

Role of edaphic factors in the development of downy mildew (*Sclerospora graminicola*) in pearl millet

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SUMMARY

Infection of pearl millet by downy mildew [*Sclerospora graminicola* (Sacc.) Schrot.] has been shown to be influenced by soil pH, soil bulk density, soil moisture content and addition of farmyard manure and nitrogen fixing bacteria. A pH value of 8.5 allowed disease to develop the most, with increases in acidity to pH 7.5 producing 70% reduction in disease. Higher soil bulk density and moisture content also led to reductions in disease but the effects were not as marked as for pH. The addition of farmyard manure to soil or the addition of *Rhizobium*, *Azospirillum* or *Azotobacter* inocula as combined seed and soil treatment also reduced disease with the best effects being from a cluster bean isolate of *Rhizobium* and from *Azotobacter chroococcum*. Assessment of rhizosphere microorganisms associated with the resistant and susceptible varieties of pearl millet showed that, overall, the fungal population was lower in the resistant varieties but that it was increased in both susceptible and resistant varieties by infection with downy mildew. Bacterial and actinomycete populations were also lower in resistant varieties but in this case downy mildew infection decreased the rhizosphere populations of both groups.

Dehydrogenase activity of rhizosphere soil was higher in susceptible varieties but was decreased in both variety types by infection with *S. graminicola*.

The results are discussed with reference to possible mechanisms to explain the observed effects.

INTRODUCTION

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is the staple diet of a vast population in tropical and subtropical countries and 26 million ha are grown annually (Singh 1995). Downy mildew, caused by *Sclerospora graminicola* (Sacc.) Schrot. is widely distributed in temperate and tropical areas of the world but it is especially important in India and Africa (Singh *et al.* 1993).

Host, environment, edaphic and biotic factors influence the processes involved from oospore infection to zoospore infection cycle of the pathogen. Both give rise to an infected crop. Growth, the infection process and survival of soil borne pathogens are greatly influenced by the physico-chemical and biotic factors of the soil (edaphic factors). Interactions between soil physico-chemical properties and biotic factors results in an extremely complex environment

in which a change in one factor leads to changes in the others (Griffin 1969). Soil moisture, along with soil temperature, organic matter and pH influence the development of antagonistic or competing microflora. All these factors directly or indirectly govern the incidence of plant diseases (Rotem 1978). Little is known about the effect of edaphic factors on the oospore phase and the initiation and the development of downy mildew disease. The present investigations were carried out to determine the influence of edaphic factors on downy mildew in pearl millet under arid environmental conditions.

MATERIALS AND METHODS

Pot and field experiments were conducted to examine the influence of various soil factors on the susceptibility of pearl millet to the incidence of downy mildew and development of the pathogen. In order to provide a conducive environment for disease development, experiments were conducted under partially controlled conditions below a shading net. Known pearl millet susceptible variety HB 3 was selected for all the studies except for rhizosphere

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microorganisms and dehydrogenase activity where Pearl millet downy mildew susceptible (HB 3 and BJ 104) and resistant (MH 179 and WCC 75) varieties were used.

Pot experiments

Soil collected from a field always free from pearl millet cultivation was used to fill earthen pots (8 kg/pot). The experimental soil was a sandy loam (1.45–1.50 g/cm bulk density, 10% moisture (w/w) at field capacity, 8.1 pH and 0.4% organic matter). Experiments were conducted over two consecutive years (1991 and 1992).

Ten grammes of one-year-old oospore powder, obtained by pulverizing dried and matured downy mildew infected leaves and heads of pearl millet and maintained in the laboratory, was incorporated in each pot and also used as a seed dressing (4 g per kg seed) by adding a little gum and water. During the experiment each pot was irrigated with 1 litre of water every 3–4 days. Observations on systematically infected and healthy plants were recorded from one day after disease appearance. The infected plants were uprooted each time and discarded to check or minimize the secondary infection. Disease incidence based on % infected plants was calculated at 35 and 42 days after sowing (DAS) and the correlation of disease incidence with variations in the soil factors at 42 DAS was determined. All the pot experiments were conducted in completely randomized design.

