Forage Yield Losses in Hybrid Pearl Millet Due to Leaf Blight Caused Primarily by *Pyricularia grisea*

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ABSTRACT

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The effects of leaf blight, caused primarily by *Pyricularia grisea*, on forage yield and digestibility of pearl millet hybrids were evaluated in 1990, 1991, and 1992. A range of disease severities on *Pyricularia*-susceptible hybrid Tifleaf 1 and on the resistant, near-isogenic hybrid Tifleaf 2 were established by inoculation with *P. grisea* or by application of chlorothalonil. Even with irrigation, no appreciable leaf blight developed in the dry 1990 season. In 1991 and 1992, disease severities (percentage of foliage with chlorosis and necrosis) in individual plots ranged from 3 to 35%. Leaf blight severity in 1991 and 1992 was negatively correlated ($P < 0.01$) with green plot yield, dry matter yield, and digestible dry matter yield. In vitro dry matter digestibility was unaffected by disease, and the response of dry matter concentration was inconsistent between years. Within the range of severities obtained, digestible dry matter yield decreased linearly with increases in leaf blight severity. Based on observed leaf blight severities of the *Pyricularia*-resistant Tifleaf 2, the regression equations estimate that minor pathogens that contribute to the leaf blight complex may reduce digestible dry matter yield of this hybrid by as much as 19%.

Pearl millet (*Pennisetum glaucum* (L.) R. Br. is a high-quality, rapidly growing summer annual forage that can be infected by several foliar pathogens. The effects of only a few of these diseases on yield and quality of pearl millet have been examined. In the southeastern United States, rust, caused by *Puccinia substriata* var. *indica*, primarily occurs late in the season and significantly reduces yield, digestibility, and digestible dry matter yield of the forage (9,15). Cercospora leaf spot, caused by *Cercospora penniseti* Chupp, is usually considered to be a minor disease, because highly susceptible pearl millets are rarely found. Burton and Wells (2) evaluated F_2 populations derived from crosses between a selected susceptible inbred, 664, and a resistant inbred, 442. Plants with moderately severe and severe infections had green forage yields reduced by 19–27%. Infection of pearl millet by *C. penniseti* usually occurs simultaneously with infections by several other pathogens (8,14), which together are manifested as a leaf blight

complex and result in foliar chlorosis and necrosis. Symptoms of foliar infection become evident early in the season, particularly as the canopy begins to close. Infection can continue throughout the season if conditions are favorable. However, leaf blight is usually most severe early in the season. Unless fully resistant and susceptible plant lines are available, effects of these individual pathogens are difficult to evaluate, because many of the organisms produce similar symptoms.

Of the organisms that contribute to the leaf blight complex, *Pyricularia grisea* (Cooke) Sacc. is the most important component (14), and infections are easily identified by symptoms. On susceptible pearl millets, gray, water-soaked lesions develop and become necrotic. Severe infection is usually accompanied by extensive chlorosis. Disease development is dependent on rainfall and humidity, and disease severity varies from season to season.

Although first identified in the United States in 1968 (13), Pyricularia leaf spot is now commonly observed at levels that attract the attention of plant breeders. Sources of resistance have been identified (12,16), and efforts have been made to incorporate resistance into improved cultivars and elite breeding lines. Highly effective resistance has been transferred from an introduction from Senegal into the cytoplasmic male sterile parent of the hybrid Tifleaf 2 (5).

Despite the prevalence and perceived importance of Pyricularia leaf spot, no information is available concerning losses of pearl millet forage due to *P. grisea* or the cumulative effect of the other less-understood fungi that contribute to the leaf blight complex. The following experiments were conducted to determine these effects. When infection by and the effects of *P. grisea* could be differentiated from the effects of other foliar pathogens, the distinction was made by designation as Pyricularia leaf spot. Otherwise, the term *leaf blight* is used to encompass the cumulative effects of infection by several fungi, including *P. grisea*, that are characterized by chlorosis and necrosis of the foliage.

