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USE OF DISEASE ASSESSMENT METHODS IN PREDICTING YIELD LOSS DUE TO NORTHERN LEAF BLIGHT OF MAIZE[1]

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ABSTRACT

Different severities of northern leaf blight were induced by inoculating maize plants once at GS 4 and 5, three times at GS 4, 5, and 6, allowing natural disease development, and by applying fungicides to deter disease development on cultivars with different levels of resistance to *Exserohilum turcicum*. Percentage leaf area affected by northern leaf blight on the whole plant, ear, first and second leaf above the ear leaf were assessed weekly for a total of six times at GS 8, 9.0, 9.1, 9.2, 9.3, and 9.4. Data obtained from the ear leaf, first leaf above the ear leaf, and second leaf above the ear leaf were used to develop a one-three-two weighted scale to account for leaf position and time of infection for the three leaves assessed and were related to yield by regression analysis. The average disease severity estimated on the ear leaf was significantly ($P \leq 0.001$) correlated with severities estimated using other disease assessment methods and loss in grain yield. Overall, AUDPC yield-loss models using percentage leaf area affected on the ear leaf gave the the best relationship ($Y = 5835–135\ AUDPC$, $R^2 = 0.42$, $P \leq 0.001$). Further analysis using leaves of various positions on the plant did not improve the yield-loss models. Critical point models, using percentage leaf area affected at GS 9.1 on A619xA632 also gave good fit ($R^2=0.53$).

Key Words: **Exserohilum turcicum, maize, northern leaf blight, yield loss**

RÉSUMÉ

Différentes sévérités de "northern leaf blight" étaient induites en inoculant des plantes de maïs une fois au stades de croissance 4 et 5 ou trois fois au stades 4, 5 et 6, soit en permettant le développement naturel de la maladie, soit en applicant des fongicides afin de freiner le développement de la maladie, et sur plusieurs cultivars avec différents niveaux de résistance au *Exserohilum turcicum*. Le pourcentage de surface foliaire atteint par le "northern leaf blight" sur toute la plante, sur l'épi et sur la première et la deuxième feuille au-dessus de la feuille d'épi était mesuré chaque semaine pour un total de six fois aux stades 8, 9.0, 9.1, 9.2, 9.3 et 9.4. Les données obtenues pour la feuille d'épi et pour la première et la deuxième feuille au-dessus, étaient utilisées pour le développement d'une échelle à poids rélatif un-trois-deux pour la détermination de la position de feuille et le moment d'infection pour les trois feuilles mesurées. De plus, ces données étaient corrélées à la productivité par analyse de régression. Il existe une corrélation significative ($P < 0{,}001$) entre la sévérité moyenne de la maladie estimée sur la feuille d'épi et d'autres méthodes d'évaluation de la maladie d'une part et entre la sévérité moyenne et la diminution de productivité d'autre part. En général,

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les modèles de diminution de productivité AUPDC utilisant le pourcentage de surface foliaire affectée sur la feuille d'épi, ont donné la meilleure rélation (Y=5835-135*AUDPC*, R^2=0,42, P < 0,001). D'autres analyses utilisant des feuilles à différentes positions sur la plante n'ont pas amélioré les modèles de diminution de productivité. Des modèles de point critique, utilisant le pourcentage de surface foliaire affectée au stade 9.1 sur A619xA632 ont donné aussi une corrélation valable.

***Mots Clés*: *Exserohilum turcicum*, le maïs, "northern leaf blight", diminution de productivité**

INTRODUCTION

Northern leaf blight, caused by *Exserohilum turcicum* (Pass.) Leonard & Suggs, is a serious leaf disease of maize (*Zea mays* L.) in warm, humid temperate and tropical regions (Ceballos *et al.*, 1991). In recent years, northern leaf blight has caused great concern among maize farmers in Uganda where the disease is widespread (Adipala *et al.*, 1993a). Commercial seed production has been interrupted for many cultivars except KWCA and its maize streak virus (MSV)-resistant derivative, KWCA-SR. This is mainly due to the susceptibility of other cultivars to northern leaf blight.

Epidemics of northern leaf blight originate from soilborne clamydospores, mycelia, or conidia on infested crop residue (Boosalis *et al.*, 1967; Leach *et al.*, 1977 where initial infection occurs on lower leaves (Robert, 1964; Levy, 1984). Under favourable conditions (Levy, 1991), conidia produced on infected leaves are blown by wind and result in secondary spread within and between fields (Meredith, 1966; Leach *et al.*, 1977; Hennessey *et al.*, 1990). In maize and other cereals, upper leaves contribute significantly to yield (Hicks and Nelson, 1977; Sabba Rao *et al.*, 1989; Levy and Leonard, 1990; Bowen *et al.*, 1991). The top, middle, and bottom leaves on maize plants contribute approximately 10:5:1%, respectively, to grain yield (Hooker, 1979). Levy and Leonard (1990) have shown that the first and second leaves above the ear contributed most to yield and their mechanical removal reduced yield by 32%. However, lower leaves are usually more severely infected by *E. turcicum* than the top leaves (Levy and Leonard, 1990). Thus, assessment of disease on the lower leaves or on the whole plant may overestimate yield losses due to northern leaf blight. However, few studies have attempted to quantify the contribution of different leaves infected by northern leaf blight to losses. One such study simulated a northern leaf blight epidemic by removing leaves in a pattern similar to normal disease development (Raymundo, 1978). Greater yield losses occurred when leaves above the ear leaf were removed indicating that the position of leaves was critical in yield-loss analysis. Similar results were reported by Bowen and Pedersen (1988). Levy and Leonard (1990) reported that greater yield losses were associated with *E. turcicum* infection on the leaves above the ear than the uppermost leaves removed by detasseling. Therefore, integration of leaf position and disease onset would provide useful information for predicting disease-yield relationships for many pathosystems (Lipps and Madden, 1989; Seck *et al.*, 1991).

Ideally, disease assessments should be obtained easily and quickly, and also be reproducible and highly correlated to yield loss (James, 1974; Campbell and Madden, 1990). Most models for northern leaf blight, whether based on critical point, or multiple point (AUDPC), utilize visual estimates of percentage leaf area affected by northern leaf blight on the whole plant. Disease assessments based on a single or few leaves that take into account leaf position, may be more accurate but this has not been well documented for northern leaf blight.