Effect of soil pH

The pH of the native soil (8.1) was brought to 9.0 and 8.5 by adding sodium bicarbonate and to pH 7.5 by adding potassium sulphate. After mixing the separate salts thoroughly, the soil was moistened and kept at equilibrium for three days under a polythene cover. The experiment had five replicates.

Effect of bulk density

Soil was added to the pots and compressed to achieve bulk densities of 1.29, 1.50, 1.80 and 2.12 g/cm. The experiment had four replicates.

Effect of organic matter

Well decomposed farmyard manure (FYM) was mixed thoroughly with soil at 160, 80 and 40 g/pot. A control (no FYM) was also maintained. The experiment had four replicates.

Field experiments

Effect of soil moisture

The experiment was conducted in 1 × 1 m microplots under a shading net using a randomized block design with three replications. Thick polythene sheets were inserted between the pot boundaries up to 1 m depth

to check the lateral inter-plot movement of soil water. Six levels of soil moisture were maintained by applying water at 4, 8, 12, 16, 20 and 24 l/plot at a regular interval of 4–5 days. The plots were protected from rain water by covering with polythene sheets at the time of rain. Soil moisture content was determined gravimetrically one day and up to 20 days after every irrigation. 200 mg of seeds coated with oospore powder by adding a little gum and water were sown in each furrow (1 m length at 20 cm apart). Oospore powder at 3 g/furrow was also applied just before sowing. As the experiment was conducted for only 35 days and the infected plants appearing from 23 DAS were to be uprooted after every count, the initial plant population maintained was rather high. Percentage disease incidence was calculated at 35 DAS. Available soil moisture (ASM), using average moisture content during 20 days was computed using the formula given by Thompson (1957).

$$\text{ASM (\%)} = \frac{\text{Total moisture} - \text{wilting point}}{\text{Field capacity} - \text{wilting point}} \times 100$$

Effect of nitrogen-fixing bacteria

Six symbiotic and free living nitrogen-fixing bacteria, *Rhizobium phaseoli*, *Rhizobium* spp. (Cluster bean strain), *Azospirillum brasilense*, *Azospirillum lipoferum*, *Azotobacter chroococcum* A and *Azotobacter chroococcum* B procured from the soil microbiology laboratory of the Central Arid Zone Research Institute, Jodhpur, India, were used and compared with an untreated control. Seeds were treated with the respective bacterial cultures and sown in furrows containing oospore powder at 3 g/m. Bacteria were also added directly to the furrow. The inoculum concentration was not recorded. 200 mg of seeds were sown in each of two 1 m rows for each treatment in triplicate in a randomized block design. Shading was provided by a net. Diseased and healthy plants were counted regularly and infected plants were then uprooted and discarded. Percentage disease incidence at 35 DAS was calculated.

Rhizosphere microorganisms and dehydrogenase activity

Ten grammes of rhizosphere soil, adhering to roots of diseased and healthy plants of susceptible (HB 3 and BJ 104), resistant (MH 179) and healthy plants of highly resistant (WCC 75) varieties in the field were assayed to determine the microbial population. Martin's rose bengal agar (Martin 1950), Kenknight's agar (Subba Rao 1986) and Thornton's agar (Thornton 1992) were used for estimating the population of fungi, actinomycete and bacteria. There were four replicates for each analysis. Dehydrogenase activity (DHA) was determined by the method of Casida *et al.* (1964). A 1 g sample of soil from the

rhizosphere was incubated with 2, 3, 5 triphenyl tetrazolium chloride and the production of triphenyl formazan was determined colorimetrically at 485 nm. The results were submitted to an analysis of variance in completely randomized design.

