87	0.67	ns	ns	0.71
R8-3	0.86	0.58	0.54	0.87	0.88	ns	0.48	0.85	0.72	0.52	0.66	0.81
R9	0.84	0.54	0.55	0.90	0.81	0.36	0.42	0.69	0.59	0.52	0.59	0.48

[a] number of plots to test correlation = 30 (5 treatments by 6 replications).
[b] ns = not significant; r value ≥ 0.36 significant at $P \leq 0.05$.

In Debre Zeit, high *r* values were obtained between rust severity and pustule density at R7A-R81. In Debre Zeit, correlations between incidence and other parameters were poor compared to Ambo, especially after R7B. This is understandable since in Debre Zeit differences between treatments were not significant after R7B, as opposed to Ambo where they remained significant at all growth stages.

Correlations between leaf area index and components of yield

Leaf area index (LAI) and pods per plant

The correlations between LAI and pods per plant were always positive (Table 5) and attained high levels between R7B and R9. For RES in Ambo and SUS in Debre Zeit, the coefficients were lower than in SUS Ambo. The developmental trend remained the same since high *r* values were found after ≥ R7B. The highest values were always found at R8. For SUS in Debre Zeit, results were significant from R7A onwards, with high *r* at the end of R8.

Leaf area index and seeds per pod

The correlations between LAI and seeds per pod were weak, especially between V4 and R7/8 for SUS and lacked a developmental trend for RES in Ambo. After R7B, especially for SUS in Ambo, the relationship became stronger but *r* did not exceed 0.58.

Leaf area index and seed weight

In SUS in Ambo, the correlation between LAI and seed weight became stronger as the crop developed with a maximum of $r = 0.56$ at R8 and R9. The *r* values were generally lower for RES than for SUS. Overall the relationship was weak. In SUS in Debre Zeit and RES in Ambo the relationship did not follow any pattern of crop development.

Leaf area index and seed yield

The *r* values were generally high for the correlation between LAI and seed yield, increasing with developmental stage. The trend was the same in all experiments. The highest *r* values (≥0.85) were obtained at R8 for SUs and RES in Ambo.

Correlations between rust and components of yield

Rust incidence and yield components

For all parameters (data not shown) variation among cultivars, locations and growth stages was high. For rust incidence and seed yield, *r* values ranged between −0.38 and −0.71 for SUS in Ambo and Debre Zeit. With RES, the *r* value was significant ($P \leq 0.05$) only at R81. For SUS *r* peaked at R7B.

A similar and consistent result was obtained for incidence and seed weight for SUS in Ambo. The relationship was significant at all growth stages with high *r* values at R8. In SUS in Debre Zeit significance was found only at R7 and early R8. At both locations *r* peaked at R7 and R8. For RES results lacked consistency, though significance was obtained at R5 to R8. The *r* values were generally lower for incidence and seeds per pod, ranging between −0.38 and −0.65. For RES in Ambo, *r* was higher for incidence and seeds per pod than for incidence and seed yield, or incidence and seed weight, and *r* peaked at R7-R8.

High *r* values were obtained for the correlation of incidence and pods per plant, ranging between −0.37 and −0.79. In SUS at Ambo, *r* was significant at all growth stages with little variation. In Debre Zeit the *r* values were significant at R5–R7. For RES the correlations of incidence with seeds per pod and pods per plant were better than with seed yield and seed weight. Differences in the relationship between location and/or year were common and variations were large for RES in Ambo and SUS in Debre Zeit.

Rust severity and yield components

The correlation coefficients for rust severity and seed yield showed variation among cultivars, growth stages, locations, and canopy layers (Table 6). For SUS in Ambo, *r* was significant at almost all growth stages with peak values at R7. In Debre Zeit, *r* was significant at R6–R8 for all three canopy layers. For RES, the relationship was weaker, with a significant *r* only in the upper canopy layer at R8.

The situation was similar for correlation between rust severity and seed weight relationships. In Debre Zeit, the *r* values were stronger at R7B–R81 in the upper canopy and middle canopy layers. In RES, significant *r* values were obtained only in the upper canopy layer at R7A, middle canopy layer at R5 and R6, and lower canopy layer at R5.

As to the correlations of rust severity and seeds per pod *r* was rarely significant in SUS in Ambo. In Debre Zeit, *r* was significant at most growth stages in the upper canopy and middle canopy layers. For RES, no consistent trend was found but significance was attained occasionally.

The correlations were better for rust severity and pods per

Table 6
Linear correlation coefficients[a] between rust severity and yield parameters

		Ambo, 1990								Debre Zeit, 1991			
		SUS				RES				SUS			
Leaf layer	Growth stage	SY[b]	SW	SP	PP	SY	SW	SP	PP	SY	SW	SP	PP
UC[c]	R5	ns[b]	ns	ns	ns	ns	ns	−0.48	ns	—	—	—	—
	R6	−0.54	−0.50	ns	−0.57	ns	ns	−0.04	−0.42	ns	ns	ns	ns
	R7A	−0.66	−0.64	ns	−0.73	−0.41	−0.39	−0.37	−0.52	ns	−0.39	−0.43	ns
	R7B	−0.64	−0.64	ns	−0.69	ns	ns	ns	ns	−0.39	−0.54	−0.55	−0.55
	R81	−0.60	−0.67	ns	−0.67	ns	ns	ns	ns	−0.45	−0.53	−0.46	−0.50
	R82	−0.61	−0.64	−0.36	−0.71	−0.41	ns	ns	−0.42	—	—	—	—
	R83	−0.52	−0.68	ns	−0.60	−0.41	ns	−0.59	−0.45	—	—	—	—
MC	R5	−0.62	−0.53	ns	−0.69	ns	−0.45	ns	−0.39	ns	ns	ns	ns
	R6	ns	−0.36	ns	−0.38	ns	−0.43	ns	−0.43	−0.42	ns	−0.40	ns
	R7A	−0.43	−0.39	ns	−0.54	ns	ns	ns	−0.37	−0.40	ns	−0.49	ns
	R7B	−0.65	−0.65	ns	−0.70	ns	ns	ns	−0.39	−0.75	−0.40	−0.54	−0.52
	R81	−0.51	−0.54	ns	−0.58	ns	ns	ns	ns	−0.81	−0.55	−0.63	−0.58
LC	R5	−0.53	−0.36	−0.44	−0.49	ns	−0.55	ns	ns	ns	ns	ns	ns
	R6	−0.42	ns	ns	−0.38	ns	ns	−0.65	−0.43	−0.40	ns	ns	ns
	R7A	−0.53	−0.43	ns	−0.62	ns	ns	ns	ns	−0.53	ns	ns	−0.52
	R7B	—	—	—	—	—	—	—	—	−0.45	ns	ns	−0.48

[a] number of plots to test correlation = 30 (5 treatments by 6 replications).
[b] ns = not significant; — = not determined; r value ≥ 0.36 significant at $P \leq 0.05$.
[c] UC = upper canopy layer, MC = middle canopy layer, LC = lower canopy layer.

plant, especially in SUS in Ambo, *r* being significant in most cases. High *r* values were obtained at R7 in all leaf layers. In Debre Zeit, the result was similar but with fewer cases of significance. For RES, rust severity was significantly correlated with pods per plant in the middle canopy layer. In the upper canopy layer, results indicated lack of consistency with the development of the crop.

Pustule density, pustule size and yield components

The correlations between pustule density or pustule size and yield components followed the general trend of rust severity and yield relationships and thus were not considered in detail.

Correlations among yield components

Significant relationships between the yield components were found (Table 7), except for seeds per pod and seed weight. *r* values were consistently higher for pods per plant and seed yield relationships. Bean yield is determined by its components,

$$SY = PP*SP*SW$$

where SY = seed yield, PP = pods per plant, SP = seeds per pod and SW = seed weight. A simple linear regression of SY with the product of PP, SP and SW gave the following equations,

$$SY_{sus} = 0.49 + 0.96_{ppspsw}; \quad R^2 = 0.92$$

$$SY_{res} = 1.13 + 0.95_{ppspsw}; \quad R^2 = 0.90$$

In a multiple regression analysis, where SY was regressed to the individual yield components, with or without two-way and three-way interactions, the complex equations did not result in a significantly higher R^2 than the simple equations shown above.