MATERIALS AND METHODS

Plots were planted 16 May 1990, 3 May 1991, and 13 May 1992 in a randomized complete block of 12 treatments (Table 1) arranged in six replications. Treatments consisted of various combinations of hybrids with fungicide applications or inoculations to produce differing levels of disease in individual plots. In 1990, all plots were planted with Tifleaf 1 (susceptible to *P. grisea*). In 1991 and 1992, three of the treatments were planted with Tifleaf 2, which is "near-isogenic" to Tifleaf 1 (Table 1). Both hybrids have the same male parent. The female parent of Tifleaf 2 (Tift $85D_2A_1$) has genes for resistance to *P. grisea* and *P. s. indica* and is a backcross derivative of the female parent of Tifleaf 1 (Tift $23D_2A_1$). These hybrids cannot be differentiated either visually or by yield in the absence of Pyricularia leaf spot or rust (5). Because fungicide application did not entirely prevent leaf blight infection in 1990, Tifleaf 2 was included to obtain data from plots with low disease severities. The remaining nine treatments were planted to Tifleaf 1. Both hybrids were planted from commercially produced seed lots. Fertilizer (5-10-15 NPK) was applied in-furrow at planting at the rate of 280 kg/ha.

Three-row plots were 4 m long in 1990 and 5 m long in 1991 and 1992. The center row of each plot was inoculated with *P. grisea* or sprayed with chlorothalonil (Bravo 720, 8 ml/L) to establish different disease severities (Table 1). Inoculum (1.4×10^5 conidia per milliliter) was sprayed into the lower canopy along the length of inoculated plots. Fungicide was sprayed to runoff with a hand-held sprayer. Rainfall was infrequent early in the season in 1990, and the plots were supplied with overhead irrigation for 1 h prior to application of inoculum at each inoculation date. Because of drought conditions, little disease developed and fewer treatments were applied than were planned at the beginning of the year, resulting in two control treatments (treatments 6 and 7). In 1991, treatment 8 was inoculated and covered overnight (17 h) with plastic. Although infection levels were high within a week, some leaf damage was observed on these plots, so no other treatments were covered after inoculation.

The outer two rows were mowed 1–4 days before harvest, and leaf blight severity was visually estimated as the percentage of foliage in the center row that was chlorotic or necrotic. No rust infection was present at the time ratings were taken. Severity of each plot in each year was estimated four times on the day of harvest. Leaf blight severity of a plot was estimated as the mean of the four ratings.

To determine the relative importance of fungi contributing to the leaf blight complex in these hybrids in 1992, five leaves with lesions were sampled from each of the untreated Tifleaf 1 and Tifleaf 2 plots before harvest. Collected leaves exhibited lesions characteristic of Pyricularia leaf spot as well as other lesion types. Five leaf pieces with lesions from each leaf (approximately 2×2 cm) were surface-disinfected for 1 min in a 0.5% NaOCL solution and plated on V8 agar (20% V8 juice and 1.5% 0.1 N NaOH). A total of 150 leaf pieces from each hybrid were incubated at 24 C under continuous fluorescent lighting. Fungi growing from leaf pieces were identified microscopically 4–6 days after plating and were subcultured to V8 agar to facilitate identification when necessary.

Pyricularia leaf spot lesions were observed in the Tifleaf 2 plots in 1992. Because the resistance to *P. grisea* in Tifleaf 2 is conferred by a single dominant gene (16) contributed by Tift $85D_2A_1$, inoculations were performed in the greenhouse to determine whether the seed lot of Tifleaf 2 was contaminated or whether a change in virulence in the pathogen had occurred to result in the infection observed on Tifleaf 2 in 1992. Six single-lesion isolates of *P. grisea* collected from Tifleaf 2 plots were used to inoculate seedlings of Tifleaf 1 and Tifleaf 2. An average of 25 seedlings of each hybrid in each of two pots (replicates) were inoculated with each of the six isolates, by methods previously described (14).

After disease ratings were made and leaf samples taken in 1992

TABLE 1. Treatments used to establish diferences in leaf blight severities in pearl millet plots in 1990, 1991, and 1992