RESULTS

Effect of soil pH

Disease incidence increased slightly with a decrease in soil pH from 9.0 to 8.5, but then declined as the pH fell to 8.1 and was much less at pH 7.5 (Table 1). Effects were consistent at both assessment times.

Effect of bulk density

Increasing the soil bulk density caused a reduction in disease (Table 2). At 1.29 g/cm bulk density the disease at 42 DAS was 21.9% lower as compared to that at 2.12 g/cm. Effects were uniform at both assessment times. Per cent disease incidence was negatively correlated ($r = -0.97$, $n - 2 = 2$) with bulk density ($P < 0.05$).

Effect of organic matter

A consistent decrease in disease was noticed with increase in the rate of FYM (Table 3). Per cent disease incidence was negatively correlated ($r = -0.97$, $n - 2 = 2$) with organic matter ($P < 0.05$). At 35 DAS, with 160 and 80 g FYM applications diseases was not statistically different but both had significantly lower disease than the 40 g and control treatments. Disease at 42 DAS was the lowest (24.4% lower than control)

Table 1. *Effect of soil pH on downy mildew incidence in pearl millet at Jodhpur, India*

pH	Downy mildew incidence (%)	
	35 DAS	42 DAS
9.0	35.74 (36.71)	38.80 (38.53)
8.5	40.18 (39.33)	43.13 (41.04)
8.1	33.44 (35.31)	38.27 (38.19)
7.5	10.25 (18.66)	12.37 (20.51)
S.E.M. (16 D.F.)	(0.75)	(0.90)
C.D. ($P < 0.05$)	(2.25)	(2.69)

Figures in parentheses are arc sine angular transformed values.
DAS, days after sowing.

Table 2. *Effect of bulk density on downy mildew incidence in pearl millet at Jodhpur, India*

Bulk density g/cm	Downy mildew incidence (%)	
	35 DAS	42 DAS
1.29	37.63 (37.82)	41.61 (40.16)
1.50	36.54 (37.18)	40.64 (39.62)
1.80	35.13 (36.34)	37.64 (37.84)
2.12	29.08 (32.61)	32.06 (34.46)
S.E.M. (12 D.F.)	(1.07)	(0.99)
C.D. ($P < 0.05$)	(3.30)	(3.04)

Figures in parentheses are arc sine angular transformed values.

DAS, days after sowing.

at 160 g application followed by 80 g (15.4% lower than control). Disease in the 40 g treatment and in the control was almost equal.

Effect of soil moisture

The negative effect of soil moisture on disease was clearly noticeable as an increase in soil moisture decreased disease (Table 4). Disease incidence at 38.53% ASM was significantly more than all other

Table 3. *Effect of farm yard manure application on downy mildew incidence in pearl millet at Jodhpur, India*

FYM (g/pot)	Downy mildew incidence (%)	
	35 DAS	42 DAS
160	29.40 (32.84)	35.81 (36.71)
80	34.04 (35.70)	40.06 (39.26)
40	40.12 (39.30)	46.03 (42.72)
Control (No application)	42.08 (40.44)	47.36 (43.49)
S.E.M. (12 D.F.)	(1.01)	(0.82)
C.D. ($P < 0.05$)	(3.10)	(2.54)

Figures in parentheses are arc sine angular transformed values.
DAS, days after sowing.

Table 4. *Effect of soil moisture on downy mildew incidence in pearl millet at Jodhpur, India*

Water applied (l)	ASM (%)†	Downy mildew incidence (%) 35 DAS
4	38.53	61.11 (51.38)*
8	52.93	60.26 (50.95)
12	63.87	57.27 (49.18)
16	78.27	40.18 (39.34)
20	88.00	41.45 (40.07)
24	96.80	37.97 (38.01)
S.E.M. (10 D.F.)	—	(1.08)
C.D. ($P < 0.05$)	—	(3.40)

* Arc sine angular transformed values.

† Mean of 20 days.