Discussion

Spray treatments

Crop growth and disease

The objective of the spray treatments was not disease control *per se*, but the generation of epidemics at different severity levels. This objective was attained. Oxycarboxin has no direct effect on the physiology of the host plant (Newby and Tweedy, 1973; Pring and Richmond, 1976). Spray treatments influenced rust intensity, and therewith, indirectly leaf area index. The magnitude of effects varied with location, cultivar, canopy layer and parameter. Spray effects on other diseases and dead tissue were negligible.

Leaf area index was most affected after pod formation. Rust, measured by either incidence, severity, pustule density or pustule size, varied with spray frequencies. Incidence was found most sensitive since differences were significant at all growth stages, whereas the impact of spraying on severity and pustule density was larger after flowering than during vegetative development.

Differences between cultivars were common for LAI, incidence, severity, and pustule density but not for pustule size. Rust epidemics began at an early stage, and the bean crop continued to produce new leaves, hence it is not surprising to see great differences between treatments for incidence from an early developmental stage onward as opposed to rust severity and pustule density. Spray treatments produced the highest variations at pod initiation and seed filling, regardless of the parameters assessed.

In most cases (LAI, incidence, severity, pustule density), there is a strong cultivar by treatment (C*T) interaction, stronger in SUS than in RES, suggesting a differential reaction to rust intensity at different levels of (partial) resistance. This is not uncommon as Lim and Gaunt (1986) suggested for the spring

Table 7
Correlation matrices[a] of pods per plant (PP), seeds per pod (SP) seed weight (SW) and seed yield (SY)

	Year	Location	Cultivar	PP	SP	SW	SY
PP	1990	Ambo	SUS	1.00			
SP				0.51[b]	1.00		
SW				0.59	ns	1.00	
SY				0.90	0.54	0.58	1.00
PP			RES	1.00			
SP				ns	1.00		
SW				0.46	ns	1.00	
SY				0.81	ns	0.38	1.00
PP	1991	Debre Zeit	SUS	1.00			
SP				0.56	1.00		
SW				0.69	ns	1.00	
SY				0.71	0.48	0.51	1.00

[a] number of plots to test correlation = 30 (5 treatments by 6 replications).
[b] ns = not significant; r value ≥ 0.36 significant at $P \leq 0.05$.

barley-leaf rust pathosystem. The result supports the suggestion to combine partial resistance with adequate fungicide management (Zadoks, 1989, 1993), but for bean production in Ethiopia one has to be cautious in recommending fungicides. The components of disease management beyond partial resistance are probably cultural (intercropping, cultivar mixtures, sowing dates).

Canopy layers

Distinction between leaf layers produced interesting results. The lower leaves died early. Treatment effects at the lower canopy layer were not as strong as in the upper canopy and middle canopy layers, but remained significant in most cases. Cultivar by treatment interaction was absent at the lower canopy layer mainly due to lack of differences between cultivars. Rust began to develop on the lower canopy layer and increased and moved upwards as the crop developed. Rust intensity seemed to decline at the lower layer because of removal (Zadoks and Schein, 1979) by death of primary pustules and subsequent appearance of many but significantly smaller pustules.

Moreover, leaves at lower canopy layer senesced and dropped early. Effects of early epidemics on lower leaves were reported by Rouse et al. (1980), Kolbe (1982) and by Lim and Gaunt (1986). In legumes, it is not always clear which nodes contribute most to yield (Wadill et al., 1984; Debouck, 1991). Rust in *Phaseolus* beans, if it comes early, will most often affect the primary and the first trifoliolate leaves which later become the lower leaves. The fact that rust was first observed in the lower leaves make these leaves epidemiologically important, despite low incidence and early removal from the infection process. This is of particular importance to any rust control strategy. The loss of leaves in the lower canopy layer *per se* may not affect yield significantly but infection at this stage acts as a source of inoculum for the upper canopy layers, suggesting the appropriateness of managing bean rust at this early stage.

Yield components

Yield depends on climate, production situation, cultivar, pathogen and disease severity (Zadoks and Schein, 1979; Daamen, 1989; Savary and Zadoks, 1992a,b). Analysis of disease effects on yield should include analysis of yield components to obtain a balanced view of their effects on final yield and their relationships. Some of these yield components were studied in the present report.

Epidemics affected seed yield, seed weight, seeds per pod and pods per plant. There was variation in the degree of response (Fig. 4), as seed yield and pods per plant were more affected than seeds per pod and seed weight. SUS was always more sensitive to spray treatment than RES, suggesting a larger effect of sprays in susceptible cultivars.

Disease effects on legumes include reduction of attainable number of plants, pods per plant, seeds per pod, seed weight and seed yield. The effects on the yield components and seed yield depend on the pathosystem. Williams (1975, 1978) and Rapwood et al. (1984) showed that rust (*Uromyces vicia-fabae*) of faba bean mainly affected seed weight and chocolate spot (*Botrytis fabae*) mainly pods per plant. In our study pods per plant was most affected.

The present report suggests the importance of rust in common bean, especially when a susceptible cultivar is attacked early. Rust is endemic in Ethiopia, especially in the Rift Valley and the southern provinces, where an outbreak of rust in combination with wide-spread cultivation of a susceptible cultivar can be devastating. The yield advantage obtained by applying fungicides frequently shows the damage potential of bean rust, but the experimental results also indicate that even minimum chemical treatment could produce economic benefits. The use of fungicides in Ethiopia is influenced by the availability and cost of chemicals, availability of sprayers and water, and the value of the crop (cash or consumption).

Relationships

Rust assessment parameters

Since disease assessment is laborious, bean breeders and extension specialists want a simple method suiting their needs. Correlations between the rust parameters incidence, severity, pustule density and pustule size depended on cultivar, location and leaf layer. Higher correlation coefficients were obtained for susceptible than for partially resistant cultivars, and *r* values were better at Ambo, where disease pressure was higher than at Debre Zeit. Linear correlations become more significant with larger ranges of rust intensities.

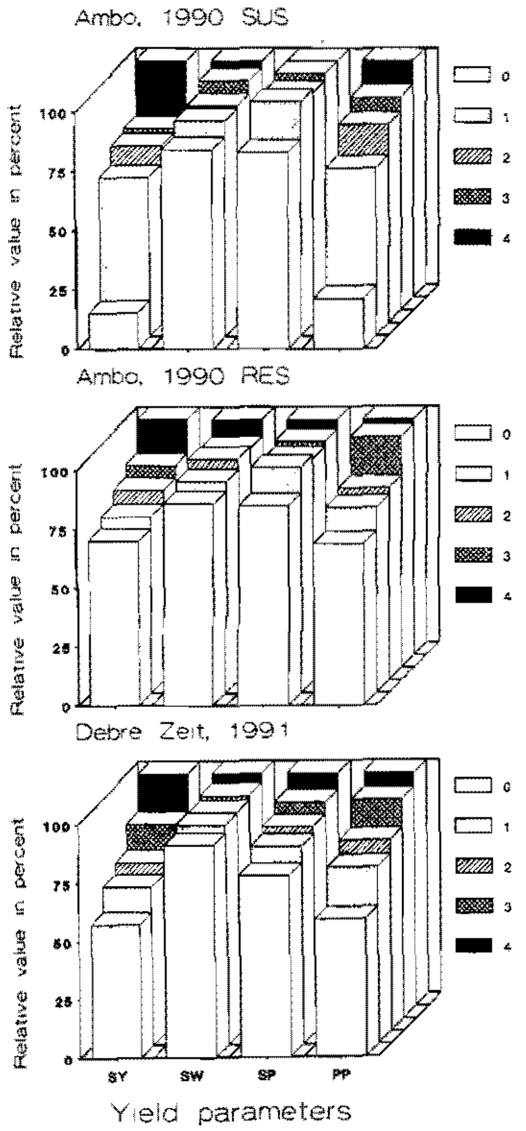

Fig. 4 Yield components in relative values. Yield values as percent of the reference (rust free plot). (A) Ambo, 1990 SUS, (B) Ambo, 1990 RES; (C) Debre Zeit, 1991 SUS. SY = seed yield; SW = seed weight; SP = number of seeds pod^{-1}; PP = number of pods plant^{-1}. Columns per item represent spray frequency from 0 (untreated control) to 4 treatments

