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Review

Downy mildews of India

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Abstract

The downy mildew diseases are caused by different fungus species in several genera in the class Oomycetes. They comprise a major group of diseases affecting a large number of crops. In India, downy mildews have been reported on several economically important crops, including maize, sorghum, pearl millet, onion, soybean, cucurbits, and grapes, causing severe economic losses in some regions and seasons. Pathogens reported to cause downy mildews in India include species in the genera, *Perenosclerospora, Perenospora, Pseudoperonospora, Plasmopara, Sclerophthora* and *Sclerospora*. In view of the economic importance of the crops, and prevalence and severity of the disease, the downy mildews have been classified into high, moderate and low research priority problems. In this article we present a brief review of the work done in India related to pathogen biology, epidemiology and management methods, and provide an outlook for future research.

Keywords: Downy mildews; Biology; Epidemiology; Management methods

Contents

1. Introduction

The fungal pathogens causing downy mildew diseases of plants belong to the family Peronoporaceae in the class Oomycetes. Several species are highly destructive to major crops, including pearl millet, sorghum, maize,

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Table 1
Major downy mildew pathogens, their hosts and economic importance in India

Genus	Species	Host	Research priority[a]
Peronosclerospora	*P. heteropogoni* (Siradhana, Dange, Rathore and Singh)	Maize	Low
	P. maydis (Rcib.) C.G. Shaw	Maize	Low
	P. sacchari (T. Miyake in Ito) Shirai & Hara	Sugarcane, maize, grasses	Low
	P. sorghi (Weston & Uppal) C.G. Shaw	Sorghum, maize, millets	Moderate
Peronospora	*P. destructor* (Berk.) Casp. ex Berk.	Onions, *Alllium* sp.	High
	P. manshurica (Naum.) Syd.	Soybean	Low
	P. parasitca (Pers. Ex Fr.) Fr.	Brassica	Low
	P. arborescens (Berk.) de-Bary	Opium popply	High
	P. pisi Syd.	Pea	Low
	P. plantaginis (Undewood)	Isabgol	High
	P. alta (Fuckel)	Isabgol	High
Plasmopara	*P. halstedii* (Farl.) Berk & de Toni	Sunflower	Moderate
	P. viticola (Berk. & Curt.) Berk. & de Toni	Grapevine	Moderate
Pseudoperonospora	*P. cubensis* (Berk. & Curt) Rost.	Cucurbits	Moderate
	P. plantaginis (?)	Isabgol	High
Sclerophthora	*S. macrospora* (Sacc.) Thirum. Shaw & Naras.	Maize, grasses	Low
Sclerospora	*S. graminicola* (Sacc.) Shroet	Pearl millet	High

[a] Based on prevalence and incidence of downy mildews, acreage and importance as food value of the crops.

sunflower, brassica, soybean, cucurbits, opium poppy, onion, grapes, and flowers, such as roses. The major genera causing downy mildews include *Peronospora*, *Plasmopara*, *Bremia*, *Pseudoperonospora*, *Sclerospora*, *and Sclerophthora*. Most of these downy mildews are prevalent in India (Table 1). A perusal of the Indian literature on downy mildews reveals that not all the reported downy mildews have caused major yield reductions, but they do have potential to cause epidemics and consequent severe damage. Information on distribution, prevalence of downy mildews and resulting yield losses in India are fragmented and inadequate. Nevertheless, the downy mildews of pearl millet, sorghum maize, rapeseed and mustard, and sunflower, because of their economic significance in India (Table 2), have received major research attention and significant advances have been made on various aspects of their management (Williams, 1984a, b; Jeger et al., 1998; Mayee, 1998; Thakur, 1998; Pande et al., 1998; Saharan, 1998; Sharma, 1998). Other downy mildews have been managed using cultural and chemical control measures, but have not received the needed research attention.