Information on the general relationship between yield of maize and severity of northern leaf blight is available (Ullstrup and Miles, 1957; Ullstrup, 1970; Fisher *et al.*, 1976; Hooker and Perkins, 1980; Raymundo and Hooker, 1981; Perkins and Pedersen, 1987; Bowen and Pedersen, 1988; Levy and Leonard, 1990) but not for tropical African conditions and cultivars. Initial estimates of yield loss, comparing inoculated and uninoculated treatments, found that the resistant hybrid yielded over 4,000 kg ha^{-1} more than the susceptible hybrid (Ullstrup and Miles, 1957). However, to characterise the relationship between disease and yield, studies must include experimental units of healthy plots as well as those with various disease levels (James and Teng, 1979). Thus, subsequent studies utilizing different disease levels have documented a significant relationship between level of northern leaf blight infection and yield losses. Estimates of yield losses have ranged from 0-60% (Elliott and Jenkins, 1946; Hughes and Hooker, 1971; Raymundo and Hooker, 1981; Bowen and Pedersen, 1988; Perkins and Pedersen, 1987). The magnitude of yield losses depends on the stage of plant growth when infection occurs, severity of disease, and the resistance level of the maize genotype (Perkins and Pedersen, 1987). Under favourable environmental conditions (Hooker and Perkins, 1980; Abadi *et al.*, 1989; Levy, 1991), early onset of northern leaf blight, usually within 2–3 wk after silking, may be expected to cause severe losses in grain yield (Elliott and Jenkins, 1946; Ullstrup and Miles, 1957; Raymundo and Hooker, 1981). In Uganda, because of the two cropping seasons a year, overlapping of growing seasons, and presence of off-season maize, epidemics of northern leaf blight often begin before tasseling and higher yield losses probably occur. However, no studies have been conducted to quantify losses due to northern leaf blight in Uganda. The objectives of this study were to determine the extent of yield loss associated with northern leaf blight in Uganda, to determine effectiveness of disease resistance in reducing yield losses, and to evaluate different disease assessment methods as to their relationships with grain yield.

MATERIALS AND METHODS

Maize germplasm. Three open-pollinated Ugandan maize cultivars EV8428-SR, KWCA-SR, and Babungo 3 were used in the study. They were selected on the basis of greenhouse studies conducted in 1990 with *E. turcicum* races 0, 1, 23, and 23*N* that indicated susceptible, intermediate, and high level of rate-reducing resistance, respectively (Adipala *et al.*, 1991, 1993b). The Ugandan genotype EV8428-SR was an introduction from the Centro Internacional de Mejoramiento de Maiz y Trigo (CIMMYT), Mexico, and Babungo 3 was obtained from the International Institute of Tropical Agriculture (IITA), Nigeria. For comparison, two hybrids from the USA with known reaction to northern leaf blight were included in the study. The hybrids, A619xA632 (susceptible), and B73xMo17 (polygenic resistant) (Perkins and Pedersen, 1987), were obtained from the Maize Breeding Germplasm, Department of Agronomy and Plant Genetics, University of Minnesota, St. Paul, and Illinois Foundation Seeds Inc., Champaign, respectively. Not all cultivars were tested at each location and/or year.

Field plots. Field plots were established at two locations, Makerere University Agricultural Research Institute, Kabanyolo, and Namulonge Research Station, Uganda. At Namulonge, plots were planted in land under cotton-groundnut-maize rotation. The plots in Kabanyolo followed soybean. In each of the two seasons, plots were plowed, disked and harrowed before planting. In 1990 plots at Kabanyolo were planted on 18 September. In 1991 plots were planted at Kabanyolo on 28 February and at Namulonge on 2 March. In 1990, plots were not established at Namulonge.

Plots at each location were set up in an identical manner. The experimental design was a split-plot with four replicates. Inoculation/fungicide treatments (see below) were main plots and cultivars were subplots. Seed of the five genotypes were planted in subplots consisting of four rows 4.5-m long (experimental units). All plots were hand-planted with 30 cm between hills within rows and 75 cm between rows and thinned to one plant per hill to a density of about 44,400 plants ha^{-1}. In order to reduce interplot dispersal of the pathogen, six rows of KWCA, a tall cultivar with high level of resistance to *E. turcicum* (Adipala *et al.*, 1993b), was planted between main plot treatments with 30 cm between hills within rows and 60 cm between rows.

Monoconidial field isolates of *E. turcicum* from Nakulabye, Kampala, Uganda, were grown on BBL Corn Meal Agar (Becton Dickson Microbiology Systems, Cockeysville, MD, USA) and Bacto Agar (Difco Laboratories, Detroit, MI, USA). After 10-12 days, the agar cultures were transferred to autoclaved sorghum seeds in 2-l glass jars. After 10-14 days the inoculum was removed and air-dried for 2 days. Plants in the two centre rows were inoculated by putting approximately 50 infested seeds into the whorl of each plant.

Different levels of northern leaf blight were induced by inoculation and fungicide treatments consisting of: a sprayed control; natural inoculum;

and inoculating plants once at growth stage (GS) (Ritchie and Hanway, 1982) 4; twice, at GS 4 and 5; and three times, at GS 4, 5, and 6. Treatments were applied only to the inner two rows of each plot. For the sprayed control, fungicide sprays were applied at each inoculation time, and at GS 7, 8, and 9.0, giving a total of six applications. The first three applications were of mancozeb (Dithane-M54 80% a.i., Rohn and Haas Company, Philadelphia, USA) at the rate of 1.6 kg a.i. ha^{-1}, and the last three applications were of benomyl (Benlate 50 WP, 50% a.i., E.I. Du Pont de Nemours & Co., Inc., Wilmington, D.E., USA) at the rate of 0.75 kg a.i ha^{-1}. Benomyl sprays were substituted for mancozeb because of an apparent poor control of northern leaf blight on mancozeb-treated plots. Fungicides were applied using a knap-sack sprayer with a delivery pressure of approximately 1.5 kg/cm^2.

Plots were hand-weeded four times at GS 2, 4, 6, and 8. At Namulonge, urea (46% N) was applied once, at the knee high stage (GS 4) at the rate of 90 kg N ha^{-1}. No fertilizers were applied at Kabanyolo. Before harvest, the total number of plants per two centre rows was determined. Maize planted in 1990 and 1991 was hand-harvested on 26 February, and on 18 July 1991, respectively. Because of late season rains in February and July 1991, grain moisture was high (ranging from 24% on A632xA619 to 39% on KWCA-SR). Therefore, ears were air-dried before shelling. Grain yield was calculated from weight of hand-shelled maize and converted to kg/ha after adjusting to 15.5% moisture content. Moisture content was determined with a hand-moisture meter (Dickey-John Corp., Auburn, IL, USA) .