There are conflicting reports on relationships of incidence and severity. The incidence-severity relationship may vary with season and leaf layer (James and Shih, 1973), with location but not with season (Chuang and Jeger, 1987), and with environmental factors (Imhoff et al., 1982). At high disease levels, the relationship between incidence and severity becomes undefined (Zadoks, 1985). The relationship between rust assessment parameters is extremely variable. A choice has to be made according to objectives. For bean breeders, rust severity may be more attractive. For epidemiological purposes, rust severity and pustule density are more appropriate. Extension specialists, who may have to deal with several crops and with diseases and insects simultaneously, may wish to select the simplest (incidence), which may be less accurate for evaluating bean rust.

Leaf area index and yield components

LAI is an important determinant of seed yield in the common bean. LAI was more closely related to pods per plant than to seed weight and seeds per pod. The correlations between LAI-pods per plant and LAI-seed yield varied with growth stage rather than with cultivar and location. The *r* values were larger at the later stages of crop development. This is understandable as differences in LAI between treatments were greatest after pod formation. The *r* values for LAI-seeds per pod and LAI-seed weight depended on location and cultivar.

Rust and yield parameters

Correlations between rust and yield parameters were affected by cultivars, growth stages, canopy layers and locations. No clear trend was visible. Relationships of rust parameters with seed yield or pods per plant were always better than with seed weight or seed per pod, especially for SUS at Ambo. The relationships were not greatly affected by the development of the crop but varied with location. The strong relationship for seed yield and pods per plant at all growth stages and canopy layers regardless of the rust parameter used, suggests the importance of all stages and canopy layers in any further epidemiological studies. The point will be elaborated in a subsequent paper.

Yield components

In dry beans the principal components of yield are pods per plant, seeds per pod, and seed weight (Adams, 1967). Our data suggest a strong correlation between pods per plant and seed yield. Early attack by rust may have affected the number of flowers. Bean rust at an early stage affects growth and development of leaves and thus the production of flowers and finally, the pod number. The effect of rust on abortion and pod filling could be partly due to the shortening of the pod-filling period by defoliation. The suggestion of Stone and Pedigo (1974), that the pod filling stage was the most sensitive to defoliation and subsequent loss of photosynthesis, explains the strong relationship between pods per plant and seed yield. The strong correlation between pods per plant and seed yield under different conditions (location, cultivar and growth stages) illustrates the overriding importance of rust attack at an early stage and its subsequent influence on the number of flowers.

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Components of partial resistance in phaseolus beans against an Ethiopian isolate of bean rust

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Abstract

Phaseolus bean cultivars, obtained from the Ethiopian national breeding programme, and cultivars widely grown in the country, 15 in total, were tested in a greenhouse for five components of partial resistance to one isolate of bean rust. The single-pustule isolate came from Ambo, a site where bean lines are tested against rust because the climate is conducive to bean rust. The components examined include latent period (LP_{50}), infection efficiency (IE), sporulation capacity (SC), infectious period (IP) and pustule size (PS). Differences in cultivar responses were found for all PR components. Differences were largest, however, for infection efficiency and sporulation capacity. Cultivars Exrico 23, A 176, Veracruz 10 and BAT 1198 had a high level of PR to the isolate tested. Mexican 142, a widely grown cultivar in Ethiopia was intermediate, whereas Red Wolaita, an important cultivar in the south, showed a low level of PR. Linear correlations between LP_{50} and IE, and between SC and PS were high. Linear correlations between IE, SC, or PS with IP were not significant. Though differences in cultivar response were found for all components, any one parameter may not suffice to explain the PR potential of a particular cultivar. The study suggests that latent period, infection efficiency and pustule size should be used in selection for PR. For the evaluation of large numbers of bean cultivars in the greenhouse, IE and PS are preferable to minimize labour requirements.

Introduction

Common beans (*Phaseolus vulgaris* L.) differ widely in their susceptibility to bean rust (Ballentyne, 1978; Coyne and Schusten, 1975; Fromme and Wingard, 1921). Genetic studies in beans have suggested most rust resistance to be monogenic (Christ and Groth, 1982; Grafton et al., 1985; Stavely, 1984, Webster and Ainsworth, 1988; Zaumeyer and Harter, 1941). Because of the ability of the bean rust fungus to adapt to new bean cultivars with monogenic resistance (high variability in terms of pathogenicity), the effectiveness of race-specific resistance is only temporary (Beebe and Pastor Corrales, 1991). Attention therefore shifted to a race non-specific type of resistance, partial resistance. Partial resistance (PR), a resistance that causes a reduced epidemic build-up of a pathogen despite a susceptible infection type (Parlevliet, 1981), can be expressed at different phases during the life cycle of a pathogen (Zadoks and Schein, 1979).

Simulated epidemics and experimental investigations suggest latent period to be the most important component of partial resistance in determining the rate of epidemic build-up (Parlevliet and van Ommeren, 1975; Zadoks, 1972). Infection frequency, sporulation capacity, pustule size and sporulation period were also used as estimates of partial resistance in several pathosystems (Mehta and Zadoks, 1970; Parlevliet, 1975; Parlevliet and Kuiper, 1977; Shaner and Hess, 1978; Statler and Parlevliet, 1987). In the bean-rust pathosystem (Statler and McVey, 1987), no differences in latent period between cultivars were found, but the number of pustules per unit area and the number of spores per pustule were associated with levels of partial resistance.

For a variable pathogen, in terms of pathogenicity, such as *Uromyces appendiculatus* (Pers.) Ung. of beans, selection for higher levels of PR might be a good alternative to selection for specific resistance, at least when PR is not race-specific and/or monogenic (Turkensteen, 1973). Selection for PR is not always easy because the expression of PR varies according to environmental factors (Zadoks and Schein, 1979). For a better understanding of the interactions between host and pathogen it is essential to evaluate components of PR. For application in a breeding programme one or two of the components have to be selected. In the bean-rust pathosystem this paper addresses the following: which components should be used for disease screening programmes and can we detect differences in the level of resistance among bean cultivars found in the advanced stages of the breeding programme with respect to the components of partial resistance and, if so, which component(s) is (are) the most effective and reliable in determining PR of rust in beans?

Materials and methods

Experimental design

The fifteen bean cultivars used for this experiment originated from the bean improvement programme of the Institute of Agricultural Research, Nazareth, Ethiopia, of which Red Wolaita and Mexican 142 are widely-grown cultivars, Exrico 23 (Awash) and A 176 (Roba) were recently released and Brown Speckled is a standard check in the large kidney bean trial. Bean plants were grown in a sterilized soil (sandy loam soil representing the soil type in the Rift Valley) in 15 cm diameter pots in the greenhouse at the Nazareth Agricultural Research Centre. The plants were grown at about 23 ± 3 °C during day time and 15 ± 3 °C at night. As the experiment was conducted in the dry season, light was not a limiting factor. No fertilizer was applied.

Two separate experiments were carried out, one for determining latent period, infection efficiency and pustule size, and the other for determining sporulation capacity and infectious period. Each experiment was performed three times in sequence (blocks), each time with four replications (subblocks). Per subblock, each cultivar was represented by one pot, four plants per pot, and pots were randomized within subblocks. Assessments were made on two of the four plants, two leaves per plant.