Among the downy mildews in India, the pearl millet downy mildew, caused by *Sclerospora graminicola* (Sacc.) Schröet is quite widespread and highly destructive. Estimated yield loss of up to 30% has been recorded (Singh, 1995; Singh et al., 1993). Epidemics of *S. graminicola* first appeared in 1970–1971, and later occurred in 1978–1980; 1984–1985; and 1992–1993 on the most popular F_1 hybrids causing major yield losses. Several hybrids were subsequently withdrawn from cultivation including NHB 3, BJ 104, MBH 110, and MLBH 104 (Singh, 1995; Thakur et al., 1999). Although

Table 2
All India area, production and productivity of major crops infected by downy mildews[a]

Crop	Area (million ha)	Production (million tonnes)	Productivity (kg/ha)
Maize	6.11	9.12	1493
Sorghum	11.75	9.20	783
Pearl millet	10.11	7.15	707
Rapeseed and mustard	6.23	5.88	944
Sunflower[b]	2.05	1.3	600
Onion	0.38	4.06	10,556

[a] *Source*: Agricultural statistics at a glance. Directorate of Economics and Statistics, Department of Agriculture and Cooperation, Ministry of Agriculture, Government of India. 1996. 140pp.
[b] Mayee, 1998.

similar epidemics have not been reported for other downy mildews, occasional significant yield losses are known to occur in sorghum, maize, sunflower, onion, opium poppy, crucifers and grapes. In sorghum, yield loss up to 78% has been reported in cv. DMS 652 (Anahosur and Laxman, 1991). The sunflower downy mildew (*Plasmopara halstedii*), recently reported in India, caused severe epidemics in cvs. Modern and EC 68414 in Maharashtra during 1984–1989, and subsequently, in Karnataka and Andhra Pradesh (Agrawal et al., 1991). The downy mildew of rapeseed and mustard, caused by *Peronospora parasitica* (Pers. Ex. Fr.) is widespread and cause significant economic loss during the seedling stage of the crop (Saharan, 1998). Downy mildew of the opium poppy (*Peronospora arborescens*) is widespread in Madhya Pradesh and Rajasthan (Fig. 1), and is reported to reduce the yields by up to 25% both for latex and seed per year (Cheema

Fig. 1. Political map of India showing different states.

et al., 1990). Onion downy mildew (*Peronospora destructor*) accounted for up to 75% yield loss during 1988–1989 in Kangra district of Himachal Pradesh (Sugha and Singh, 1991). *Peronosclerospora sorghi* infects both maize and sorghum and can cause considerable loss in both crops (Payak, 1975a). Isabgol (*Plantago ovata* Forsk.), a crop of medicinal value, is grown in several parts of Gujarat and Rajasthan, and is attacked by three species of downy mildew pathogen, namely *Peronospora plantaginis* Underwood, *P. alta* Fuckel, and *Pseudoperonospora plantiginis Underwood* (Sain and Sharma, 1999). Information on prevalence and economic loss for other downy mildews are not well documented.

In this paper, we attempt to highlight the major research advances made in India towards managing downy mildews of economic significance, the major gaps in our knowledge, and suggest future research needs.

2. Biology, epidemiology and pathogenic variability

A large volume of information is available on various aspects of downy mildews (Safeeulla, 1976; Ingram, 1981; Kenneth, 1981; Williams, 1984a; Lucas et al., 1995), which is relevant to the Indian situation. The diploid vegetative stage of downy mildew pathogens contrasts with the haploid state of the true fungi, which

represent most other obligate pathogens (e.g. powdery mildews). As obligate biotrophs downy mildews are host-dependent. Coevolution with plant hosts over a long period has lead to divergent forms of pathogen adapted to different host taxa.

