Downy Mildew Disease of Pearl Millet (Bajra): Infection, Damage and Management Strategies

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Article History

Manuscript No. 251b
Received in 16th January, 2011
Received in revised form 25th February, 2012
Accepted in final form 6th March, 2012

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Keywords

Pearl millet, downy mildew disease, Damage, management

Abstract

Systemic symptoms downy mildew disease of pearl millet (*Pennisetum glaucum* L.) generally appear on the second leaf, subsequently leaves and panicles also develop symptoms. Leaf symptoms begin as chlorosis (yellowing) at the base of the leaf lamina, and successively higher leaves show a progression of greater leaf coverage. Inoculation of plants by spraying with a suspension of zoospores (released from sporangia of *Sclerospora graminicola*) induced immediate encystment of the zoospores and drastically reduced their ability to cause disease. The earliest symptom expression and the highest downy mildew were recorded when oosporic powder was placed below and above the seeds in furrows. Genetic resistance is the most economic and feasible method for control. Cuticular and epidermal thickness were significantly higher in leaves of the highly resistant cultivar (P-310-17) compared with the highly susceptible cultivar (7042 DMS). Seed treatment with 6 g Apron 35 WS kg^{-1} of seed + spray of 4 g Ridomil MZ l^{-1} recorded the lowest disease incidence at 30 days after sowing and at the dough stage.

1. Introduction

The downy mildew (DM) disease of pearl millet [*Pennisetum glaucum* (L) R. Br.] sometimes referred to as 'green ear' disease is caused by *Sclerospora graminicola*, which is the type species of the genus *Sclerospora*. It is the most widespread and destructive diseases of pearl millet in India and Western Africa (Rachie and Majmudar, 1980). This disease, first reported in India (Butler, 1907), is present in more than 20 countries (Safeeulla, 1976) and is a major factor limiting the full exploitation of the high yield potential of hybrids in India (Singh et al., 1993).

2. Symptoms

Bajra downy mildew systemic symptoms generally appear on the second leaf, and once these appear, all the subsequent leaves and panicles also develop symptoms (Sing and King, 1988). The disease can appear on the first leaf also under favorable conditions of severe disease development. Leaf symptoms begin as chlorosis (yellowing) at the base of the leaf lamina, and successively higher leaves show a progression of greater leaf coverage by symptoms. The half-leaf symptom, characterized by a distinct margin between the diseased (basal portion) and non diseased areas towards the tip, occurs in pearl millet genotypes. It is similar to the half-leaf symptoms caused by *Peronosclerospora sorghi* on sorghum and maize. Under conditions of high humidity and moderate temperature, the infected chlorotic leaf areas support a massive amount of sexual sporulation, generally on the abaxial surface of leaves, giving them a downy appearance. Severely infected plants are generally stunted and do not produce panicles. The name 'green ear' stems from the appearance of green panicles due to transformation of floral parts into leafy structures, which can be total or partial. This is sometimes referred to as virescence. These leafy structures can also be chlorotic, and sometimes support sporulation. In certain cases, green ear is the only manifestation of the disease. There is a report of artificially induced localized 'green ear' symptoms resulting from panicle inoculation under green house conditions (Semisi and Ball, 1989). Symptoms are rarely seen as local lesions or isolated spots on leaf blades (Saccas, 1954). Spots vary in shape and size, and are at first chlorotic and produce sporangia and later become necrotic.

3. Causal Organism

The disease causing pathogen is *Sclerospora graminicola* produces two types of spores, asexual spores known as sporangia and sexual spores knows as oospores. The whitish downy growth of the pathogen on the leaf surface is the 'asexual phase'. This

phase is generally followed by the 'sexual phase' in which oospores are produced within leaf tissues.

3.1. Asexual phase

Sporangiophores are short, stout, determinate and dichotomously branched structures that emerge from systemically infected leaves through stomata. Sporangia are reproduced on sterigmata located at the tips of sporangiophore branches. Fully developed sporangia are hyaline, thin-walled, ellipsoid or broadly elliptic and papillae, with dimensions of 15-22 x 12-21 µm (Saccas, 1954; Jouan and Delassus, 1971). It was recently determined that sporangial production can occur between 10 and 30ºC with an optimum production at 20ºC (Singh et al., 1987). Sporangia germinate indirectly by producing zoospores. The number of zoospores per sporangium may vary from 1-12 (Shetty, 1987). Zoospores swim for 30-60 min, encyst, and then germinate by forming a germ tube. Sporangia liberate zoospores at a wide temperature range (10-45ºC). Similarly, germ tube grows at temperatures ranging from 15 to 35ºC. Zoospores retain their infectivity for about 4 h at 30ºC, and for a longer period at lower temperatures (Singh and Gopinath, 1990).