Disease assessments. Ten plants, five from each of the two centre rows, were randomly selected and tagged with orange ribbons for successive disease evaluations. The percentage leaf area covered by disease lesions on the ear leaf, the first leaf above the ear leaf (leaf 1), the second leaf above the ear leaf (leaf 2), and on the whole plant was assessed weekly at GS 8, 9.0, 9.1, 9.2, 9.3, and 9.4, for a total of six times, using a disease scale of 0, 0.5, 1, 5, 10, 25, 50, and >75% leaf area affected by northern leaf blight (Elliott and Jenkins, 1946). The data obtained from the ear, leaf 1 and leaf 2 were used to develop a 1–3–2 weighted disease severity scale to account for the relative leaf position and time infection occurred on the ear, leaf 1, and leaf 2, respectively. Lesion numbers were also counted on the ear leaf, leaf 1, and leaf 2. For each experimental unit, the average number of lesions and percentage leaf area occupied by lesions per plant was determined for the three leaves evaluated. The number of disease ratings varied with genotype maturity. In 1991, leaf rust, caused by *Puccinia polysora*, also was assessed on 22 June (GS 9.3) based on a disease scale of 0, 1, 5, 10, 25, and 50% leaf area visibly infected on the ear, leaf 1, and leaf 2. A similar scale is available for wheat rust (James, 1974).

Data analysis. Area under disease progress curves (AUDPC) was calculated for each plot with time expressed in days; values were standardized by dividing by the number of days from the first to the last disease assessment (Campbell and Madden, 1990). Analysis of variance (ANOVA) was used to determine effects of inoculation/fungicide treatment (whole plot), cultivars (subplot) and cultivar x treatment interaction on yield, AUDPC, and percentage leaf area affected on the ear leaf at GS 9.3. The error terms used for treatments were variances of replicate x treatment interactions. When ANOVA indicated that main effects (cultivar and inoculation/fungicide treatments) or interactions were significant, Fisher's Least Significant Difference (LSD) at $P \leq 0.05$ was used to compare means. Single-degree-of-freedom contrast comparisons were also made between sprayed and unsprayed treatments, unsprayed and inoculated treatments, and among inoculation treatments.

Correlation analysis was conducted to evaluate relationships among disease assessments. Linear regression analyses were performed to determine the relationships among disease ratings and yield loss. Yield was used as the dependent variable and disease assessments or AUDPC were the predictors (independent variables). Critical point and AUDPC models were evaluated using least square regression analysis. Multiple point models were evaluated by selecting predictors with a stepwise method. Relation between leaf rust and northern leaf blight was evaluated by including leaf rust severity as an independent variable in the yield loss model. Percentage reduction in each yield for each location was calculated using intercepts of the regression models. Criteria for

TABLE 1. Overall means and ranges of severity of northern leaf blight (*Exserohilum turcicum*), standardised area under the disease progress curve (AUDPC), and yield of three maize cultivars grown in two locations of Uganda in 1990 and 1991.

Variable, year and location	Cultivar KWCA-SR Mean^a	Range	EV8428-SR Mean^a	Range	A619 x A632 Mean^a	Range
Severity^b						
1990 Kabanyolo	3.1	1.6–08.6	15.0	4.0–35.9		
1991 Kabanyolo	6.2	3.1–13.8	24.0	10.0–41.7	30.3	11.0–52.5
1991 Namulonge	2.7	0.8–0.95	7.5	0.5–30.0	38.5	13.6–43.0
AUDPC^c						
1990 Kabanyolo	0.3	0.2–0.4	1.8	1.0–03.0		
1991 Kabanyolo	6.2	2.2–9.0	24.0	3.3–34.5	22.2	6.0–26.7
1991 Namulonge	2.0	0.4–6.6	7.5	2.0–16.0	18.1	13.1–43.0
Yield (kg/ha)^d						
1990 Kabanyolo	7.0	4.2–8.9	4.5	2.8–7.8		
1991 Kabanyolo	5.9	3.9–8.8	4.6	2.1–5.4	0.9	0.4–3.1
1991 Namulonge	5.3	3.3–8.9	4.4	1.8–7.1	1.0	0.5–1.7

[a] Data are means of 20 plots and only for cultivars showing significant yield-loss relationships (Babungo 3 and B73 x Mo17 excluded); A619 x A632 not grown at Kabanyolo in 1990.

[b] Percentage leaf area affected on the ear leaf assessed at GS 9.3 (Elliott and Jenkins, 1946; Ritchie and Hanway, 1982).

[c] AUDPC calculated using percentage leaf area affected for the ear leaf at GS 8.0, 9.0, 9.1, 9.2, 9.3, and 9.4; values standardise by dividing by the number of days between the first and the last disease assessment times (Campbell and Madden, 1990).

[d] Grain yield (10^3 kg ha^{-1})

selecting the best fitting model for estimating yield included examination of coefficient of determination (R^2), which indicated proportion of total variation explained by the model, visual inspection of the residual plots, F-statistic, which tested the significance of the regression model, and the t-statistic of each partial regression coefficient, which tested the contribution of each independent variable to predicting the dependent variable (Campbell and Madden, 1990). All statistical analyses were conducted using SAS (SAS Institute Inc., Cary, NC. USA). The GLM procedure was used for ANOVA. REG and CORR (Pearson's) procedures were used for regression and correlation analyses, respectively.

RESULTS

The 1990 and 1991 growing seasons presented conducive environmental conditions for growth of maize and development of northern leaf blight (Fig. 1). Susceptible cultivars reached severities of 63% but resistant cultivars had low disease (<5%) and were generally excluded from further analyses. Effects of inoculation/ fungicide treatment and cultivar were significant for yield, AUDPC and disease severity at GS 9.3 (Tables 2 and 3). On susceptible genotypes, disease development was extensive with both natural inoculum and with artificial inoculations. No plots were free of disease in any one location by the last assessment date. Single-degree-of-freedom contrasts indicated that natural infection or inoculation with *E. turcicum* resulted in higher disease level at GS 9.3 compared to the fungicide-treated plots (Table 2). Differences between yields of fungicide treated and inoculated plots were significant ($P \leq 0.001$) at Kabanyolo in 1990 and in Namulonge in 1991 but not at Kabanyolo in 1991. There were no significant differences in yield, AUDPC, and disease severity at GS 9.3 among one, two or three inoculation times and, sometimes, with natural inoculum (Table 2).