Reproduction is usually both by sexual and asexual means. During the sexual phase oospores are formed which are thick-walled and long-lived, and enable the pathogens to survive the crop-free, adverse periods (Payak, 1975b; Ramalingam and Rajasab, 1981; Singh, 1995). Oospores are the primary inoculum source. The asexual phase occurs in periods of conducive weather conditions. Asexual reproduction is through production of conidia or sporangia. Sporangia produce zoospores which are the infecting propagules, while conidia germinate directly. Several pathogens, such as *Perenosclerospora sorghi*, *Perenospora parasitica*, and *P. tabacina* produce conidia while others, such as *S. graminicola* and *Pseudoperonospora cubensis* produce sporangia and zoospores. Conidia-producing pathogens are thought to be evolutionarily more advanced than those producing sporangia (Williams, 1984a), however, the epidemiological advantages of conidia over sporangia have not yet been established.

All Peronoporaceae require surface wetness for spore germination and infection, and high relative humidity (RH) for spore production. Thus rainfall and high RH are critical weather factors for epidemics to develop. The downy mildew pathogens infecting maize, sorghum, and pearl millet have similar environmental requirements for asexual reproduction. Prior to sporulation the host tissue requires exposure to high light intensity for photosynthetic energy. At 20°C in the dark a systemically infected sorghum leaf produced 10,800 conidia cm^2 at 100% RH, but only 3600 conidia cm^2 at 85% RH, and none at 80% RH (Shetty and Safeeulla, 1981). A minimum of 3 h at 25°C and 95% RH is essential to initiate sporulation in *S. graminicola* (Singh et al., 1993). Production of conidia and sporangia in the field has a marked periodicity of release and has a close relationship with temperature and RH. Most sporulation occurs when temperatures are around 20°C and RH > 95% (Payak, 1975b; Shetty, 1987).

Asexual spores of the downy-mildew pathogens are ephemeral, therefore rapid dispersal and infection is essential. Wind speed, RH, temperature, sunshine, and leaf wetness can influence viability and dispersal of spores. Sporangia of *S. graminicola* remain viable for 2.5–6 h depending on temperature, RH and wind speed (Shetty, 1987), and under favourable conditions they can be transported up to 3 km by wind. In sunflower downy mildew, rain immediately after sowing was crucial for disease initiation and spread (Patil et al., 1993).

Disease symptoms can develop under a range of temperature and RH conditions for different downy mildews. *P. parasitica* on cabbage can be very destructive at 10–15°C, and symptoms can develop at 24°C, but sporulation is limited beyond 24°C (Saharan et al., 1997). Bains and Jhooty (1976) reported higher incidence in mustard at 14°C and 152 mm rainfall than at 17°C and 51 mm rainfall. Infection was reduced at 25°C, with no infection at 30°C. Infection frequency and disease development was positively correlated with increasing leaf wetness duration (Mehta et al., 1996). In sorghum, pearl millet, and maize symptoms of downy mildew infection develop at 25°C, but incidence is reduced below 20 and above 35°C.

The role of seed in pathogen transmission and dispersal is important. Seed transmission of *S. graminicola* through oospores and mycelium has been reported (Shetty et al., 1978), but subsequent studies indicated that if the seed was dried to a moisture level of 12% the seedborne transmission could be eliminated (Williams, 1984a). *P. sorghi* has been reported to be transmitted internally in sorghum and maize seed either as mycelium (Kaveriappa and Safeeulla, 1978) or as oospores (Upadhyay, 1987), and *P. heteropogoni* as mycelium in maize seeds (Rathore et al., 1987). Seed transmission of *P. parasitica* has also been reported for rapeseed-mustard and radish (Vishunavat and Kolte, 1993). Disease transmission in onion occurs with seedlings from one area to the other (Sugha and Singh, 1991). In northern India *P. cubensis*, the cucurbits downy mildew pathogen, perpetuates in the form of active mycelium on self-sown or cultivated sponge gourd vines (Bains and Jhooty, 1976). Dew is the most important environmental factor affecting infection and disease spread. Oospores have a major role in survival and spread of *P. cubensis*, but their occurrence has been erratic (Bains and Jhooty, 1976).