Treatment number	Hybrid[a]	Treatment[b]	Treatment dates 1990	Hybrid[a]	Treatment[b]	Treatment dates 1991	Treatment dates 1992
1	TL1	F	6-19, 6-27, 7-5, 7-13, 7-26	TL2	F	5-31, 6-10, 6-18, 6-24, 7-3	6-3, 6-10, 6-25, 7-1, 7-9, 7-16
2	TL1	F	6-19, 6-27, 7-5, 7-13	TL2	U		
3	TL1	F	6-19, 6-27, 7-5	TL2	I	5-30, 6-11, 6-18, 6-24	6-3, 6-10, 6-16, 6-25, 7-2
4	TL1	F	6-19, 6-27	TL1	F	5-31, 6-10, 6-18, 6-24, 7-3	6-3, 6-10, 6-25, 7-1, 7-9, 7-16
5	TL1	F	6-19	TL1	F	5-31, 6-10	6-3, 6-25, 7-9, 7-16
6	TL1	U		TL1	F	5-31	6-3, 7-9
7	TL1	U		TL1	U		
8	TL1	I	7-11	TL1	I	5-30 + cover[c]	6-25
9	TL1	I	7-2, 7-11	TL1	I	5-30	6-16, 6-25
10	TL1	I	6-26, 7-2, 7-11	TL1	I	5-30, 6-11	6-10, 6-25
11	TL1	I	6-20, 6-26, 7-2, 7-11	TL1	I	5-30, 6-11, 6-18	6-3, 6-10, 6-25
12	TL1	I	6-14, 6-20, 6-26, 7-2, 7-11	TL1	I	5-30, 6-11, 6-18, 6-24	6-3, 6-10, 6-16, 6-25, 7-2

[a] TL1 = Tifleaf 1, susceptible to *Pyricularia grisea*; TL2 = Tifleaf 2, resistant to *P. grisea*.
[b] F = fungicide (chlorothalonil) treated, U = untreated, I = inoculated with *P. grisea*.
[c] Plot covered with plastic for 17 h after inoculation.

to identify component fungi contributing to leaf blight, center rows were harvested at a 10-cm height with a forage chopper 31 July 1990 (75% anthesis), 12 July 1991 (10% anthesis), and 30 July 1992 (70% anthesis). Green yield was determined at harvest. To determine dry matter concentration, weights of samples (approximately 300 g each) from each plot were taken at harvest and were dried to constant weight in a forced-air oven at 60C for 48 h. Dry matter yield was calculated as the product of green yield and dry matter concentration. Digestibility was determined from samples used to determine dry matter concentration with a two-stage in vitro incubation, as described previously (15). Digestible dry matter yield was calculated as the product of green yield, dry matter concentration, and digestibility.

Data from each year were analyzed by analysis of variance and regression analysis. Sums of squares were partitioned into replication and treatment effects. Before analysis of variance, leaf blight severities for 1991 were transformed to log(percent severity + 1); and the 1992 data for green yield, dry matter concentration, dry matter yield, and digestible dry matter yield were transformed to log(variable + 1) to reduce associations between means and variances. Treatment means were tested for differences by Fischer's least significant difference. Pearson's correlation coefficients between leaf blight severity and components contributing to digestible dry matter yield were calculated for 1991 and 1992 data. Digestible dry matter yields were regressed on final disease severities, and yield reductions associated with disease were determined by linear regression. Data for both hybrids were included in the correlation and regression analyses. One sample from the 1991 test was misplaced before digestibility analyses, so only 59 digestible dry matter yields could be calculated and included in the correlation and regression analyses. After the intercept was determined, digestible dry matter yields were transformed as a percentage of the intercept to compare results based on a percentage loss with increasing disease severity.

RESULTS

Early-season drought in 1990 was unfavorable for leaf blight development. Treatment influenced ($P \leq 0.10$) leaf blight severity and dry matter concentration. Treatment means ranged from 9 to 16% affected foliage, but much of the necrosis appeared to be due to drought rather than leaf blight. There were few differences among treatment means for any other yield or quality variables examined in this experiment. No relationships between leaf blight severities and digestible dry matter yields were detected in 1990.

Conditions were more favorable for disease development in 1991 and 1992. Pyricularia leaf spot was observed in Tifleaf 2 plots in 1992. Inoculations in the greenhouse performed to determine whether the presence of the disease was due to seed contamination or selection for virulence to the resistance in Tifleaf 2 revealed that approximately 15% of the Tifleaf 2 plants were susceptible (infection types 3 or 4 [17]) to six isolates of *P. grisea*. The remainder of the plants were fully resistant with infection type 0. No evidence for virulence on Tifleaf 2 was observed from these inoculations.