In the 1990 growing season, yield and AUDPC were significantly affected by cultivar and treatment (Table 2, Fig. 2). The treatment by

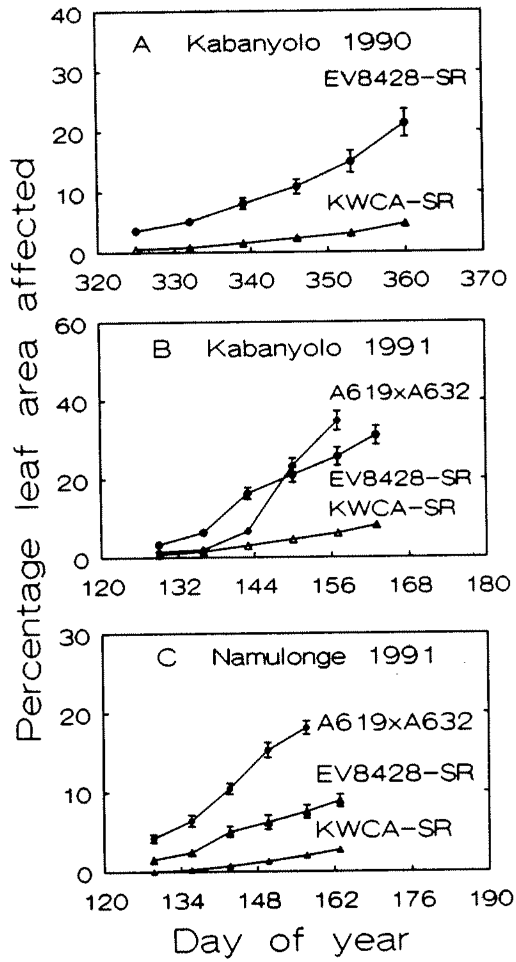

Figure 1. Disease progress curves of northern leaf blight caused by *Exserohilum turcicum* on two cultivars of maize in 1990 (A) and three in 1991 (B, C) at two locations of Uganda, Kabanyolo (A, B) and Namulonge (C). Bars indicate standard errors.

cultivar interaction was significant only at Kabanyolo. The interactions for yield were due to the greater reduction in yield of plots planted to EV8428-SR which had high level of disease (multiple inoculations) compared to low disease level (fungicide-treated). In the 1991 growing season at Kabanyolo, only the main effects of treatment and cultivar were significant ($P \leq 0.05$) for yield but the interaction effects were significant ($P \leq 0.05$) for AUDPC and disease severity at GS 9.3. At Namulonge, only the main effects of cultivar and treatment were significant ($P \leq 0.0.05$). Although disease intensity was not significantly lower under natural inoculum compared to the fungicide-treated control, yields of control plots were significantly higher than for plots under natural inoculum.

Correlation coefficients among the six assessment methods were high and significant ($P \leq 0.001$) (Table 3). Disease assessments on the ear leaf were highly correlated with disease assessments on the whole plant and with the average disease ratings for the three leaves combined. Subsequently, different disease assessment methods were evaluated for their relationships to yield by regression analysis. No significant relationships among yield and severity of northern leaf blight were found in any analyses in each year or location for Babungo 3 and B73xMo17, cultivars with high levels of rate-reducing resistance (Perkins and Pedersen, 1987; Adipala *et al.*, 1993b). Thus, yield-loss regression models were constructed only for KWCA-SR, EV8428-SR, and A619xA632, cultivars which had significant correlations between yield and disease (Figs. 3 and 4).

Considerable variation on disease-yield relationship with assessment methods occurred across genotypes and locations (Table 4). For the moderately resistant KWCA-SR, disease assessments on the ear leaf were generally more correlated with yield than other assessment methods, except in 1991 at Namulonge. R^2 for the weighted assessment (0.24) was only slightly higher than for the ear leaf assessment at Kabanyolo in 1991 (0.22). For EV8428-SR, the best estimates were obtained with the whole plant assessment in 1991 at Kabanyolo (R^2=0.51) but the results were comparable to the ear leaf assessment (R^2=0.42). The best relationship for A619xA632 was obtained with disease assessment on the whole plant at Kabanyolo (R^2=0.64) but the relationship was better described by the ear leaf assessment at Namulonge (R^2=0.38). The weighted assessment system had a higher or lower correlation with yield compared to the other assessments, depending on the location and year. The coefficient of determination for the data combined over the 2-yr period for the averages of the three leaves (0.31) was higher than that for the unweighted scale (0.25) but lower than for the ear leaf assessment (0.42) (Fig. 5). Yield reduction, for the 2-yr period and three maize cultivars, was best explained by the model Yield=5835-135 AUDPC (R^2=0.42, $P \leq 0.001$). Because the

TABLE 2. Analysis of variance table for grain yield, standardised area under the disease progress curve (AUDPC), and percentage leaf area affected by northern leaf blight (*Exserohilum turcicum*) on the ear leaf of three maize cultivars at growth stage 9.3 at two locations in Uganda[a].

	Mean squares[c]				
Source	df	Yield	df	AUDPC	Severity[b]
1990 Kabanyolo:					
Block	3	84.8	3	0.1	35.7
Treatment[d]	4	940.5^{***}	4	0.9^{*}	74.5^{*}[f]
Error A (BLock x cultivar)	8	109.8	12	0.2	16.7
Cultivar[e]	2	3140.0^{***}	1	20.7^{***}	1373.8^{***}
Cultivar x Treatment	12	321.1^{***}	4	0.5^{*}	37.5NS
Error B	30	71.1	14	0.16	23.4
Contrast					
1 vs 3–5	1	3435.5^{***}	1	3.0^{***}	198.6^{**}
2 vs 3–5	1	7.4 NS	1	1.1^{**}	167.1^{**}
1 vs 2	1	2507.8^{***}	1	0.3 NS	0.98 NS
1991 Kabanyolo:					
Block	3	504.0	3	85.9	164.4
Treatment	4	425.0^{*}	4	107.4^{**}	407.4^{***}
Error A (BLock x cultivar)	12	19.7	12	16.9	30.7
Cultivar	3	7998.1^{***}	2	1364.0^{***}	3109.1^{***}
Cultivar x Treatment	12	19.7 NS	8	50.8^{**}	156.9^{**}
Error B	45	114.5	30	15.5	41.8
Contrast					
1 vs 3–5	1	1603.5^{***}	1	289.2^{***}	1348.2^{***}
2 vs 3–5	1	350.3^{*}	1	153.6^{**}	512.6^{***}
1 vs 2	1	303.2 NS	1	14.2 NS	132.1^{*}
1991 Namulonge:					
Block	3	124.0	3	168.4	15.6
Treatment	4	1717.4^{***}	4	250.4^{*}	54.7^{*}
Error A (BLock x cultivar)	12	90.4	12	66.4	6.0
Cultivar	4	2049.0^{***}	2	5452.8^{***}	1339.9^{***}
Cultivar x Treatment	16	90.7 NS	8	54.3 NS	6.5NS
Error B	60	62.0	30	47.7	5.4
Contrast					
1 vs 3–5	1	6117.7	1	677.9^{**}	154.9^{***}
2 vs 3–5	1	2113.5	1	456.2^{**}	92.5^{***}
1 vs 2	1	693.1	1	7.1 NS	5.3 NS