With *P. parasitica* on crucifers, oospores are produced in necrotic tissues of cotyledons and the fungus can be maintained on young cauliflower seedlings and detached cabbage cotyledons (Silué et al., 1996). Oospores develop on the seed surfaces and in the hypodermis of the seed coat tissue in sarson, toria and Indian mustard. The pathogen was seed transmitted non-systemically in sarson and toria with 0.9% and 0.4% seed infection, respectively (Vishunavat and Kolte, 1993). With *P. sorghi*, oospores are formed abundantly on *H. contortus*, which form the sole source of primary inoculum for maize (Dange, 1976).

Pathogenic variability in downy mildew fungi is well known, but no systematic research has been done in India. In *S. graminicola*, the pearl millet downy mildew pathogen, at least four distinct pathotypes have been established (Thakur et al., 1999). These pathotypes have evolved by host cultivar-directed selection under farmers' field conditions (Thakur et al., 1992). Pathogenic variability has been demonstrated in single-oospore and single-zoospore isolates of *S. graminicola* (Thakur and

Shetty, 1993; Thakur et al., 1998a) and among isolates from several pearl millet cultivars India (Thakur and Rao, 1997; Thakur et al., 1998b, 1999). DNA fingerprinting of cultivar-specific pathotypes revealed distinct restriction fragment length polymorphisms (RFLP) of DNA (Sastry et al., 1995; Thakur et al., 1999). Various races of *P. cubensis* are known to exist (Bains and Jhooty, 1976), but these need to be clearly defined. In other downy mildews races have not been well documented in India. Five races of *P sorghi* infecting sorghum have been identified in the Americas (Craig and Odvody, 1992), but there is no such report from India. There are evidences of existence of variable pathotypes in *P. parasitica* to rape seed mustard (Nishaat and Awasthi, 1995) and to *Brassica oleracea* and *B. rapa* (Silué et al., 1996).

3. Management methods

3.1. Host plant resistance (HPR)

HPR is a practical and economic method of control for downy mildews. This is a unique technology embedded in seed, without direct cost to farmers and does not require extra efforts and understanding for its use. The use of HPR requires: an effective screening technique; good sources of genetic resistance; a proper breeding method to efficiently incorporate the resistance; a sound strategy for cultivar deployment; and effective monitoring system for pathogen virulence and resistance durability.

Effective field and greenhouse screening methods have been developed for downy mildews of pearl millet (Singh et al., 1997; Williams et al., 1981), sorghum (Williams, 1984a; Narayana et al., 1995), maize (Williams, 1984b), and field-screening methods for other downy mildews are generally based on sick-plot method. Field screening using a combination of spreader rows and oospore-infested plots has been used effectively to screen for resistance to the downy mildews of sorghum and pearl millet at several locations in India. To develop an effective screening method sound knowledge of pathogen biology, epidemiology, and host-pathogen interaction is essential. Although it sounds simple, a great deal of efforts are needed to develop sick plot, including the decision on use of a particular race or pathotype, monitoring disease incidence, providing favorable environment, particularly RH and temperature optimal for the pathogen growth, infection and disease spread, and use of an effective disease rating scale to clearly discern between resistant and susceptible lines. Screening of a large variable germplasm is done to identify resistant lines. Resistance of these lines is confirmed by repeated screening at and across locations over a number of years. In the process, lines with stable resistance can be identified. A large number of resistant lines have been identified for most downy mildews. Stability of resistance of these lines have been variable depending on the evolution of new pathotypes or races of the pathogen.