Inoculation

All cultivars were inoculated with urediniospores of a single-pustule isolate at the primary leaf stage, 10–12 days after sowing. The isolate originated from Ambo, where the relatively cool and moist climate is conducive to bean rust. Inoculation was carried out by spraying suspensions with about 2×10^4 urediniospores ml^{-1} over both sides of the primary bean leaves. Microscope slides greased slightly with Vaseline^{TM} were placed horizontally near the plants to check the resulting spore density (spores cm^{-2}). After inoculation, all plants were placed in a near-saturated atmosphere. Twenty-four hours after the deposition of spores, plants were returned to a bench in the greenhouse where they remained for the duration of the experiment.

Progress curve

Numbers of pustules per cultivar were counted daily once white flecks had been observed. The change in number of pustules with time was plotted to see variation among cultivars.

Latent period and infection efficiency

The latent periods were calculated by counting the number of visible pustules every day until no more pustules appeared (Parlevliet, 1975). Latent period, LP_{50}, was calculated as the time in days between inoculation and the moment at which 50% pustules were open. The infection efficiency (IE), the ratio between the number of resulting pustules and the number of spores applied, both per unit area (Zadoks and Schein, 1979), was determined by counting the number of pustules per unit leaf area (sum of the upper and lower surfaces) of the leaves about 15 days after inoculation. For both parameters counts were made on 2×2 cm^2 area.

Sporulation capacity and infectious period

Sporulation capacity (SC, weight of spores produced per unit area) and infectious period (IP, period in days from the appearance of the first open pustule until the end of sporulation) were determined per cultivar.

Table 1. Latent period (LP_{50}), infection efficiency (IE), sporulation capacity (SC), infectious period (IP) and pustule size (PS) of primary leaves of 14 cultivars, inoculated with a bean rust isolate from Ambo

Cultivars	LP_{50}	IE	SC	IP	PS
ICA 15441	9.4a	2.5d	0.34ef	27.6a	4.0c
Jalisco 33	9.6a	3.1bcd	1.12a	14.6d	6.0a
Red Wolaita	9.6a	3.5bc	0.76cd	15.2d	5.0b
Brown Speckled	9.7a	3.9b	0.38ef	15.2d	5.0b
KY Wonder 765	9.7a	5.4a	0.44de	24.3b	5.0b
Diacol Calima	9.9ab	2.4d	0.58cd	27.3a	4.0c
Mexican 142	9.9ab	2.9cd	0.53de	23.6b	3.5cd
US # 3	9.9ab	3.4bc	0.50de	21.5bc	3.5cd
Mexico 6	10.1ab	2.4d	0.51de	21.5bc	4.0c
CSW	10.2ab	3.6bc	0.47de	15.5d	3.5cd
BAT 1198	10.7ab	0.8ef	0.04g	19.6c	2.5e
Veracruz 10	11.4b	1.2e	0.19fg	22.4b	3.0de
Exrico 23 (Awash)	17.0c	0.2f	0.04g	14.4d	2.5e
A 176 (Roba)	18.6c	0.1f	0.04g	15.0d	2.5e

Cultivar means within each component followed by the same letter are not significantly different at $p \leq 0.05$.

Spores were collected every 3 days (until no more sporulation occurred) by means of a spore collector, beginning the first day of sporulation. Spores were collected from two areas of 4 cm^2, one at either side of the leaf. The data were converted to mg spores cm^{-2}.

Pustule size

Pustule size (PS) was assessed when it reached its maximum, at about 14 days after inoculation for most of the cultivars, according to the scale of Stavely et al., 1983 (1 = no visible symptoms, 2 = necrotic spots without sporulation, 3 = diameter of sporulating pustule < 300 μm, 4 = 300–500 μm, 5 = 500–800 μm and 6 = > 800 μm).

Statistical analysis

All data were subjected to ANOVA and mean values were separated by LSD at $p \leq 0.05$.

Results

Data compaction

Each experiment was performed 3 times sequentially (blocks), with 4 replications (subblocks) per time. Since no significant differences were found between blocks and subblocks, data were averaged over replications and times.

Progress curves for pustule production

In some cultivars minute, raised, white flecks appeared on both sides of the leaves about 7 to 8 days after inoculation. A day or two later the epidermis ruptured and reddish brown coloured sporulating pustules appeared. All cultivars showed asymptotically sigmoidal curves (Fig. 1), except BAT 338–1c which was immune to the Ambo isolate. In most cultivars a maximum was reached asymptotically 15 days after inoculation but about 24 days for Exrico 23 and A 176. The cultivars can be grouped, *ex post facto*, into four classes. Group 1 is represented by KY Wonder 765, group 2 by Brown speckled, Red Wolaita and Mexican 142, group 3 by Veracruz 10, and group 4 by Exrico 23. The other lines are not shown to avoid blurring the picture.

Latent period

LP_{50}, varied between 9.4 days for ICA 15441 and 18.6 days for A 176 (Table 1). The cultivars can be grouped into 3 LP_{50} classes (Fig. 2). Most cultivars are in group 1 with latent periods ranging from 9.4 to 9.9 days. In group 2 are Mexico 6, CSW, BAT 1198 and Veracruz

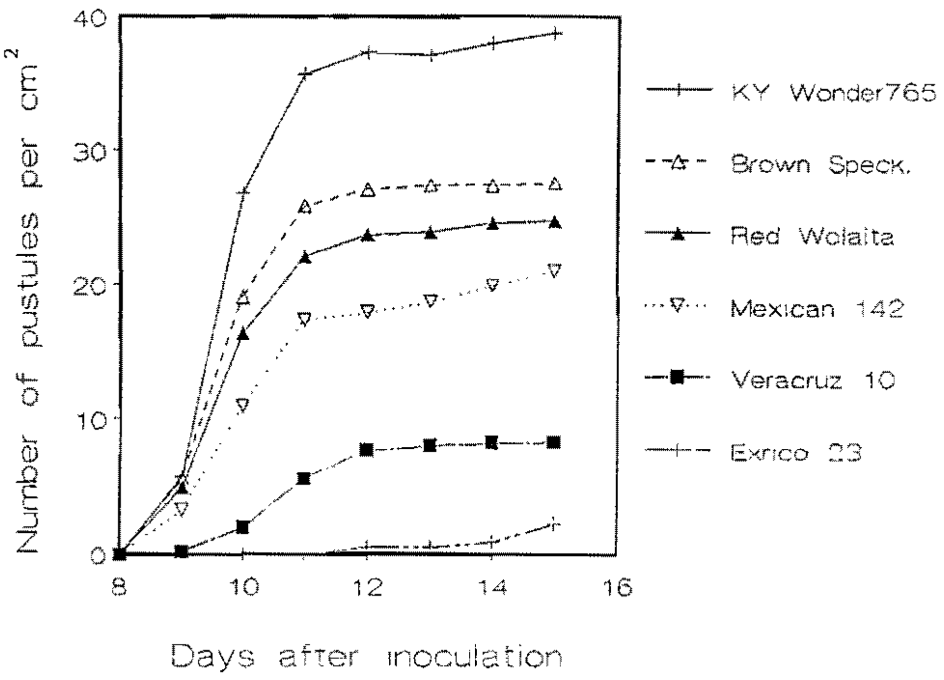

Fig. 1. Progress curves of number of pustules cm^{-2} with time in days for 6 representative cultivars, primary leaves.