3.2. Sexual phase

The process of sexual reproduction in *Sclerospora graminicola* is initiated in antheridia (male) and oogonia (female) and culminates in the formation of oospores. Oospores are produced in large numbers. As a rule, in *Sclerospora* spp. the oogonial wall is fused with the oospore wall, which is a major identifying feature of this genus. The mature oospore is spherical and brownish yellow and measures 32 µm (22-35 µm) in diameter. Two mating types have been identified and are considered to be necessary for the production of oospores, illustrating the heterothallic nature of the pathogen (Michelmore et al., 1982). Many workers have reported on the germination of oospores, both directly by germ tubes and indirectly by the liberation of zoospores, with great variation in the frequency of germination (Nene and Singh, 1976). However, these results have generally not been reproducible. Recently, however, Panchbhai et al. (1991) reported obtaining up to 76% germination when oospores were treated with sodium hypochlorite (clorox).

4. Infection

Inoculation of plants by spraying with a suspension of zoospores (released from sporangia of *Sclerospora graminicola*) induced immediate encystment of the zoospores and drastically reduced their ability to cause disease. Chilling suspensions of sporangia prior to spraying delayed zoospore release and was an effective method for maintaining infection potential. Chilling resulted in some abnormal zoospore structures being released from sporangia before zoospore release, a small reduction in diseases incidence was observed when chilled inoculums was used, probably due to cold disruption of zoosporogenesis. For large scale disease resistance screening, this reduction is outweighed by the benefit of uniform and adequately high disease pressure that can be obtained over many hours using chilled spore suspension (Jones et al., 2001). The inheritance of avirulence in *Sclerospora graminicola* was studied by hybridizing the isolates Sg 139-4 (Mat A), highly virulent, and Sg 110-9 (Mat B), avirulent, on pearly millet genotype IP 18292 under pot culture experimentation with artificial inoculation. Downy mildew incidence was recorded two weeks after inoculation. Avirulence was dominant over virulence and a single gene pair (AA/Aa) controlled avirulence in isolate Sg 110-9 to a corresponding resistance gene *Rsg1*. The pattern of segregation of virulence: avirulence suggested the presence of a gene-for-gene interaction between *Sclerospora graminicola* and *P. glaucum* (Pushpavathi et al., 2006).

5. Epidemiology

The studies on epidemiological aspects of downy mildew of pearl millet reveals that the earliest symptom expression and the highest downy mildew were recorded when oosporic powder was placed below and above the seeds in furrows. Incorporation of oospores over the seed in furrow gave better results than the present practices of pre-sowing furrow application of oospores below the seed for field screening of pearl millet cultivars for downy mildew resistance. The amount of oosporic powder applied was correlated positively with disease incidence and negatively with the time taken to express disease symptoms. A high negative correlation between the age of seedlings at the time of sporangial inoculation and disease incidence was observed. The infection rate ('r') of the disease was highest in the unprotected plot. The magnitude of reduction in 'r' with Ridomil (metalaxyl) spray was greater than seed treatment with Apron (metalaxyl) (Gupta and Singh, 2000).

6. Management Strategies for the Control of Downy Mildew

6.1. Genetic resistance

Genetic resistance is the most economic and feasible method for control for downy mildew (*Sclerospora graminicola*) of pearl millet. To identify genes for DM resistance with diverse origin, a total of 539 accessions of 12 wild *Pennisetum* spp. from 17 countries evaluated in green house and field-disease nurseries. Out of these, 223 accessions were found DM free in all the tests. DM resistance genes from these wild species will be useful in the control of this disease, if found different from those of pearl millet (Singh and Navi, 2000). The inheritance of resistance to downy mildew disease and the defense-related enzymes β-1,3-glucanase and peroxidase was studied in crosses of pearl millet using a generation-mean analysis. The significance of scaling tests revealed the existence of non-allelic interactions in the inheritance of resistance to downy mildew as well as with the enzymes. Among the gene effects, both additive and dominant effects were significant. All the