Several foliar pathogens were isolated from Tifleaf 1 and Tifleaf 2 in 1992. Known pathogens among the 295 fungi isolated from Tifleaf 1 were *P. grisea* (41.4% of isolations), *C. penniseti* (6.8%), *Exserohilum rostratum* (4.4%), *Gloeocercospora sorghi* (5.1%), *Drechslera dematioidea* (3.4%), *Phyllosticta penicillariae* (1.0%), and *Bipolaris setariae* (0.7%). The remainder of the isolated fungi were either saprophytic or unidentified, or untested for pathogenicity. When only the minor pathogens (those other than *P. grisea*) were considered, isolation frequencies from Tifleaf 2 were nearly identical to those from Tifleaf 1.

Treatment was a significant ($P \leq 0.01$) source of variation for leaf blight severity, green yield, and dry matter concentration in 1991 (Table 2) and for leaf blight severity, dry matter concentration, dry matter yield, and in vitro dry matter digestibility in 1992 (Table 3). Treatments affected disease severities in individual plots. However, there was variation in the effectiveness of treatments used to establish different levels of disease. Frequent inoculations did not increase mean leaf blight severity significantly in either 1991 or 1992, possibly due to variation in microenvironmental conditions within plots. Replication was significant ($P \leq 0.05$) for green yield, dry matter concentration, dry matter yield, and digestible dry matter yield in both years. Replication significantly affected leaf blight severity in 1992 ($P \leq 0.01$) and in vitro dry matter digestibility in 1991 ($P \leq 0.10$) and 1992 ($P \leq 0.01$).

When relationships for individual plot data from 1991 and 1992 were examined, leaf blight severity was negatively correlated with green plot yield, dry matter yield, and digestible dry matter yield (Table 4). No relationship existed between leaf blight severity and in vitro dry matter digestibility, and correlations with dry matter concentration were inconsistent in these two years.

Based on linear regression, there was a decrease of digestible dry matter yield with increasing leaf blight severity (Fig. 1). Because digestibility was not affected by leaf blight infection, the regression equations relating dry matter yield and digestible dry matter yield to disease were nearly identical. The relationships between disease and digestible dry matter yield are presented to facilitate comparisons with previously obtained data on the effects of rust (15).

DISCUSSION

From these data we conclude that leaf blight can cause a significant reduction of forage yield, although there was a lack of precision in determining these effects, evident in the distribution of observations about the regression lines. The variability in the data is most likely due to differences in inherent levels of fertility in the experimental plot land. It was apparent that plots in

TABLE 2. Treatment means for leaf blight and components contributing to digestible dry matter forage yield of pearl millet hybrids in 1991

Treatment	Leaf blight log(% + 1)	Green yield (kg)	Dry matter concentration (%)	Dry matter yield (kg)	In vitro dry matter digestibility (%)	Digestible dry matter yield (kg)
1	0.95	10.3	24.9	2.56	64.1	1.65
2	0.97	13.2	24.9	3.26	62.9	2.03
3	0.94	13.5	24.7	3.34	60.3	2.00
4	0.90	11.9	24.5	2.86	63.2	1.80
5	1.33	9.0	24.2	2.17	63.9	1.38
6	1.18	10.4	25.5	2.73	60.2	1.57
7	1.23	11.9	25.0	2.96	59.6	1.76
8	1.03	13.3	24.7	3.24	57.0	1.84
9	1.33	11.4	26.0	2.93	58.5	1.71
10	1.30	9.9	25.6	2.54	59.6	1.51
11	1.16	13.4	25.1	3.34	58.8	1.96
12	1.14	12.2	24.8	3.00	61.3	1.85
LSD ($P = 0.05$)	0.21	4.0	1.5	0.92	4.8	0.56

TABLE 3. Treatment means for leaf blight and components contributing to digestible dry matter forage yield of pearl millet hybrids in 1992

Treatment	Leaf blight (%)	Green yield log(kg + 1)	Dry matter concentration log(kg + 1)	Dry matter yield log(kg + 1)	In vitro dry matter digestibility (%)	Digestible dry matter yield log(kg + 1)
1	6.5	1.10	1.372	0.47	59.2	0.247
2	11.0	1.04	1.378	0.41	61.7	0.200
3	11.9	1.03	1.365	0.40	58.2	0.160
4	7.6	1.04	1.388	0.43	59.5	0.201
5	9.8	1.04	1.380	0.42	55.3	0.159
6	15.6	1.08	1.365	0.44	60.2	0.220
7	19.1	1.06	1.359	0.42	55.0	0.163
8	19.4	1.10	1.377	0.48	57.7	0.240
9	20.6	1.02	1.365	0.38	51.8	0.096
10	19.0	1.14	1.371	0.51	56.9	0.262
11	20.7	1.00	1.368	0.37	54.2	0.106
12	21.0	1.06	1.386	0.44	56.8	0.192
LSD ($P = 0.05$)	5.2	0.12	0.028	0.14	3.1	0.140