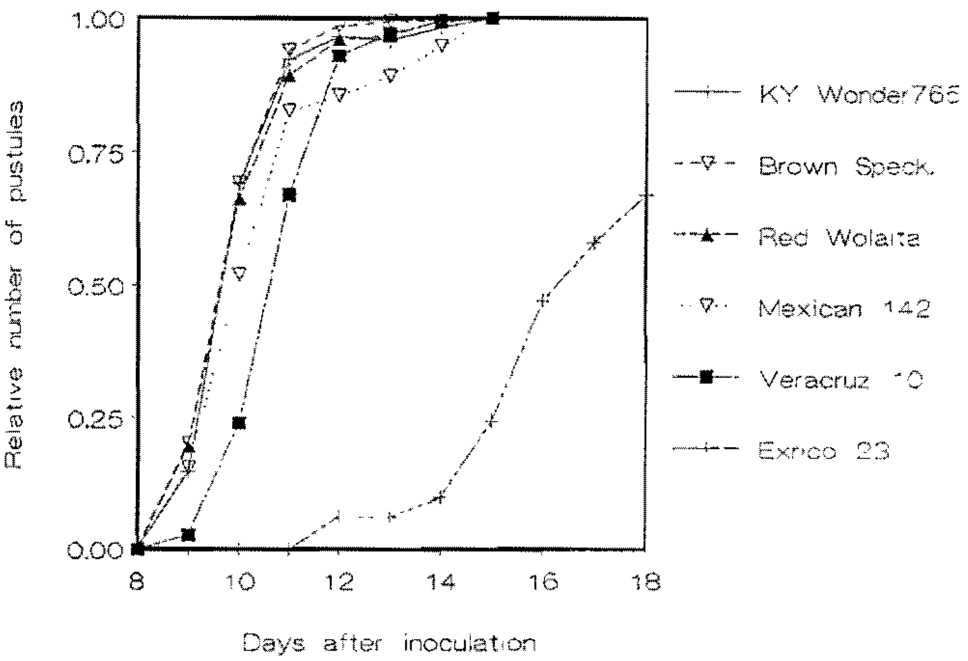

Fig. 2. Relative number of pustules per cultivar plotted with time in days for determination of latent period (LP$_{50}$); graph showing six representative cultivars.

Table 2. Correlation matrix of latent period (LP_{50}), infection efficiency (IE), sporulation capacity (SC), infectious period (IP) and pustule size (PS). Number of observations (Table 1) = 14. $p \leq 0.05$. Entries are linear correlation coefficients

	LP_{50}	IE	SC	IP
IE	−0.74			
SC	−0.62	0.62		
IP	−0.43	ns	ns	
PS	−0.62	0.77	0.85	ns

10 with an LP_{50} between 10.1 and 11.4 days. In group 3 are A 176 and Exrico 23 with an LP_{50} of 17.0 or more days.

Infection efficiency

IE varied between 0.1% for A 176 to 5.4% for KY Wonder 765 (Table 1). IE was below 1% for A 176, BAT 1198 and Exrico 23, between 1 and 2% for Veracruz 10, 2–3% for 4 cultivars and greater than 3% for the remainder. Differences in IE were mainly due to the small numbers of pustules observed in A 176, BAT 1198 and Exrico 23.

Sporulation capacity

Total amount of spores produced during one infection cycle varied between 0.04 mg cm^{-2} for A 176 to 1.12 mg cm^{-2} for Jalisco 33 (Table 1). Total amount of spores produced was high for Jalisco 33 and Red Wolaita, moderate for Mexican 142, Diacol Calima and Mexico 6, and low for A 176, Exrico 23 and BAT 1198.

Infectious period

Infectious period varied considerably (Table 1). Six varieties had a short IP in the range 14–16 days, whereas the remainder had 20 days or more. The longest IPs ($\geq$ 27 days) were found with Diacol Calima and ICA 15441.

Pustule size

Pustule size, classified in micrometers, shows variation between cultivars (Table 1). Pustule sizes were small ($\leq$ 3.0 μm) for cultivars A 176, BAT 1198, Exrico 23 and Vera Cruz 10, small-medium (3.1–4.0 μm) for ICA 15441, CSW, Mexican 142, Mexico 6 and US # 3, large (4.1–5.0 μm) for Brown speckled, KY 765 and Red Wolaita, and very large (> 5.0 μm) for Jalisco 33.

Relationships between the pr components

All paired correlations (Table 2) between LP, IE, SC and PS were significant and relatively high. However, correlations of IP with these parameters were not significant with the single exception of IP with LP.

Discussion

Context

Partial resistance is usually supposed to be polygenic, manageable by breeders, and durable (e.g. Lamberti et al., 1983; Jacobs and Parlevliet, 1992). In some cases, however, PR is monogenic (Turkensteen, 1973) and thus liable to be overcome by a new and adapted physiologic race. The genetic background of the resistance in the varieties tested here is not known. When grown widely, some lines such as Exrico 23 and A 176 could possibly exert such a high selection pressure on the rust that new and adapted races might appear. Selection for the highest possible partial resistance could be risky.

The experiments reported were designed to represent Ethiopian conditions. An array of varieties, used in the Ethiopian breeding programme, was tested. The widely grown cultivars Mexican 142 and Red Wolaita were included for comparison. Due to constraints imposed by technical, financial and political factors only one rust isolate could be tested. Though it came from Ambo, the breeders' testing site for rust resistance, its representativeness cannot be guaranteed. In fact, unpublished results suggest that the Ethiopian bean rust population is rather diverse. No fertilizer was applied as it is not recommended for beans. The soil type (sandy loam) used represents the soils of the bean growing area in the Rift Valley.

The experiment was monocyclic, testing young plants in a greenhouse with a single isolate, at low soil fertility level. Thus, its results cannot be generalized. Rather, they should be considered as a methodological excercise, in the wake of the pioneer study by Fromme and Wingard published in 1921.

Variations in components

Latent period, infection efficiency, sporulation capacity, infectious period and pustule size are important components of partial resistance. Zadoks (1972) demonstrated the importance of latent period by means of dynamic simulation. In experiments, latent period was found to be an important component in some pathosystems (Parlevliet, 1975; Neervoort and Parlevliet, 1978; Savary et al., 1988), among which the bean rust pathosystem (Fromme and Wingard, 1921: 10–15 days). In other pathosystems (Statler and McVey, 1987; Roumen, 1993) no important differences in LP were found, among which bean-rust (Statler and McVey, 1987). In the 15 cultivars of beans studied here, important differences in latent period were found. The differences were largely due to two cultivars, A 176 and Exrico 23, with latent periods exceeding 16 days. The difference between groups 1 and 2 is roughly one day. If the bean season is 90 days and the rust season is 80 days (primary leaf infected), the rust can complete 8 cycles in group 1 and 7 cycles in group 2, with multiplications up to 10^8 and 10^7, respectively. The use of a partially-resistant cultivar in an area of origin could play an important role in reducing the amount of rust inoculum migrating to other parts of the country. Exrico 23 and A 176, in group 3, are newly released cultivars tested under a wide range of environmental conditions in Ethiopia. Despite their susceptibility to anthracnose (Habtu, unpublished), limiting wider acceptance, they showed a high level of partial resistance to bean rust at all test sites. Collaborative activities, either in the area of regional rust nurseries or bean yield regional trials, currently ongoing in Eastern Africa, should help to determine the performance of these cultivars under varying climatic conditions.

Differences in infection efficiency among cultivars were found in most pathosystems studied (Groth and Urs, 1982; Ahn and Ou, 1982; Parlevliet and Kuiper, 1976; Statler and McVey, 1987; Roumen, 1993). Our study also supports such findings. Sporulation capacity was highly correlated with partial resistance in the field (Aust et al., 1984; Neervoort and Parlevliet, 1977). Small pustule size was associated with slow rusting of wheat (Ohm and Shaner, 1976) and high partial resistance in beans (Statler and McVey, 1987). In our study cultivars A 176 and Exrico 23, with long latent periods, low infection efficiencies and low sporulation capacities had small pustules. BAT 1198 and Vera Cruz 10 had somewhat shorter latent periods but were otherwise similar.

This study has indicated wide differences between cultivars in five components of partial resistance. Ideally, a high degree of resistance implies long latent period, low infection efficiency, low sporulating capacity, short infectious period and small pustule size. Exrico 23 and A 176 seem to possess such ideal characteristics, closely followed by BAT 1198 and Vera Cruz 10.

Conversely, a highly susceptible cultivar will have a short latent period, high infection efficiency, high sporulation capacity, long infectious period and large pustule size. Of the 15 cultivars tested none showed such characteristics. Mexican 142, the widely grown cultivar, showed a moderate infection efficiency. Red Wolaita, the most dominant cultivar in southern Ethiopia, showed a high infection efficiency. Note that Mexican 142 is in the higher intermediate category if all components are considered. In a crop loss study (Habtu and Zadoks, 1995), where Mexican 142 was used as a susceptible check, a seed yield loss of up to 85% was obtained. This difference could be due to a high damage potential expressed by Mexican 142. One cultivar could be more susceptible to damage than another.