[a] AUDPC calculated using percentage leaf area affected (Elliott and Jenkins, 1946) on the ear leaf at GS 8, 9.0, 9.1, 9.2, 9.3, and 9.4 and standardised by dividing by the number of days between first and last disease assessment times (Campbell and Madden, 1990).

[b] Percentage leaf area affected at GS 9.3

[c] Mean squares (10^4) for yield

[d] Single-degree-of-freedom contrasts: treatment 1 = fungicide treated; treatment 2 = natural inoculum; treatment 3 = inoculation at GS 4; treatment 4 = inoculation at GS 4 and 5; treatment 5 = inoculation at GS 4, 5, and 6.

[e] Cultivars (Babungo 3 and B73 x Mo17) indicating non-significant disease-yield relationships were excluded from AUDPC and severity analyses.

[f] Astericks indicate statistical significance, $^{*}P \le 0.05$; $^{**}P \le 0.01$; $^{***}P \le 0.001$, and NS = not significant.

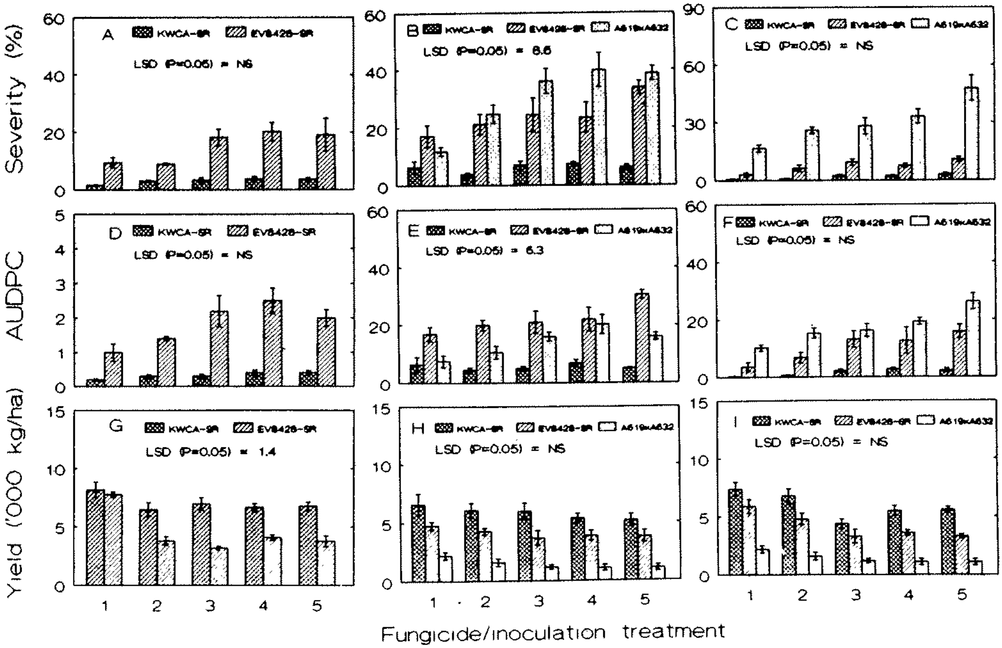

Figure 2. Interaction of cultivar and inoculation/fungicide[a] on yield, standardised area under the disease progress curve (AUDPC[b]), and disease level at GS 9.3 of *Exserohilum turcicum* on two maize cultivars in 1990 and three in 1991 at two locations of Uganda[c].

[a]Treatment 1 = fungicide sprayed check; treatment 2 = natural inoculum; treatment 3 = one inoculation at GS 4, 5, and 6. Data are means of four replicates; F values provided where significant F values were determined by ANOVA, and bars indicate standard errors. [b]AUDPC calculated using percentage leaf area affected on the ear leaf at GS 8, 9.0, 9.1, 9.2, 9.3, and 9.4; values were standardised by dividing by the number of days between the first and last disease assessment times. [c]Experiments were conducted at Kabanyolo and Namulonge, Uganda.

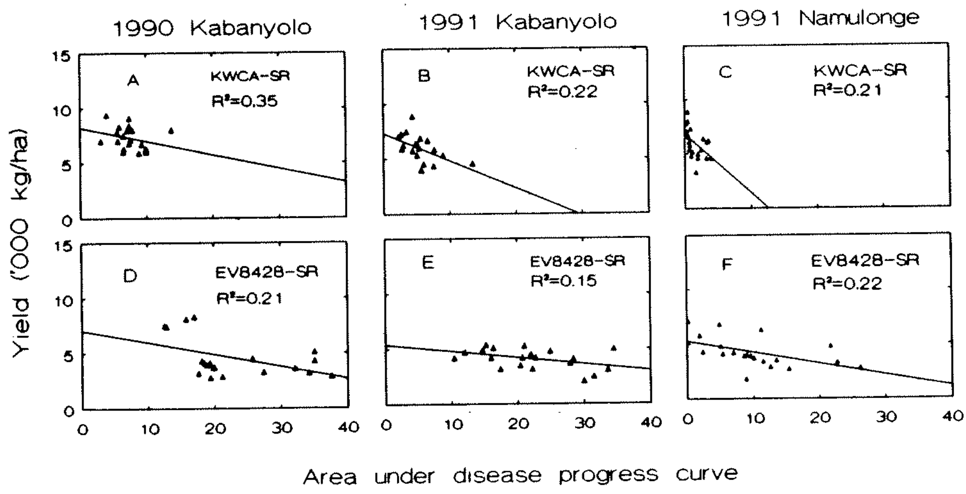

Figure 3. Relationships among yields and standardised area under the disease progress curve (AUDPC[a]) for percentage leaf area infected by northern leaf blight on the ear leaf for two maize cultivars in 1990 and1991 at two locations in Uganda[b].