DAS, days after sowing; ASM, available soil moisture.

Table 5. *Interaction of downy mildew pathogen with N fixing bacteria in pearl millet at Jodhpur, India*

Subject number	Treatment	Downy mildew incidence (%) 35 DAS
1	<i>Rhizobium phaseoli</i>	26.41
2	<i>Azospirillum brasilense</i>	28.36
3	<i>A. lipoferum</i>	25.46
4	<i>Azotobacter chroococcum</i> A	18.61
5	<i>A. chroococcum</i> B	14.53
6	<i>Rhizobium</i> spp. (Cluster bean isolate)	14.88
7	Control	43.79
S.E.M. (12 D.F.)		0.98
C.D. ($P < 0.05$)		3.02

DAS, days after sowing.

moisture levels except at 52.93% ASM. At 96.8% ASM, disease was the lowest (37.9% lower than at 38.53% ASM) but statistically similar to that at 88% and 78.27% ASM. A correlation study revealed a highly significant ($P < 0.01$) negative relationship ($r = -0.94$) between variation in soil moisture and PDI ($n - 2 = 4$).

Effect of nitrogen-fixing bacteria

All nitrogen-fixing bacteria treatments reduced the downy mildew infection compared to the uninoculated plants (Table 5). The best effects came from the crops grown with *Azotobacter chroococcum* B (66.9% lower disease than control) or *Rhizobium* spp. (cluster bean isolate) with 66% lower disease as compared to

control, although significant effects were also observed with *Azotobacter chroococcum* A and to a lesser extent with *Azospirillum brasilense*, *A. lipoferum* and *Rhizobium phaseoli*.

Rhizosphere microorganisms and dehydrogenase activity

Overall the fungal population was significantly lower in resistant varieties than in the susceptible varieties (Table 6). Increase in fungal population by downy mildew was significant in susceptible varieties, HB 3 and BJ 104 but not in resistant variety MH 179. The bacterial and actinomycete populations were also significantly lower in resistant varieties than in susceptible varieties but their populations decreased

Table 6. Rhizosphere population and dehydrogenase activity of healthy and infected resistant and susceptible varieties of pearl millet at Jodhpur, India

Subject number	Rhizosphere population (per g soil)			DHA ($\mu\text{g TFP/g/h}$)
	Fungal ($\times 10^3$)	Bacterial ($\times 10^4$)	Actinomycete ($\times 10^4$)	
Susceptible varieties				
1 HB healthy	70.50	36.25	42.50	5.71
2 HB 3 infected	90.00	22.75	30.25	4.48
3 BJ 104 healthy	65.50	42.75	63.00	5.97
4 BJ 104 infected	110.25	24.50	30.00	4.65
Resistant varieties				
5 MH 179 healthy	39.25	21.75	29.00	4.93
6 MH 179 infected	55.50	16.25	22.75	4.25
7 WCC 75 healthy	36.75	24.75	24.50	4.98
S.E.M. (21 D.F.)	6.14	3.14	3.85	
C.D. ($P < 0.05$)	18.07	9.23	11.33	

DHA, dehydrogenase activity.

significantly in infected susceptible varieties, while in one resistant variety (MH 179) the decrease was non-significant.

Dehydrogenase activity was higher in susceptible varieties than in the resistant varieties. With infection, a decrease in DHA was noticed in both types of varieties. Bacteria and actinomycetes were found to have a significant positive correlation with DHA [$r = 0.96$ ($P < 0.01$) and 0.87 ($P < 0.05$), respectively ($n - 2 = 5$)].