Correlation of components

The relationships between the components are not considered to be high, 0.85 being the highest r obtained). This is probably due to mutual compensation (Yarwood, 1961; Zadoks and Schein, 1979) of PR components. For each component, except maybe IP, variations among cultivars are gradual. Nevertheless, practically every pair of cultivars has at least one component with a significant difference, the two most resistant cultivars (Exrico 23 and A 176) excepted. Determination of PR is laborious and also sensitive to environmental conditions. The expression of partial resistance is complex and so is its measurement (Zadoks, 1972; Roumen, 1993), depending on environmental factors (Imhoff et al., 1982). The differences between cultivars for the various components may point to a race-non-specific type of resistance (Shaik, 1985), which is often believed to be durable (Parlevliet and Zadoks, 1977; Parlevliet, 1993).

Without genetic analysis of the varieties, exposing them to many phenotypically different rust isolates, nothing definite can be said about the genetic basis of PR and its durability. The significant correlations between various components of PR could even point to oligogenic PR. If so, its durability becomes questionable.

Relative importance of components

Any one parameter may not suffice to explain the PR potential of a particular cultivar. Our result suggests the inclusion of latent period, infection efficiency and pustule size in the selection for partial resistance. Determination of latent period is time-consuming. For the evaluation of large numbers of bean cultivars in the greenhouse, infection efficiency and pustule size are preferable to minimize labour. As pustule size and sporulation capacity are strongly correlated there is no need to include the latter for screening purposes. Infectious period showed poor correlation with other components and should thus be handled with care. Severely infected leaves dropped early, before spore production came to en end. Small pustules can continue to produce spores for a long period and nonetheless have low sporulation. These results underline the importance of testing for PR components at low infection density for a better expression of PR, as suggested earlier (Parlevliet, 1976).

Research implications

Because of the different responses of cultivars for the different parameters it is unlikely to find one measure representative for all components. The result suggest differences, however small, in all the components studied. For polycyclic diseases such as rust (Parlevliet, 1975; Zadoks and Schein, 1979), even small differences as found here may benefit integrated bean rust management. The existence of such differences in all parameters provides possibilities to identify PR cultivars at an early stage in the Ethiopian national bean breeding scheme. Before drawing far-reaching conclusions, studies need to be made (i) on the relationship between component response in a monocyclic study on seedling leaves and polycyclic disease progress in the field on adult plants, (ii) correlation between component response at seedling and adult plant stages, (iii) correlation between component response and disease progress in the field, and (iv) testing a range of PR cultivars with various rust genotypes (Habtu and Girma, unpublished) prevalent in Ethiopia and, eventually, in East Africa.

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Focus expansion of bean rust in cultivar mixtures

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Radial expansion of foci in mixtures of susceptible and resistant bean cultivars was studied at two sites in Ethiopia. The foci expanded in a wave-like fashion. At Ambo (1990), radial expansion velocity ranged from 6 cm per day in mixtures with 20% susceptible plants to 15 cm per day in plots with the susceptible plants only. At Debre Zeit, the velocity ranged from 3 cm per day in a mixture with 20% susceptible plants to 16 cm per day in plots with 100% susceptible plants. At both sites the radial expansion velocity of foci correlated linearly with the logarithm of the fraction of susceptible plants in the mixture. Velocities of focus expansion at Ambo and Debre Zeit were approximately equal in plots consisting of susceptible plants only. At lower proportions of susceptible plants the velocities at Debre Zeit were lower than at Ambo. Indications were given as to the environmental factors responsible for the observed difference between sites. At each site, the variation between plots showed a clear spatial pattern, probably due to environmental factors.

INTRODUCTION

Modernization of agricultural practice has resulted in a drastic decline in inter- and intraspecific crop diversity. The widespread use of single resistance genes over large areas led to an increase in the frequency and intensity of epidemics (Zadoks & Schein, 1979; Mundt, 1989). Alternative approaches for the management of diseases and disease resistance genes, such as mixed populations (Borlaug, 1958), intercropping (Van Rheenen *et al.*, 1981) and inter- and intra-specific diversity (Jensen, 1952; Zadoks, 1958, 1959; Groenewegen & Zadoks, 1979; Wolfe, 1985), were suggested.

The use of varietal mixtures and their potential to control diseases and stabilize yield have been extensively studied. The effectiveness of varietal mixtures in reducing the rate of disease progress was established both experimentally (Zadoks, 1958; Barrett, 1978; Jeger *et al.*, 1983; Panse *et al.*, 1989; Pyndji & Trutmann, 1992) and by computer simulation (Kampmeijer & Zadoks, 1977; Mundt & Leonard, 1986; Mundt *et al.*, 1986). The rate of disease progress can be measured by the velocity of focus expansion (Minogue & Fry, 1983a, 1983b; Van den Bosch *et al.*, 1988a, 1988b, 1988c). Focal expansion reaches a constant velocity, after an initial phase of focus build-up (Kampmeijer & Zadoks, 1977). Factors such as level of resistance, genetic heterogeneity, plant density, temperature, wind and stochasticity of spore dispersal can influence the velocity of focus expansion, as was illustrated experimentally (Buiel *et al.*, 1989), analytically (Minogue & Fry, 1983a, 1983b; Van den Bosch *et al.*, 1990; Van den Bosch, 1993) and by computer simulation (Zadoks & Kampmeijer, 1977; Zawolek, 1989; Zawolek & Zadoks, 1992).

Van den Bosch *et al.* (1988c) developed a model to describe the relationship between the velocity of focus expansion, c, and the proportion of susceptible plants in a mixture, f. They showed that

$$c = A + B\ln(f) \qquad (1)$$

The velocity of focus expansion, c, increases linearly with the logarithm of the proportion of susceptible plants in a mixture, f. The purpose of the present study is to examine this relationship for bean rust (*Uromyces appendiculatus*), in mixtures of resistant and susceptible common bean (*Phaseolus vulgaris*) cultivars, in two different environments.

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MATERIALS AND METHODS

The experiment was conducted during the main crop growing seasons (June to October) in the research stations of the Phytopathological Laboratory at Ambo (1990) and the Institute of Agricultural Research at Debre Zeit (1991), Ethiopia. The two locations represent two different environments. Ambo (2150 metres above sea-level), representing the higher altitudes, has more rainy days, more cloud cover, less radiation, cooler nights and higher rust pressure than Debre Zeit (1850 metres above sea-level), which represents the intermediate altitudes.

Experimental design

The experiment was carried out in a 5 × 5 latin square design. The plot size was 4 m × 4 m. Each plot was surrounded by a strip 2·4 m wide planted with wheat. There were five treatments with the mixing proportions of 1 : 0 (twice, one treatment as a control without a focus and the other one with focus), 1 : 1, 1 : 2 and 1 : 4 susceptible (Mexican 142) to resistant (Negro Mecentral) plants. Seeds of the susceptible and resistant cultivars were mixed manually. From this mixture one seed at a time was drawn randomly and placed along the row at a distance of 10 cm between seeds. Each plot consisted of 10 rows of bean plants, planted with a distance of 40 cm between rows. One row of resistant beans was planted around each plot to reduce interplot interference.

Establishment of infected plants

Four seeds of the susceptible bean cultivar were sown along with the test seeds at the centre of each plot. At about 3 weeks after sowing, in four of the five treatments, two of the four plants were removed and the remaining plants were inoculated with rust suspensions to establish the foci. Inoculated plants were covered with plastic bags for 24 h to ensure conditions of high humidity for infection. A plot planted with only the susceptible cultivar was left uninoculated to serve as a control

Observations

Observation grids (made of plastic string) with grid cells of 0·40 m × 0·40 m were placed over the plots, with the inoculated plants in the central cell. Thus each plot was divided into 100 cells. The development of the foci was monitored weekly by counting the number of open pustules per grid cell. The numbers of pustules were counted on three trifoliolate leaves at the third, fifth and ninth leaf positions (from the top), representing the top, middle and bottom canopy layers, respectively. When the number of pustules per leaf exceeded 50, the numbers were estimated in intervals of ten. To prevent cross-infection between plots during observation, the boots and hands of observers were cleaned before entering the next experimental plot. The observations continued until the bean plants reached full maturity, although the leaves were still green. Data were expressed as the mean number of pustules per leaf and per grid cell for each plot, after averaging over the three canopy layers.