3.2. Resistance expression

Resistance to downy mildews in different pathosystems is expressed in different forms. Resistance conferred by single dominant alleles is expressed in seedlings as well as in adult plants and is characterized by a hypersensitive reaction-type due to accumulation of some defense compounds, such as phytoalexins. Most *Allium* species and their hybrids resistant to *Peronospora destructor* exhibit a hypersensitive reaction following inoculation, but in some host genotypes inhibition of pathogen growth occurs without any obvious cell reaction (Kofoet and Zinkernagel, 1991). Phenylalanine ammonia-lyase (PAL) activity increased in downy mildew resistant lines of pearl millet 24 h after inoculation, but decreased in susceptible lines. The activity was greater in the shoot than in the root or mesocotyl of resistant lines, whereas it was low in all three parts in a susceptible line (Nagarathna et al., 1993).

Race non-specific (field) resistance occurs in some pathosystems, which is typified by a reduced rate of disease development, leading to less severe symptoms and reduced pathogen reproduction. The response of pea cultivars with different levels of resistance to *Peronospora viciae* showed no apparent difference until 4 days after inoculation, when the rate of pathogen growth in the host varied, leading to reduced sporulation in the more resistant genotypes (Dickinson and Singh, 1982).

Systemic Acquired Resistance (SAR) is a contrasting type of resistance expression in downy mildew pathosystems. This was first described in tobacco infected by *Peronospora tabacina* (blue mold); infection of stem tissues by the fungus reduced the severity of disease on leaves subsequently challenged with the same pathogen (Cruickshank and Mandryk, 1960). Protection is associated with a necrotic reaction in inoculated stem tissues and takes 2–3 weeks to develop (Cohen and Kuc, 1981). A similar phenomenon has been observed in the pearl millet downy mildew system (Kumar et al., 1993), which is associated with induction of pathogenesis-related proteins and increases in the activity of chitinase B-1, 3-glucanase, and peroxidase (Tazun et al., 1989; Ye et al., 1990).

Induced systemic resistance to *S. graminicola* was demonstrated in pearl millet (Kumar et al., 1993). Root-dip inoculation of pearl millet seedlings (3-day-old) with 6000 zoospores ml^{-1} of *S. graminicola* caused infection in all plants but symptoms were visible on only 18%

plants. These plants, when challenged 4–6 d later with 4×10^4 zoospores ml^{-1}, remained predominantly healthy compared with the control. This suggests induction of resistance by the suboptimal dose of inoculum used. The induced resistance was systemic and protected tillers and inflorescences (Kumar et al., 1993).

Recovery resistance has recently been demonstrated in pearl millet infected with downy mildew (Singh and King, 1988; Singh and Talukdar, 1996) and a similar resistance mechanism has also been reported for sorghum downy mildew in Zimbabwe (Singh and de Milliano, 1989) and for maize downy mildew in Nigeria (Olanya and Fajemisin, 1992).

3.3. Sources of resistance

Lines resistant to downy mildews are available in most pathosystems. Relatively large numbers of resistant lines are available for pearl millet, sorghum, and maize compared to other crops. In these three crops world germplasm collections have been screened at several locations with the involvement of international agricultural research centers, and many stable sources of resistance are available. However, field screens have been done for other downy mildews, and resistant lines are available for sunflower (Patil et al., 1993; Mayee, 1998), crucifers (Saharan et al., 1997), brassica (Kolte, 1985), opium poppy (Kandulkar et al., 1993) and isabgol (Sain and Sharma, 1999). In pearl millet, sorghum and maize resistance breeding has received major attention from the Indian programs and consequently, disease resistant, high yielding cultivars are available. A number of resistance lines of pearl millet have recently been characterized against the pathogenically diverse isolates of *S. graminicola* (Thakur et al., 1997a, b). Several sources of resistance have been utilized in breeding programs to produce downy mildew resistant parental lines and hybrids (Hash et al., 1997; Thakur et al., 2001).

3.4. Inheritance of resistance

There are several published reports on the inheritance of resistance, but these are limited to some of the downy mildews, particularly of pearl millet, sorghum and maize. Most studies on inheritance of resistance have been inconclusive because of large variation that exist both in the pathogen and host populations, and use of different disease rating scales.