DISCUSSION

A pH of 8.5 was found to be optimum for downy mildew development in pearl millet. The effect of soil pH on downy mildew may be direct either through its lethal influence on the oospores as such or on germinating oospores. The indirect effect of pH on downy mildew incidence may be through the former's influence on the microbial population (including antagonists) in the rhizosphere (Waksman 1959; Kaufman & Williams 1965) and also on the solubility, availability and uptake of nutrients (Barber 1984). The pH directed micronutrient changes in the soil are indirectly supported by the findings of Gupta (1989) who observed a reduction in primary infection with the soil application of boron, and in secondary infection by foliar sprays of Cu, Zn, Fe and Mo in downy mildew of pearl millet under native soil having pH 8.1. At pH 8.1 the disease was about three times more than at pH 7.5 in the present study. Kaufman & Williams (1965) observed a greater development of the antagonists *Penicillium funiculosus* and *P. oxalicum* to *Fusarium* and *Verticillium* wilt at pH 6.5 to 7.3 rather than at pH 4.9 to 5.4. Woltz & Jones (1973) found that at pH 6.0, application of superphosphate beyond the optimum dose in tomato increased wilt

incidence while at pH 7 or 7.5 wilt did not increase which may be due to a decrease in the availability of phosphorus.

Bulk density is a measure of pore space in the soil. Higher bulk densities can result in reduced oxygen diffusion (Craig 1992). This decrease in oxygen level in the soil might have proved lethal to oospores and their germination. Tasugi (1933) reported higher oospore germination of *Sclerospora graminicola* incubated in an oxygen-rich water medium. The decrease in disease with increased bulk density seen in the present study can thus possibly be attributed to the reduction in soil aeration. The low bulk density (1.45 to 1.50 g/cm³) of the soil of this region could thus be one of the predisposing factors for downy mildew disease in pearl millet.

Addition of organic matter (FYM) discouraged the development of downy mildew. Qian & Leander (1987) found a positive correlation between the oospore lysis of *Pythium ultimum* and percentage organic matter of the soil, so it is possible that FYM might have proved lethal to the oospores of the fungus. The negative effect of FYM on disease may also be attributed to chemical gradients (Bowen & Rovira 1976), an altered nutrient balance in soil, host and pathogen (Saxena 1980), or by altering soil structure (Tsunio 1991), and cation exchange capacity of the soil (Barber 1984). The organic matter might have also played some role in discouraging downy mildew disease by developing intense competition for the space and nutrients through activation of general soil microflora and antagonistic microorganisms (Rangaswami 1988). Several soil-borne microorganisms are known to parasitize oospores of many downy mildew pathogens (Person *et al.* 1955; Kenneth & Shahor 1974). However, the role of FYM in

lowering downy mildew infection by inducing more vigorous growth of the pearl millet plants cannot be ruled out. Better root development, including root elongation, branching, root hair development and fresh root weight at early growth stages in maize, soybean and wheat with FYM application has been reported (Tsunio 1991).

The fact that the incidence of downy mildew is not favoured by high soil moisture is in general agreement with the observations of Kenneth (1981), Balasubramaniam (1974) and Gupta & Gupta (1988) in downy mildew and by Stover (1953), and Edmund (1964) in other soil-borne diseases. Low soil moisture may predispose the host to the attack by the pathogen (Edmund 1964), either by reducing plant vigour through harmful physiological or metabolic changes, or by weakening the cellular defence mechanism by depleting roots' carbohydrates (Dodd 1980).

Inversely high soil moisture affects the growth and also the survival of resting spores of the pathogen (Shokes *et al.* 1977). High soil moisture made the soil environment favourable for the host by influencing soil temperature, soil aeration and availability of minerals and nutrients. This may be either through accelerated diffusion of plant exudate which alters the antagonism within soil microflora in rhizosphere and non-rhizosphere (Griffin 1963); increased bacterial and actinomycetes population (Ramarao & Raja 1980), or altered oxygen diffusion (Craig 1992). Lochhead (1959) postulated that at high soil moisture levels the growth factor necessary for the pathogen to initiate infection probably gets diluted and is not available in sufficient quantities and this in turn stimulates antagonistic fungi around the rhizosphere decreasing the chances of the colonization of the root by the pathogen. Thus, at a low water potential, soil borne pathogens become free from the antagonistic influence from the soil microbiota by limiting the growth of other organisms more than that of the pathogen itself. The growth of uninfected pearl millet plants was similar at all moisture levels. Oospore germination was not observed in the *Sclerospora sorghi* when they are surrounded by almost 100% water (Balasubramanian 1974).