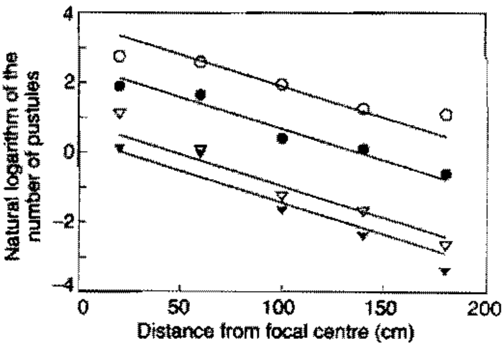

Fig. 1. Focus development of bean rust in cultivar mixtures. The natural logarithm of the number of pustules is plotted against distance from the focal centre in cm. Parallel lines are fitted at four successive dates: (▼), 10 days after inoculation (DAI), day 0; (▽), 17 DAI, day 7; (●), 24 DAI, day 14; (○), 31 DAI, day 21.

Velocity of focus expansion

The rate of focus expansion was large compared to the plot size used. This implies that the area within which disease severity exceeded a chosen value increased from zero to more than the plot area within 1 to 1·5 weeks In such situations the area method of Van den Bosch *et al.* (1990) cannot be used. We therefore applied the gradient method described by Buiel *et al.* (1989). Using the observation grid, the average number of pustules was calculated at distances of 20, 60, 100, 140 and 180 cm from the focal centre.

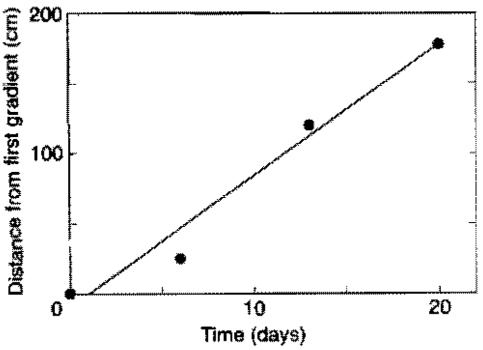

Fig. 2. Focus development of bean rust in cultivar mixtures. The distance in cm of a disease gradient in Fig. 1 from the first disease gradient is plotted against time in days. The radial velocity of focus expansion per plot was calculated from the straight line. Dots represent successive observations.

These averages were based on a variable number of grid cells. Theoretically, the tail of the disease profile is exponential. For each plot the logarithm of the number of pustules was plotted as a function of the distance from the focal centre (Fig. 1). Parallel straight lines were fitted using the program STATGRAPHICS (Statistical Graphics Corporation, 1986). From these lines the horizontal distance travelled by the disease profile was measured relative to the first observation date. Plotting these distances as a function of time (Fig. 2) gave a straight line from which the velocity of focus expansion was calculated.

RESULTS

Beans at Debre Zeit grew more vigorously and matured earlier than those at Ambo. The bean rust epidemics originating from the point sources, established by inoculation, continued to intensify and expand throughout the growing season at both locations. Disease intensity at and near the focal centres was higher at Ambo than at Debre Zeit. At Debre Zeit, due to waterlogging of some plots in one of the replications, only four replications were used in the analysis. The rust infection in the control plots was negligible, and therefore we did not adjust the data for interference by inoculum from outside sources.

Velocity of focus expansion was plotted as a function of the natural logarithm of the fraction of susceptible plants (Fig. 3). The velocity of focus expansion at Ambo ranged from 6 cm to 15 cm/day, and for Debre Zeit from 3 cm to 16 cm/day. The velocity of focus expansion, c, showed variation between plots (wide scattering of dots) and within plots (high standard deviations). The fitted line for Debre Zeit was steeper than that for Ambo. The calculated probability that the two lines had the same slope was $P = 0\cdot08$. In plots with susceptible plants only $(f = 1)$, the velocities, c, did not differ between locations. When the fraction of susceptible plants

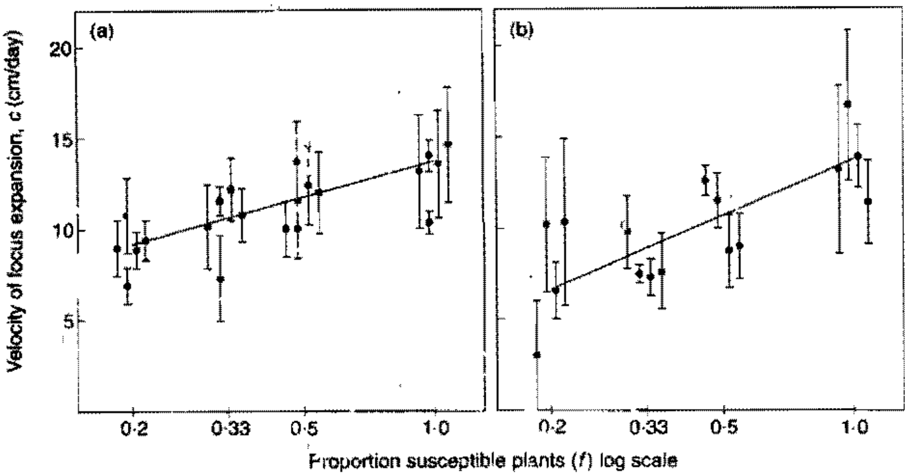

Fig. 3. The velocity of focus expansion, c, as a function of the proportion of susceptible plants, f, in the experimental plots. Dots represent observed c values (means per plot), vertical bars represent their standard deviations. Data points are scattered slightly in the horizontal direction to avoid obscuring data points in similar positions. The drawn line is fitted according to Equation 1. (a) Ambo, (b) Debre Zeit.

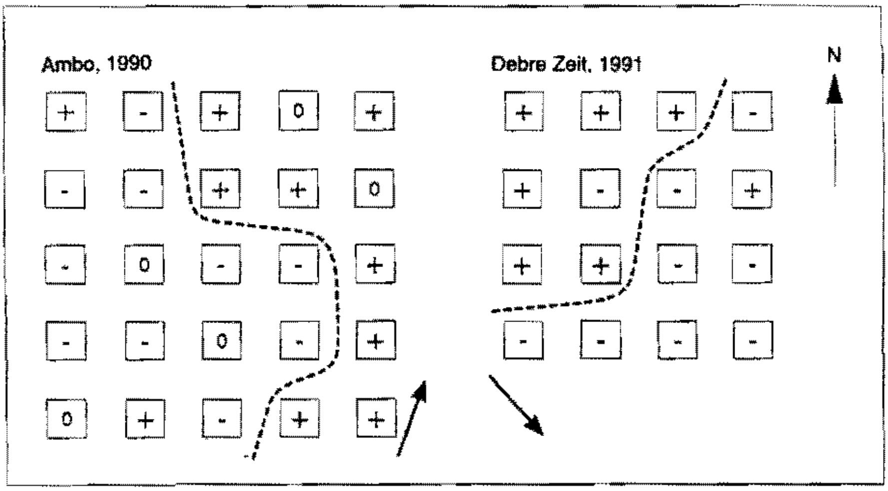

Fig. 4. Positions of bean plots. The signs at each plot indicate whether the numerical values of the observed velocity of focus expansion, c, are larger (+) or smaller (−) than the values calculated by Equation 1. (0) = non-inoculated control.

was low ($f = 0{\cdot}2$), the velocity, c, at Debre Zeit was smaller than that at Ambo. The agreement between the observed data and the model was reasonable for both locations

The spatial arrangement of the plots is shown in Fig. 4. The signs indicate whether the observed velocity is larger (+) or smaller (−) than the velocity calculated from the fitted lines. The clustering of positive and negative signs in the field is noticeable. At Ambo (1990), most of the negative signs are clustered in the west of the field as indicated by the broken curve. At Debre Zeit (1991), most of the negative signs are located in the south-eastern section of the field.