Several studies of the inheritance of resistance to pearl millet downy mildews have provided inconclusive results because both host and pathogen are allogamous (Thakur et al., 1992), and segregation for HPR generally shows continuous variation (Basavaraju et al., 1981; Dass et al., 1984; Deswal and Govila, 1994; Kataria et al., 1994). More recently, when a highly homogenous host lines and a pathogen isolate were used, a clear monogenic dominant resistance was demonstrated in a pearl millet line IP 18292 against a Patancheru isolate of *S. graminicola* (Singh and Talukdar, 1998).

In sorghum, resistance to *P. sorghi* has been reported to be dominant, major gene, and of complementary effect (Rana et al., 1982; Reddy et al., 1992). Inheritance of resistance to three pathotypes of *S. sorghi* indicated two dominant genes for resistance in QL 3 and one in SC 414-12 (Sifuentes and Frederiksen, 1988). In various studies the number of genes and gene actions were variable depending on the sorghum lines and pathotypes involved (Thakur et al., 1997a, b). In maize, resistance to sorghum downy mildew (*P. sorghi*) is reported to be monogenic dominant, recessive or polygenic additive depending on the lines studied (Frederiksen and Ullstrup, 1975; Jinahyon, 1973; Schmitt et al., 1977). Resistance to brown stripe downy mildew in maize is inherited polygenically with additive effects (Handoo et al., 1970; Singh and Asnani, 1975). The resistance in opium poppy to *P. arborescens* is reported to be both additive and non-additive, the latter being more important in cvs. Uo185 and MoP539 (Kandulkar et al., 1993).

In pearl millet there is clear evidence that the A_1 cytoplasm is not associated with susceptibility or resistance to downy mildew (Anand Kumar et al., 1983; Yadav et al., 1993; Yadav, 1996). However, there is also evidence for genes in the nucleus controlling host plant reaction to this disease (Basavaraju et al., 1981; Deswal and Govila, 1994; Singh and Talukdar, 1998). Recent inheritance studies using molecular marker based genetic linkage maps are yielding useful results (Hash and Witcombe, 1994; Jones et al., 1995) that will facilitate genetic manipulation of disease resistance.

3.5. Utilization of resistance

Conventional breeding procedures use the greenhouse or field screening methods to incorporate adequate levels of downy mildew resistance into breeding populations, parental lines, and varieties that have superior agronomic performance and product quality. Pure line selection (selection within partially inbred lines), pedigree selection, backcrossing, induced mutation, and recurrent selection procedures have all been used in breeding for resistance to downy mildews, with varying degrees of success.

Marker-assisted selection (MAS), in which selection is for the presence of molecular 'tags' tightly linked to the gene(s) controlling resistance, is a new tool for plant breeders. MAS will permit more effective pedigree and backcross improvement of downy mildew resistance in the future. Pedigree and recurrent selection methods

have been most widely and successfully used for improving downy mildew resistance in pearl millet (Andrews et al., 1985; Weltzien and King, 1995).

Backcrossing procedures have been used in breeding for resistance to downy mildews using effective screening procedures. In pearl millet, the Indian Agricultural Research Institute used backcrossing to breed downy mildew resistant seed parents MS 5054 and MS 5141 in the elite genetic background of Tift 23B (Pokhryal et al., 1976; Murty et al., 1983).

Selection within lines for resistance variability has been used as a pure line breeding method for downy mildew in pearl millet. Selection for downy mildew resistance is done within a susceptible line using pedigree procedures. A large population of a susceptible line is grown in the disease nursery or inoculated in the greenhouse. Disease-free plants are selfed and the selfed progenies of these are screened panicle-to-row against the disease. The process of selection and selfing is repeated for several generations until several progenies with the desired level of resistance and the morphological characters of their susceptible progenitor have been identified. A notable success with this method was the development of ICMA 841 and ICMB 841 from the susceptible 5141A and 5141B (Singh et al., 1990). ICMA 841, the male-sterile counterpart of the maintainer line ICMB 841, has been exploited commercially in India as a female parent of several F_1 hybrids including ICMH 423, Pusa 23, and Pusa 322. Currently, Pusa 23 is the most widely grown public-bred hybrid in India.