TABLE 4. Pearson's correlation coefficients between leaf blight severity and components contributing to digestibile dry matter yield of pearl millet forage[a]

Component	Correlation with leaf blight severity	
	1991	1992
Green yield	−0.54**[b]	−0.48**
Dry matter concentration	0.37**	−0.32**
Dry matter yield	−0.50**	−0.48**
In vitro dry matter digestibility	0.02	0.13
Digestible dry matter yield	−0.53**	−0.52**

[a] Data for Tifleaf 1 and Tifleaf 2 were pooled.
[b] ** = Correlation significant at $P = 0.01$.

particular areas within the field had poorer growth than others, and replication was a significant source of variation for many of the variables measured in the experiments in 1991 and 1992.

Soil fertility effects on infection by *P. grisea* have been documented for other crops. In susceptible varieties, high nitrogen levels result in more severe infection in napier grass (*P. purpureum* Schumach) (1), ragi (finger millet, *Elusine coracana* G.) (10,11), and rice (*Oryza sativa* L.) (7). Increased phosphorus increases blast severity in rice (4). Potassium reduces severities in ragi (10), and silicon content of soils is negatively correlated with infection in rice (3).

The response to nitrogen is likely due to differences in canopy density. Poor infection levels obtained in 1990 suggest the limiting factor in infection by *P. grisea* may be humidity or free moisture. A dense canopy will reduce air circulation and penetration by sunlight, thereby retaining free moisture longer. If these assumptions are correct, low nitrogen could result in poor plant and canopy growth, leading to low yields with low disease levels. The data in Figure 1 indicate that this probably occurred in several of the plots, so that the losses due to leaf blight in well-fertilized pastures may have been underestimated.

Because Tifleaf 2 is resistant to *P. grisea*, leaf blight on this hybrid was the result of the cumulative effect of the minor pathogens described above. Untreated Tifleaf 2 plots had mean leaf blight severities of 10.2 and 11.0% in 1991 and 1992, respectively. If the intercept is considered to be an accurate estimate of yield from completely disease-free plants, loss of digestible dry matter yield due to the minor pathogens estimated from the regression equations was 16 and 22% in 1991 and 1992, respectively. The estimate obtained in 1991 may be more accurate, because the Tifleaf 2 plots in 1992 were contaminated with *Pyricularia*-susceptible plants. These calculated losses due to minor pathogens are considerably more than expected. However, they may be accurate since minor pathogens comprised about one-third of the total isolations of known pathogens from Tifleaf 1. These estimates may have implications in pasture-management practices that affect canopy density (such as grazing frequency or row spacing) and suggest that breeding for resistance to the minor pathogens is warranted.

Losses of pearl millet forage to leaf blight differed from the response to rust (15). In the present evaluations, leaf blight infection was detrimental only to growth of pearl millet. No effect on digestibility of the whole-plot forage was observed. Leaf blight infection resulted in a simple relationship expressed as reduced growth with increased infection. Rust infection of pearl millet reduces both growth, measured as dry matter yield, and digestibility of the forage. The detrimental effects of rust infection interact to result in a logarithmic relationship between rust severity and digestible dry matter yield (15).

Tifleaf 2 yields up to 22% more forage than Tifleaf 1 in environments with high disease pressure (5). This estimate of forage yield does not account for differences in digestibility of the forage infected with rust. Hill et al (6) evaluated the grazing performance of yearling heifers on Tifleaf 1 and Tifleaf 2 in a 2-yr study. When tester grazing days and average daily gains were used to determine weight gain of heifers ($kg \cdot ha^{-1}$), that of heifers on Tifleaf 1 was about 30% less than on Tifleaf 2.