DISCUSSION

In this paper we showed the velocity of focus expansion, c, to be proportional to the logarithm of the fraction of susceptible plants in the mixture, f, as predicted by the model of Van den Bosch *et al.* (1988c). There are, however, clear variations between and within experiments. In the following discussion we suggest possible explanations for these variations.

There were *within-plot variations*. The sequential observations as plotted in Fig. 2 show variation around the regression line which can be expressed in terms of a standard deviation. Figure 3 shows that these within-plot standard deviations are relatively high, suggesting high variability of c in time. In calculating the focus expansion velocity, c, two methods, the area method (Van den Bosch *et al.*, 1990) and the gradient method (Buiel *et al.*, 1989), can be used. Studies made on cereal rusts indicated that standard deviations in the gradient method, which was rather sensitive to the presence of daughter foci and background noise, were much larger than those in the area method. The area method is generally recommended for calculating c, but for relatively small plot sizes, as in this study, it was not applicable.

Variability between plots of similar experiments was evident, suggesting systematic differences between plots. Differences between plots can be caused by several factors, including wind speed and direction, experimental position relative to ditches, waterlogging, the presence or absence of trees in the surrounding areas, etc. Wind influences the speed and shape of epidemics (Gregory, 1973; Okubo, 1980; Zawolek, 1993). During the crop-growing season (June to October) the prevailing wind direction was south-west. Figure 4 shows no obvious relationship between the wind direction and the + or − signs. The differences in velocity of focus expansion between plots within locations did not depend on wind direction. The experiment at Ambo was surrounded by tall trees on the west side and up-hills on the south, and the experiment at Debre Zeit was in an open field We were unable to explain the spatial variation observed at the two locations in terms of field environment. Both fields had a light slope and the spatial distribution of the signs rather corresponded with the direction of the slope of the fields.

The most likely explanation of the sign clusters was a gradient in the experimental field created either by waterlogging (Debre Zeit) or by erosion (Ambo) due to water. Both could result in low availability of nutrients, mainly N, to the plant, in Debre Zeit at the lower end of the field, and in Ambo at the upper end. Several studies suggest an increase in rust and mildew diseases is associated with increasing application of nitrogen fertilizers (Nazim *et al.*, 1982; Jenkyn *et al.*, 1983; Leich *et al.*, 1987). At low N concentrations, biotrophic fungi such as rust develop poorly (Zadoks & Schein, 1979), which would result in lower values of c. Systematic differences between plots resulting in variation in c have also been observed in other studies (Van den Bosch *et al.*, 1990).

The difference in slope between the regression lines of Fig. 3 may be explained by variation in environmental conditions. Differences in velocity between locations could arise from variations in crop growth, wind speed, turbulence, periods of leaf wetness, etc. At low f the velocity c is higher at Ambo than at Debre Zeit, but at high f the velocity is about equal.

Van den Bosch *et al.* (1988c) showed that the velocity of focus expansion is proportional to the logarithm of the fraction of susceptible plants. The formula does not give insight into the dependence of the velocity on parameters other than the fraction of susceptible plants in the mixture. The difference between the two experiments, in the slope of the regression lines relating focus expansion velocity to the logarithm of the fraction of susceptible plants, can only be attributed to the effect of other parameters. Thus, the formula of Van den Bosch *et al.* (1988c) must be extended.

Consider a line source parallel to the front of the focus. The number of pustules produced by this line source at a distance x from this source is

$$N(x) = \gamma S_0 f \frac{1}{\sqrt{2}} \frac{1}{\sigma} \exp\left[-\sqrt{2}\frac{1}{\sigma}|x|\right] \qquad (2)$$

where σ is the standard deviation of the distance of daughter lesions from the line source, f is the proportion of susceptible plants in the mixture, and γS_0 is the net reproductive number of the disease (Van den Bosch *et al.*, 1990). This net reproductive number is the total number of daughter lesions produced by one mother lesion during the whole course of its life if it is continuously surrounded only by susceptible plants. Define the effective distance, X_{eff}, as the distance beyond which $N(x)$ decreases below a certain number, κ. Then

$$X_{eff} = \frac{\sigma}{\sqrt{2}} \ln\left[\frac{\gamma S_0 f}{\kappa \sigma \sqrt{2}}\right] \qquad (3)$$

The effective distance is a measure of the distance travelled by the focal front in one generation. Therefore the velocity of focus expansion is proportional to the effective distance

$$c = \frac{X_{eff}}{T} \qquad (4)$$

where T is the generation time. Rearrangement of Equation 3 leads to

$$c = B + A\sigma \ln\left(\frac{\gamma S_0}{\sigma}\right) + A\sigma \ln(f) \qquad (5)$$

where

$$A = \frac{1}{T}\frac{\sigma}{\sqrt{2}}. \qquad (6)$$

$$B = A \ln\left(\frac{1}{\kappa\sqrt{2}}\right) \qquad (7)$$

and c is the velocity of focus expansion. Since both the generation time, T, and the parameter κ are undetermined, then A and B can be treated as arbitrary parameters.

For plots consisting of susceptible plants only, $f = 1$. This implies

$$c = B + A\sigma \ln\left(\frac{\gamma S_0}{\sigma}\right) \qquad (8)$$

Using these formulae we can find an explanation for the observed differences in the slope of the regression lines in Fig. 3. Weather conditions are much more favourable for infection and sporulation at Ambo than at Debre Zeit. Favourable temperature and dependable rain resulting in long periods of wetness lead to a higher net reproduction rate, γS_0, for Ambo than for Debre Zeit. Increasing wetness periods may increase the germinability of rust spores (Imhoff, 1981). Prolonged periods of rain can also reduce the dispersal of the urediniospores, which is essentially dependent on wind (Amorim *et al.*, 1994). The experimental field at Ambo was partly bordered by high earth walls and tall trees, which reduced the effects of wind and turbulence and thus also reduced σ in Ambo more than in

Debre Zeit. Such interacting conditions could result in almost equal velocities for $f = 1$ at the two locations (Equation 8), yet at the same time result in different slopes of the regression lines in Fig. 3. The standard deviation of the distance travelled by spores at Ambo is smaller than that at Debre Zeit,

$$\sigma_A < \sigma_{DZ}, \text{ as argued above.}$$

Low σ results in small slopes and high σ results in large slopes (Equation 5). We conclude that the differences in slopes at the two sites might be explained by differences in environmental factors.

The potential of cultivar mixtures for reducing foliar fungal disease has been extensively studied in cereals (Jeger *et al.*, 1983; Mundt & Leonard, 1986a; Buiel *et al.*, 1989; Van den Bosch *et al.*, 1990) and in beans (Mundt & Leonard, 1986b; Panse *et al.*, 1989; Pyndji & Trutmann, 1992). On the basis of the results obtained from replicated focal epidemics in two locations, we conclude that cultivar mixtures have potential for reducing foliar fungal diseases in beans as well. Farmers grow cultivar mixtures for different purposes (Clawson, 1985). The disease suppressive potential may be one reason why farmers in Ethiopia used cultivar mixtures (Westphal, 1974; Institute of Agricultural Research, 1991). Thus, as part of integrated crop and disease management, traditional Ethiopian farmers can benefit more by supplementing rust resistance cultivars in their cultivar mixture strategy. We also conclude that both at Ambo and at Debre Zeit radial expansion of bean rust epidemics in bean cultivar mixtures originating from a point source was proportional to the logarithm of the proportion of susceptible plants in the mixture, as described by Van den Bosch *et al.* (1988c). We believe that more can be gained by incorporating other parameters such as wind, canopy (LAI or LAD), leaf wetness duration or a measure of partial resistance into the model.

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