non-allelic interaction effects were significant in the crosses. Studies on the isoenzyme patterns of the enzymes substantiated the results of the disease incidence experiments inmost of the generations. The results indicated that the inheritance of downy mildew disease resistance and the expression of β 1,3-glucanase and peroxidates in pearl millet is not only under the control of additive and dominant genes but are also governed by complex non-allelic interactions (Shetty et al., 2001). Dieng et al. (1999), when they screened 26 varieties of pearl millet from different countries of Western and Central Africa in two localities in Senegal, they identified some sources of resistance to the disease. The control variety 7042 had an incidence of 97%. In general, the different varieties presented low disease incidence and severity and reactions differed between the localities, it indicates that existence of physiological strains. A protein was identified by Sishupala et al. (1996) from a virulent pathotype of *Sclerospora graminicola*, the binding reaction of which differentiated susceptible and resistant cultivars of pearl millet to downy mildew disease. This protein and corresponding antibody were used in an enzyme-linked immunosorbent assay (ELISA) to screen suspension cells of pearl millet cultivars for their resistance to the downy mildew pathogen. Screening results for 31 pearl millet cultivars correlated positively with the established field screening method. The anatomical studies conducted on leaves of three different cultivars of pearl millet (*Pennisetum glaucum*) having varying degrees of resistance and susceptibility to downy mildew disease caused by *Sclerospora graminicola* reveals that cuticular and epidermal thickness were significantly higher in leaves of the highly resistant cultivar (P-310-17) compared with the highly susceptible cultivar (7042 DMS). However, the highly resistant cultivar had a significantly lower stomatal index and higher epicuticular wax content when compared with the highly susceptible cultivar. These anatomical characteristics seem to provide a greater degree of defense against penetration and invasion by *S. graminicola* in the highly resistant cultivar (Yadav and Thakur, 2001).

6.2. Screening for resistance

Use of resistant cultivars is the most cost-effective method for the control of downy mildew. Considerable progress has been made in the development of identification of sources of resistance and breeding of resistant cultivars. Ramesh et al. (2003) screened eleven forage composites and their parents against 6 diverse pathotypes of *Sclerospora graminicola* in greenhouse conditions and also in field nursery, using infector row system at Patancheru. Three genotypes (DRSB 3, DRSB 7 and IP 14305) of pearl millet (*Pennisetum glaucum*) were resistant with <5% mean downy mildew incidence. Seven genotypes (DRSB 6, DRSB 7, DRSB 10, Giant Bajra, IP 9294, IP 14188 and IP 14305) had <10% downy mildew incidence. Average linkage cluster analysis broadly classified the 17 genotypes into 3 groups- resistant, moderately resistant and susceptible. The reaction to downy mildew of 11 pearl millet lines were evaluated at 17 locations in India from 1995 to 1999 and found that the disease incidence varied significantly among lines, locations and years. The tested pearl millet lines exhibited significant differential resistance. Resistance in lines IP 18292, IP 18293, 700651 and P310 17 was most stable regardless of the location or season. Based on the reaction of the 11 pearl millet lines, the 17 *Sclerospora graminicola* populations were grouped into six putative pathotypes by Thakur et al. (2004). Rao et al. (2005) evaluated 585 pearl millet fields during 2001-04 in Rajasthan of India, of the 585 pearl millet fields, 59% were infected by DM. The mean DM incidence varied from low to moderate (1-21%). Of the 26 hybrids encountered during the survey, 6 hybrids (Pusa 23, JKBH 26, Proagro 9444, Pioneer 7688, PAC 931 and HHB 67) were highly resistant (mean DM incidence of <5%) and 13 hybrids were disease free. Significant variation in disease incidence of downy mildew was observed in 147 germplasm lines evaluated for their resistance and disease incidence ranged from 0 to 90%. The data indicated that more than 60% genotypes were susceptible or highly susceptible. Out of 147 lines, 25 were highly resistant (out of these, 10 lines: IP 9, IP 55, IP 104, IP 253, IP 262, IP 336, IP 346, IP 498, IP 545 and IP 558 were completely free from DM infection at both the growing stages, i.e. 30 and 60 DAP in both the years of testing 2005 and 2006), 32 resistant, 52 susceptible and 38 highly susceptible to DM (Sharma et al., 2007). Zarafi (2007) screened 152 pearl millet genotypes for resistance to downy mildew under field conditions during 2000, 2001 and 2002 wet seasons. The disease incidence and severity were assessed 65 days after sowing. The results indicate that, 70 genotypes showed resistance, 43 were moderate resistance, 35 were moderate susceptibility and 3 genotypes were susceptible. The results indicate that, availability of germplasm with resistance to DM.