The reduction in downy mildew incidence owing to free living nitrogen-fixing bacteria (*Azotobacter* spp. and *Azospirillum* spp.) may be ascribed to their role on both host and pathogen while the affectivity of *Rhizobium* spp. may be only through their effects on the pathogen. These bacteria were found to be very responsive in sandy soils (Dobereiner 1977). The increased growth rate of pearl millet in response to these free living nitrogen-fixing bacteria might have helped in escaping the disease incidence. Under similar soil and agroclimatic conditions, elongation of radicle and plumule, advancement of initiation in lateral root primordia, marked increase in lateral roots and root hairs in pearl millet seedlings by presowing seed

inoculation with *Azospirillum brasilense* under pot and laboratory experiments (Venkateswarlu & Rao 1983) and increase in tillers, test weight and grain yield of pearl millet under field conditions (Joshi & Rao 1989) have been observed. The induced growth was attributed to the better nitrogen fixation and production of growth hormones by the bacteria. The positive effects of *Azotobacter* inoculation on growth of pearl millet was reported by Reddy & Reddy (1981). Action of nitrogen fixing bacteria (both free and symbiotic) on the pathogen may be another possible cause of reduction in disease incidence. Bacterial action may be direct on the pathogen by posing competition for nutrients and space by fast multiplication, and indirectly by the activation of soil microflora including the antagonists. Rangaswami (1988) reported that when seeds carrying a pretreated load of microorganisms are sown, certain microorganisms are selectively activated while the others are suppressed and the organisms loaded through pre-treatment of seeds become dominant. Thus *Rhizobium*, *Azotobacter* and *Azospirillum* applied as seed treatment established on the root surface of germinating seed.

Presence of higher microbial populations found in the rhizosphere of susceptible varieties in pearl millet suggests that the number of antagonistic organisms have an overriding role in suppressing the development of disease over the microbial population. Rangaswami (1988) has isolated organisms, specifically antagonistic to the relevant pathogen from the rhizosphere of resistant varieties but not from susceptible varieties in some crops. He also indicated that it was not possible to establish a pathogen in the rhizosphere of a non-host or resistant host varieties, whereas it could readily be accomplished in susceptible varieties. A resistant cultivar of pea became susceptible to *Pythium debaryanum* when its seed was treated with the exudate from the seed of a susceptible variety which was found to release significantly more sucrose during germination than the seeds of resistant varieties (Wood 1980). Thus, it seems that nutrients of plant origin in the rhizosphere vary in amount and chemical spectrum with the varieties and physiological conditions of the plant. Presence of more total microbial populations in rhizosphere of susceptible varieties of pearl millet may be ascribed to production of more exudates by susceptible varieties and less and antagonistic growth promoting exudates by resistant varieties, making the pathogen incapable of infecting root or underground parts of the resistant host. Further increase in fungal populations and decreases in bacterial and actinomycete populations due to infection indicate that the root exudates may change not only quantitatively but also qualitatively due to the disease infection. Rangaswami (1988) also stated that the complex system of biological and biochemical relationships in the rhizosphere continuously change

because of the change in physiological condition of the plant.

The DHA increases with an increase in microbial population (Skujins 1973), therefore, in the present study susceptible varieties were found to have more DHA than the resistant varieties as the former varieties had more rhizospheric microbial

populations. The decrease in DHA with infection was mainly due to reduction in the population of bacteria and actinomycetes as indicated by positive correlation between DHA and bacterial and actinomycete population. The study clearly indicates that soil environment plays a definite role in influencing the incidence of downy mildew in pearl millet.

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