[a]AUDPC calculated using percentage leaf area affected on the ear leaf at GS 8, 9.0, 9.1, 9.2, 9.3, and 9.4 and values were standardised by dividing by the number of days from the first to the last disease assessment times (Elliott and Jenkins, 1946; Campbell and Madden, 1990).

[b]Experiments were conducted at Kabanyolo (A, B, D and E) and at Namulonge (C and F) in 1990 (A and D) and in 1991 (B, C, E and F); coefficients of determination (R^2) indicated were significant ($P \leq 0.05$).

TABLE 3. Correlation coefficients (*r*) for the relationships among six disease assessment indices[a] used to assess severity of northern leaf blight (*Exserohilum turcicum*) on two maize cultivars in 1990 and three in 1991 at two locations of Uganda[b].

	Ear	Plant	Leaf 1	Leaf 2	Weighted average	Average
1990 Kabanyolo:						
Plant	0.85[c]					
Leaf 1	0.92	0.84				
Leaf 2	0.87	0.84	0.94			
Leaf average	0.91	0.79	0.93	0.88		
Weighted average	0.84	0.84	0.95	0.92	0.97	
1991 Kabanyolo:						
Plant	0.90					
Leaf 1	0.94	0.88				
Leaf 2	0.91	0.82	0.91			
Leaf average	0.97	0.88	0.96	0.95		
Weighted average	0.94	0.83	0.96	0.97	0.96	
Lesion	0.77	0.71	0.75	0.71	0.76	0.73
1991 Namulonge:						
Plant	0.92					
Leaf 1	0.91	0.93				
Leaf 2	0.89	0.92	0.98			
Leaf average	0.91	0.93	0.98	0.99		
Weighted average	0.89	0.94	0.99	0.97	0.98	
Lesion	1.00	0.92	0.91	0.89	0.91	0.88

[a] Percentage leaf area affected by nothern leaf blight (Elliott and Jenkins, 1946) assessed at growth stage (GS) (Ritchie and Hanway, 1982) 8, 9.0, 9.1, 9.2, 9.3, and 9.4 on whole plant (Plant), ear leaf (Ear), first leaf above the ear leaf (Leaf 1), second leaf above the ear leaf (Leaf 2), average on the ear, leaf 1 and leaf 2 (leaf average), 1–3–2 weighted average to account for disease onset and leaf positions of the ear leaf, leaf1 and leaf 2, respectively, and average number of lesions (lesion) on the ear, leaf 1 and leaf 2. Lesion numbers were not assessed at GS 9.4.

[b] 400 and 600 plants assessed on two maize cultivars in 1990 and three in 1991, respectively.

[c] All correlation coefficients are significant at $P \leq 0.001$.

disease-yield relationship was significant for assessment of disease on the ear leaf of moderately and susceptible genotypes at each location and year (Table 3) and satisfactory residual plots were obtained, further analyses are presented only for data from the ear leaf.

Critical point models were developed with disease severity assessed on the ear leaf to determine the assessment time that had the highest correlation with yield (Table 4). Relationships between yield and severity of northern leaf blight were inconsistent when disease was assessed at GS 8 or 9. For the moderately resistant KWCA-SR, disease assessment at GS 9.2 or later were often significantly correlated with yield. R^2 for the critical point models for EV8428-SR in 1990 were low and mostly not significant and provided relatively poor residual plots. In 1991, critical point models for all six assessment dates for EV8428-SR were significant but higher R^2 values were associated with later disease assessments. For A619xA632 at Namulonge, high R^2 values were obtained at several assessment times, although the best relationship was obtained with disease assessed at GS 9.1 (R^2=0.53).

Regression statistics (intercept and slope) describing the relationship between yield and AUDPC varied for different genotypes (Table 5). Although higher disease levels developed on EV8428-SR than on KWCA-SR, loss in grain

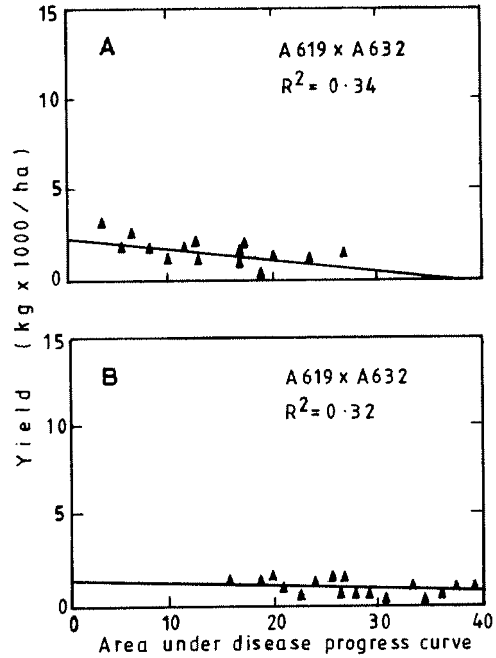

Figure 4. Relationships among yields and standardised area under the disease progress curve (AUDPC[a]) for percentage leaf area infected by northern leaf blight on the ear lea fof the maize cultivar A619 x A632 in 1991 at two locations in Uganda[b].

[a]AUDPC calculated using percentage leaf area infected on the ear leaf at GS 8, 9.0, 9.1, 9.2, 9.3, and 9.4 and values were standardized by dividing by the number of days from the first to the last disease assessment times (Elliott and Jenkins, 1946; Campbell and Madden, 1990).

[b]Experiments were conducted at Kabanyolo (A) and at Namulonge (B); coefficients of determination (R^2) indicated were significant ($P \leq 0.05$).

yield per unit increase in AUDPC (b_1) were generally higher for KWCA-SR than for EV8428-SR or A619xA632.

Attempts were made to relate yield to northern leaf blight severity at more than one assessment time by multiple regression analysis (Campbell and Madden, 1990). Most models resulted in only single significant assessment periods similar to the ones obtained with critical point models (data not presented). Similarly, inclusion of rust severity as a term in disease-yield models did not improve the model R^2 except for B73xMo17, which indicated considerable susceptibility to rust infection.