6.3. Transgenic studies

Transgenic pearl millet lines expressing pin gene exhibiting high resistance to DM pathogen, *Sclerospora graminicola* were produced suing particle-inflow-gun (PIG) method. T_1 plants resistant to DM invariably exhibited tolerance to Basta suggesting co-segregation of *pin* and *bar* genes. Further, the downy mildew resistant T_1 plants were found positive for *pin* gene in Southern and Northern analyses thereby confirming stable integration, expression and transmission of *pin* gene. T_2 progenies from T_0 confirmed to dihybrid segregation of 15 resistant: 1 susceptible plant (Lata et al., 2006).

6.4. Induced resistance

Innate defense mechanisms in plants can be triggered and enhanced by certain agents which were referred to as inducers. Inducing resistance against a broad spectrum of pathogens in otherwise susceptible plants is seen as a potentially safer

alternative to other methods of chemical control of plant diseases. Cerebrosides, which are glycosphingolipids extracted from various plant pathogens, have been reported as resistance elicitors. It elicited resistance against downy mildew disease (*Sclerospora graminicola)* of pearl millet (*Pennisetum glacum*) that was highly significant. The resistance was of systemic nature and the time required for the resistance to build up was from 2nd day onwards (Deepak et al., 2003). Pre-treatment of pearl millet seedlings with a suboptimal concentration of *Sclerospora graminicola* induced resistance that protected plants (62%) from subsequent infection by the optimal concentration of the pathogen moreover, it enhances the vegetative and reproductive growth parameters of resistance-induced plants. The resistance achieved through this was independent of cultivar and was not related to its constitutive resistance. No adverse effect either on the host or pathogen when Nitric oxide (NO) used for its effectiveness in protecting pearl millet plants against downy mildew disease caused by *Sclerospora graminicola*. Aqueous sodium nitroprusside (SNP) seed treatment with or without polyethylene glycol (PEG) priming was the most effective in inducing the host resistance against downy mildew both under greenhouse and field conditions. Spatio-temporal studies corroborated that the protection offered by NO donor treatment was systemic in nature and a minimum of 3-day time gap between the inducer treatment and subsequent pathogen inoculation was necessary for maximum resistance development (Manjunatha et al., 2008). Seed treatment and foliar sprays with Ind-Ile-Me (1-oxo-indanoyl-L-isoleucine methyl ester) were tested for inducing resistance against downy mildew disease caused by the phytopathogenic oomycete *Sclerospora graminicola* in pearl millet and found that, under greenhouse conditions, a 50% protection, under field conditions 60% protection achieved moreover, the induction of resistance was correlated with the enhanced activities of defense-related proteins such as phenylalanine-ammonia-lyase, peroxidase and enhanced level of hydroxyproline-rich glycoproteins. Ind-Ile-Me can be used as a valuable protection compound in downy mildew disease management (Shantharaj, 2007). In search of suitable alternative to the otherwise perilous chemical control strategy of disease management, the amino acid proline was evaluated for its efficacy to elicit resistance in pearl millet against downy mildew disease caused by *Sclerospora graminicola* both under greenhouse and field conditions by Raj et al. (2004). Seed treatment with proline at 50 mM for 3 h significantly enhanced seed germination and seedling vigor of pearl millet compared to the control and also it protected the plants from downy mildew by offering 58% protection under greenhouse and 67% protection under field conditions. Three days were required for proline-treated plants to develop resistance, which was systemic and was sustained throughout the life of the plants. The studies carried out by Babitha et al. (2002) revealed that, when superoxide dismutase (SOD) was inducted, the differential reactions are noticed in resistant (IP 189292) and susceptible (23 B) pearl millet seedlings inoculated with *Sclerospora graminicola*, the SOD activity was greatest in roots and 2 fold increase recorded in resistant seedlings upon inoculation with the pathogen. Induction of resistance in pearl millet against downy mildew disease was studied by (Geetha and Shetty, 2002) treating seeds of highly susceptible pearl millet cultivars with plant activator benzothiadiazole (BTH) (CGA 245704), calcium chloride ($CaCl_2$) and hydrogen peroxide (H_2O_2). BTH at 0.75%, $CaCl_2$ at 90 mM and H_2O_2 at 1 mM were efficient in managing the disease by giving 78, 66 and 59% protection respectively. To develop maximum resistance a gap of 4 days is required between inducer treatment and inoculation of the pathogen. Inducer treatment not only offered protection but also increased the vegetative and reproductive growth parameters and enhanced grain yield. BTH gave more protection than calcium chloride and hydrogen peroxide. Seedlings raised from inducer-treated seeds recorded an early and increased hypersensitive response as a reaction to *Sclerospora graminicola* inoculation.