Regression equations from the present experiments and previously published data on the effects of rust (15) can be used to compare our estimates of the total loss of digestible dry matter yield due to Pyricularia leaf spot and rust with the studies above. Leaf blight is primarily an early-season disease and rust is a late-season disease. We generally harvest twice to evaluate the performance of hybrids. Because Tifleaf 1 and Tifleaf 2 are near-isogenic hybrids differing in their reactions to Pyricularia leaf spot and rust, the reduction of digestible dry matter yield of Tifleaf 1 compared to Tifleaf 2 in the first harvest can be attributed to Pyricularia leaf spot, and reductions in the second harvest can be attributed to rust.

Using the mean leaf blight severities of untreated Tifleaf 1 and Tifleaf 2 in Tables 2 and 3 and the regression equations in Figure 1, it can be determined that the digestible dry matter yield of the first harvest of Tifleaf 1 over 2 yr averaged 18% less than that of Tifleaf 2. From mean rust severities in untreated plots of Tifleaf 1 and Tifleaf 2 in 1988 and 1989 tests (15) and the appropriate regression equations from that study, it can be determined that the digestible dry matter yield of the second harvest of Tifleaf 1 over 2 yr averaged 43% less than that of Tifleaf 2.

Approximately 67% of total harvested yield of Tifleaf 2 accumulates before the first harvest, with the remaining 33% removed in the second harvest (*unpublished data*). By combining this yield distribution with the calculated digestible dry matter loss attributable to Pyricularia leaf spot (−18%) for the first harvest and rust (−43%) for the second harvest, it can be estimated that Tifleaf 1 should yield 26% less digestible dry matter than Tifleaf 2. The similarity between our estimates and those of Hill et al (6) is an initial confirmation of the validity of our yield loss equations.

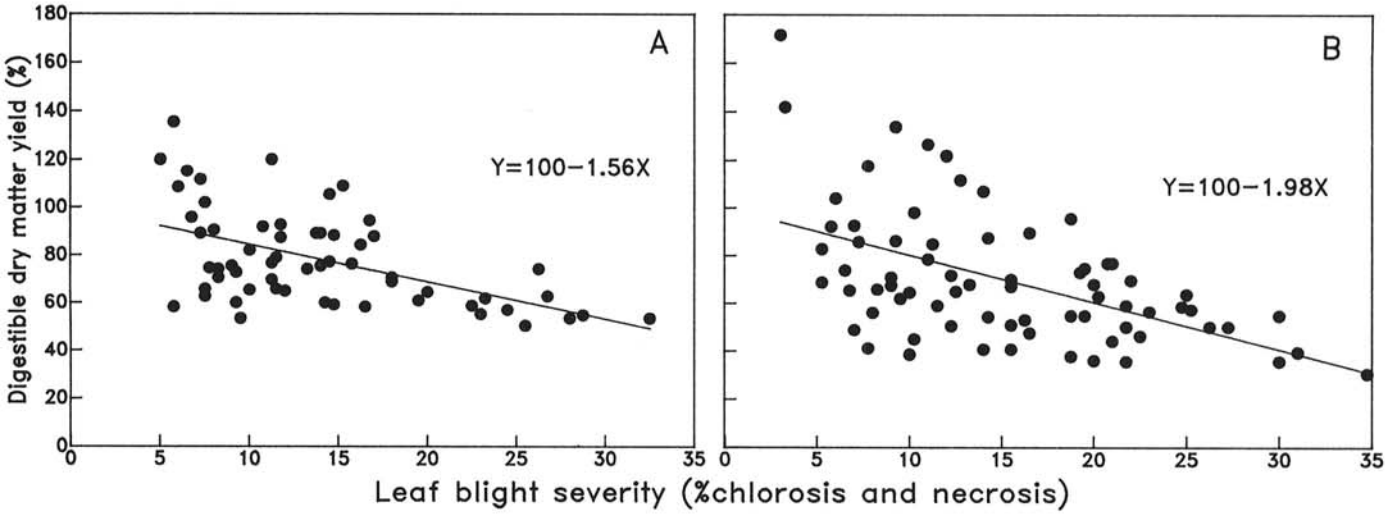

Fig. 1. Effect of leaf blight infection, caused primarily by *Pyricularia grisea*, on digestible dry matter yield of pearl millet forage in **A,** 1991 ($R^2 = 0.29$; $P \leq 0.01$), and **B,** 1992 ($R^2 = 0.28$; $P \leq 0.01$). Data for Tifleaf 1 and Tifleaf 2 are pooled and are expressed as digestible dry matter yield of individual plots as a percentage of the calculated intercept.

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