DISCUSSION

The various disease assessment methods were highly correlated with each other. Because of this, there was not a single assessment method that best predicted yield. Disease on the ear leaf tended to have R^2 values as high or higher than those of other methods. Similar results were obtained with disease assessed on the whole plant. An average or weighted average of disease on leaf positions sometimes improved R^2 values but not in a consistent manner. Thus, disease assessment on the ear leaf appeared as adequate as any of the assessments for developing disease-yield relationships of both susceptible and moderately resistant genotypes, given the high variability in disease and yield in Uganda. Waggoner and Berger (1987) believed that differences between leaves at different positions on the maize plants did not greatly affect yield of maize infected with *E. turcicum*. However, results of Hooker (1979) and Levy and Leonard (1990) indicate that consideration of leaf position is important. In studies with wheat leaf rust caused by *Puccinia recondita* f. sp. *tritici*, the flag, penultimate and antepenultimate leaf were found to contribute 26, 12, and 13%, respectively, to potential grain yield per tiller (Simmons and Jones, 1985). Disease-yield relationships were better estimated when leaf positions were considered. In a related study, Lipps and Madden (1989) used different assessment methods to account for leaf position to determine the relationship between powdery mildew severity and grain yield of winter wheat. Their results indicated that several assessment methods that account for leaf position were useful for quantifying disease-yield relationships. Thus, for studies that require high precision, inclusion of leaf position would be necessary. However, our data indicate that evaluation of disease on the ear leaf is sufficient for Uganda field experiments, especially for rapid disease assessments.

Over the 2-yr period, there was generally a linear relationship between disease severity and yield. Although the regression coefficients were significantly different from zero, they were relatively low. The susceptible Ugandan genotype EV8428-SR had a significant relationship between yield and disease severity in 1990 but only in one of the two locations (Namulonge) in 1991.

TABLE 4. Coefficients of determination (R^2) from regression of grain yield and standardised area under the disease progress curve (AUDPC[a]) for northern leaf blight (*Exserohilum turcicum*) severity based on different assessment methods[b] for two maize cultivars in 1990 and three in 1991 grown at two locations in Uganda[c].

Year and assessment indice	Cultivar		
	KWCA-SR	EV8428-SR	A619 x A632
1990 Kabanyolo:			
Ear	0.31**	0.16*	–
Plant	0.26**	0.18*	–
Leaf 1	0.12	0.12	–
Leaf 2	0.20*	0.14*	–
Leaf average	0.22**	0.20*	–
Weighted average	0.24**	0.19*	–
Lesion	0.19**	0.09	–
1991 Kabanyolo:			
Ear	0.22*	0.42***	0.34***
Plant	0.04	0.51***	0.64***
Leaf 1	0.04	0.22*	0.44**
Leaf 2	0.04	0.02	0.27**
Leaf average	0.22*	0.11	0.47***
Weighted average	0.24**	0.37***	0.41***
Lesion	0.03	0.14*	0.20*
1991 Namulonge:			
Ear	0.21*	0.22*	0.38***
Plant	0.27**	0.28**	0.16*
Leaf 1	0.23**	0.17*	0.13
Leaf 2	0.00	0.00	0.01
Leaf average	0.23**	0.21*	0.15*
Weighted average	0.24**	0.24*	0.22**
Lesion	0.31**	0.41***	0.19*

[a] AUDPC calculated using percent leaf area affected by northern leaf blight (Elliott and Jenkins, 1946) or number of northern blight lesions at growth stages (GS) 8, 9.0, 9.1, 9.2, 9.3, and 9.4 (Ritchie and Hanway, 1982); values were standardised by dividing by the number of days from the first to the last disease assessment time. Lesions were counted at GS 8, 9.0, 9.1, 9.2, and 9.3.

[b] Severity rated on whole plant (plant), ear leaf (ear), first leaf above ear leaf (leaf 1), second leaf above ear leaf (leaf 2), average of percent leaf area affected on the three leaves rated (leaf average), and average number of lesions on the three leaves (lesion). Weighted scale of 2–3–1 was designed to account for leaf position, contribution to yield, and disease onset on the ear leaf, leaf 1, and leaf 2, respectively.

[c] Experiment was conducted in 1990 at Kabanyolo and in 1991 at Kabanyolo and Namulonge.

[d] Astericks indicate significance of R^2, $^{*}P \le 0.05$, $^{**}P \le 0.01$, and $^{***}P \le 0.001$ (12 degrees of freedom in 1990 and 1991).

Evaluation of critical point models indicated that the most appropriate time to estimate potential yield loss varied with resistance level of the cultivar. Late disease assessments were more correlated with yield loss than early season assessments for moderately or resistant genotypes. For susceptible genotypes, critical point models, 2–4 wk after mid-silking gave better estimates than late season assessments. Thus, early season assessment may adequately predict yield loss for susceptible genotypes.

Relationships between yield and assimilate accumulation at various stages of maize plant have been reported (Fairey and Daynard, 1978; Levy and Leonard, 1990). Most assimilates contributing to yield are formed after silking. Thus, results of disease assessments at GS 8 and 9.0 (tasseling) sometimes indicated no significant relationship with yield. Although late disease assessments were more correlated with yield than earlier assessments, disease levels at the end of the epidemic reflect cumulative effect of disease

TABLE 5. Coefficients of determination (R^2) for the relationship between grain yield and percentage leaf area affected by northern leaf blight (*Exserohilum turcicum*) on the ear leaf at different stages on two maize cultivars in 1990 and three in 1991 at two locations in Uganda[a].

Growth stage	Cultivar		
	KWCA-SR	EV8428-SR	A619 x A632[b]
1990 Kabanyolo:			
8	0.14^{**c}	0.10	–
9.0	0.04	0.12	–
9.1	0.33^{***}	0.10	–
9.2	0.31^{***}	0.14^{**}	–
9.3	0.38^{***}	0.02	–
9.4	0.33^{***}	0.13^{**}	–
1991 Kabanyolo:			
8	0.11	0.27^{***}	0.02
9.0	0.05	0.18^{**}	0.10
9.1	0.19^{**}	0.25^{***}	0.21^{**}
9.2	0.47^{***}	0.33^{***}	0.26^{***}
9.3	0.16^{**}	0.38^{***}	0.25^{***}
9.4	0.19^{**}	0.40^{***}	
1991 Namulonge:			
8	0.02	0.17^{**}	0.00
9.0	0.05	0.14^{**}	0.34^{***}
9.1	0.34^{***}	0.14^{**}	0.53^{***}
9.2	0.22^{**}	0.21^{**}	0.16^{**}
9.3	0.32^{***}	0.24^{***}	0.31^{***}
9.4	0.26^{**}	0.25^{***}	

[a] Percentage leaf area affected on the ear leaf at GS 8.0, 9.0, 9.1, 9.2, 9.3, and 9.4 (Elliott and Jenkins, 1946; Ritchie and Hanway, 1982).