6.5. Plant products

Watery extracts of forty plant species commonly growing in across India have been screened for anti-sporulant activity against *Sclerospora graminicola*, the causative agent of pearl millet downy mildew. The crude extracts of 12 species *Agave Americana*, *Aloe vera*, *Artemisia parviflora*, *Citrus linon*, *Citrus sinensis*, *Eucalyptus globosus*, *Euphorbia hirta*, *Leucas aspera*, *Murraya koenigi*, *Ocimum sanctum*, *Santalum album* and *Zingiber offinale* completely inhibited the zoosporoorangium formation. The anti-sporulant activity of commercialized *Azadirachta* preparation (nutri-neem) was more pronounced than that of *Reynutria* based one (milsana) and *Sabadilla* (veratrin), however, these botanical preparations held off synthetic fungicides and the most active watery extracts (Deepak et al., 2007). The leaf extract of *Datura metel* protected pearl millet plants against downy mildew disease caused by *Sclerospora graminicola*, the highest seed germination and seedling vigor was recorded when seeds were treated with a 2% extract for 3 h. when tested for induction of resistance against downy mildew disease. Seed treatment with *Datura metel* extract resulted in 79 and 67 % protection under greenhouse and field conditions, respectively. The resistance offered by this, to be systemic acquired resistance (SAR) and was active at both early and later stages of plant growth (Devaiah et al., 2009).

6.6. Biological control

Pearl millet seeds when soaked in sporulated culture of biological control agents *Trichoderma viride*, *Trichoderma harzianum*, *T. hamatum*, *Pseudomonas fluorescens*, maximum seed emergence was recorded with *P. fluorescens*, *T. harzianum* and *T. viride* also reduced disease incidence up to 52.40% compared to the control. None of the formulations matched the

level of metalaxyl in offering protection against downy mildew. Soil amendment was the most suitable and desirable way of delivering formulations (Mane et al., 2007). Similar findings were recorded by Latake and Kolase (2007). Studies on downy mildew management resulted in varied degrees of protection by the PGPR both under greenhouse and field conditions. With fresh suspensions, treatments with INR7 (*Bacillus pumilus*) resulted in the highest protection (57%), followed by *Bacillus pumilus* strain SE34 and *B. subtilis* strain GB03, which resulted in 50 and 43% protection, respectively, compared with the untreated control. With powdered formulation, PGPR strain INR7 suppressed downy mildew effectively, resulting in 67% protection, while SE34 resulted in 58% protection, followed by GB03 with 56% protection. The tested PGPRs both as powdered formulations and fresh suspensions can be used within pearl millet downy mildew management strategies and for plant growth promotion (Raj et al., 2003).

6.7. Chemical control

Seed treatment with 6 g Apron 35 WS Kg^{-1} of seed + spray of 4 g Ridomil MZ l^{-1} recorded the lowest disease incidence at 30 (1.83%) days after sowing and at the dough stage (6.73%). Copy yield (1617 kg ha^{-1}) and percentage increase over the control (160%) were also highest for this treatment (Pandya et al., 1999). The formulations of metalaxyl when tested as seed treatment or foliar spray controlled downy mildew of pearl millet. Control depends on the rate of application and on varietal susceptibility, more fungicide being required on more susceptible cultivars. When metalaxyl used at >2 g a.i. kg^{-1} seed it is toxic to germination, particularly with Apron 35 SD formulation (Singh and Shetty, 1990). Seed treatment with metalaxyl (Apron 35 WS) @ 2 g a.i. kg^{-1} seed controlled downy mildew up to 20-22 days after sowing (DAS). Seed treatment by Apron 35 WS 2 g a.i. kg^{-1} seed followed by one spray of Ridomil MZ 72 WP (metalaxyl + mancozeb) at 4 g l^{-1} at 20 DAS gave the best results, with the disease incidence 4.63 and 41.59% as compared to 39.10 and 69.92% in control at 30 and 60 DAS, respectively. Seed treatment with Aliette (fosetyl-ammonium) alone at 5 g kg^{-1} seed was ineffective in controlling the downy mildew (Pandya et al., 2000).

7. Conclusion

Downy mildew disease of pearl millet is one of the most important diseases in almost all growing areas of the country. Though genetic resistance is one of the best ways, however breeder may fail to focus on achieving potential yield. So, fungicide may help not only to control the disease incidence below threshold level but also to get economic return.

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