[b] Disease was not rated at GS 9.4 on A619 x A632.

[c] Astericks indicate statistical significance of R^2, where $^{**}P \leq 0.05$, $^{***}P \leq 0.01$, and $^{***} P \leq 0.001$.

epidemic (Campbell and Madden, 1990).

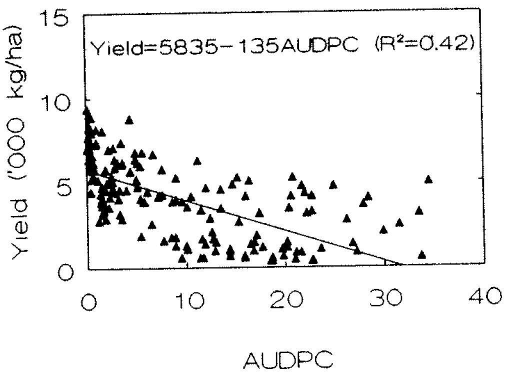

Figure 5. Relationship between yield and standardised area under the disease progress curve (AUDPC) for percentage leaf area affected by northern leaf blight (*Exserohilum turcicum*) on the ear leaf of two maize cultivars grown in Uganda in 1990 and three in 1991. Data based on 160 data points and the coefficient of determination was significant ($P \leq 0.001$).

In this study, northern leaf blight adversely affected yield, as has been documented previously (Ullstrup and Miles, 1957; Ullstrup, 1970; Raymundo and Hooker, 1981; Levy and Leonard, 1990). Yield of susceptible genotypes were reduced by 18–64%. Yields were significantly lower in plots under natural inoculum compared to fungicide-treated plots indicating that considerable yield loss does occur on susceptible genotypes in Uganda. High levels of disease developed with natural inoculum indicating that considerable inoculum was present and/or substantial spread occurred from inoculated plots. In the 2-yr study, northern leaf blight severity was low on resistant genotypes, Babungo 3 and B73xMo17, and these cultivarss showed no significant yield response to infection. Reductions in yield of Babungo 3 and B73xMo17 were usually <1% compared to EV8428-SR, KWCA-SR, and A632xA616 (unpublished). Our data, therefore, confirm the usefulness of resistance in the control of northern leaf blight (Perkins and Pedersen, 1987; Meyer *et al.*, 1991).

Often there was a significant cultivar by treatment interaction for disease and yield. This indicated that yield or disease response to treatment varied from cultivar to cultivar, and that some cultivars showed greater yield depression at high northern leaf blight severities. In 1990, the significant interaction was due to the response of EV8428-SR to different disease levels (treatments). In 1991, the interactions were significant in only one of the two locations. Also, lower R^2 values of the yield loss relationships to disease severity were obtained for EV8428-SR in 1991 at Kabanyolo compared to in 1990 and at Namulonge in 1991. The interactions from ANOVA and the distinct regression coefficients (b_0 and b_1) indicated that models must be constructed for each cultivar seperately. None of the regression equations of grain yield on disease severity resulted in a high R^2, indicating that much of the variability in yield could not be attributed to northern leaf blight. Overall, models based on AUDPC gave the best estimates of

TABLE 6. Regression statistics describing the relationship between grain yield and standardised area under the disease progress curve (AUDPC) for percentage leaf area affected by northern leaf blight (*Exserohilum turcicum*) on the ear leaf for two maize cultivars in 1990 and three in 1991 at two locations in Uganda[a].

Cutivar	Statistics[b]					
	b_o	$s(b_o)$	b_1	$s(b_1)$	MSE ($\times 10^4$)	R^2
1990 Kabanyolo:						
KWCA-SR	8886	713	-248	90	660^{***}	0.35
EV8428-SR	7007	1131	-108	47	1363^{*}	0.22
1991 Kabanyolo:						
KWCA-SR	7285	608	-249	909	781^{*}	0.22
EV8428-SR	7329	538	-277	125	1723^{**}	0.42
A619 x A632	2425	312	-68	20	311^{**}	0.34
1991 Namulonge:						
KWCA-SR	6904	464	-361	226	912^{*}	0.21
EV8428-SR	5269	500	-102	40	949^{*}	0.22
A619 x A632	2393	252	-25	14	498^{*}	0.32
Pooled[c]						
KWCA-SR	6849	208	-221	56	2213^{***}	0.20
EV8428-SR	7329	538	-277	124	1723^{***}	0.42
A619 x A632	2425	312	-22	8	312^{**}	0.34

[a] AUDPC calculated using percentage leaf area affected on the leaf ear (Elliott and Jenkins, 1946) at growth stage 8, 9.0, 9.1, 9.2, 9.3, and 9.4; values were standardized by dividing by the number of days between the first and the last assessment times (Campbell and Madden, 1990).

[b] b_o and b_1 are the intercept and slope, respectively; $s(b_o)$ and $s(b_1)$ are their standard errors, MSE is the mean square error; R^2 is the coefficient of determination.

[c] Pooled data for one year (A619 x A632) and two years (KWCA-SR and EV8428-SR).

[d] Astericks indicate the statistical significance of the regression model: $^{*}P \leq 0.05$, $^{**}P \leq 0.01$, and $^{***}P \leq 0.001$.

relationship between yield of susceptible and moderately susceptible genotypes. Similar results have previously been reported (Raymundo, 1978; Raymundo and Hooker, 1981; Bowen and Pedersen, 1988). Raymundo and Hooker (1981) found AUDPC models to predict yield only under high disease levels. However, in the study of Perkins and Pedersen (1987), AUDPC models were the best predictors of yield (R^2=0.66). Critical-point models were also useful for describing the relationship between yield and northern leaf blight severity on susceptible genotypes. Although the relationship between yield and severity of northern leaf blight were best described by AUDPC models, critical point models were the better predictors of the reduction in individual grain yield components (Bowen and Pedersen, 1988).

Our data suggests that considerable yield loss due to northern leaf blight does occur in Uganda. However, use of cultivars with high level of rate-reducing resistance, appears effective for control of northern leaf blight. Differences in yield-loss models of susceptible genotype EV8428-SR between years and locations accentuate the difficulties in estimating yield-loss relationships, and emphasize the need for yield-loss estimation over several years and in many locations (James, 1974; James and Teng, 1979).

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