Recurrent selection procedure has been effective for breeding durable resistance to downy mildew in pearl millet (Weltzien and King, 1995). Widespread adoption of improved open-pollinated pearl millet cvs. WC-C75 and ICTP 8203 in India are good examples of the success of this procedure. For any recurrent selection scheme based on S_1 or full-sib progenies, selection for resistance between progenies will be much more effective than selection within them.

MAS uses as selection criteria 'tags' having high heritability that are genetically linked to portions of the genome controlling characters of interest. These markers can be morphological traits, proteins, including isozymes, or DNA markers such as RFLPs, randomly amplified polymorphic DNAs (RAPDs), and others. To date, markers have been identified for at least 22 different putative downy mildew resistance QTLs in pearl millet. The effectiveness of MAS is now being evaluated at ICRISAT in collaboration with the Center for Arid Zone Studies, University of Wales, Bangor, UK. Since MAS for downy mildew resistance is currently being tested, one can now contemplate ways of deploying downy mildew resistance genes that were not previously practical (Hash and Witcombe, 1996; Witcombe and Hash, 2000).

3.6. Cultural

Cultural methods for controlling downy mildews are largely aimed at sanitation and manipulation of the environment to the advantage of host and to the detriment of the pathogen. Since the pathogens survive in the form of oospores in the host tissues, removal, destruction and burning of the infected plant debris along with weeds serves to reduce the primary inoculum (Butler, 1918; Vasudeva, 1958). Clean, well-drained soils with a two-year crop rotation with a non-host crop have been recommended. Avoidance of monoculture and growing the same variety in particular fields reduces the inoculum buildup and restricts virulence selection in the pathogen population. Roots of non-host plants have been shown to stimulate germination of oospores of *P. sorghi*, the sorghum downy mildew pathogen, thus reducing the primary inoculum load in the soil for the next sorghum crop (Pratt, 1978). For the control of pearl millet downy mildew, Thakur (1992) suggested the cultivation of a highly susceptible cultivar as a trap crop between cropping seasons. The trap crop would be harvested soon after symptoms appeared to prevent production and addition of sexual spores in the soil. However, this is neither practiced nor can be feasible at the farmers' level.

Crop sanitation, deep tillage, over-planting and rouging of diseased plants, manipulation of planting dates, host nutrition, crop rotation, and inter- and mixed cropping have been suggested to reduce the primary inoculum load and secondary spread of the disease. Significant reduction in oospore density in soil and incidence of sorghum downy mildew has been reported in the US by deep tillage, rouging infected plants (Tuleen et al., 1980; Janke et al., 1983). Such operations would be difficult to be followed by resource-poor farmers in India. Late planting of sorghum in Dharwad increased downy mildew incidence in the crop (Balasubramaniyan, 1974). In this case the inoculum was provided by the early grown sorghum in the area. In general, early planting has resulted in reduced disease incidence and increased yield. Preparatory tillage, soil solarization and crop rotation have been reported to be effective in reducing sunflower downy mildew (Mayee, 1998).

Late sown crops of rapeseed-mustard have been reported to have higher DM incidence than the early sown crops (Kolte, 1985; Saharan, 1992). Soil amendments with oil cakes of *Pongamia glabra* and *Azadirachta indica* were effective in controlling both systemic and non-systemic infection of opium poppy downy mildew and increasing the yield of latex and seed (Anila and Thakore, 1991).

3.7. Chemical

The advent of metalaxyl (methyl *N*- (2,6-dimethylphenyl)-*N*- (methoxyacetyl)-DL-alaninate), a systemic

fungicide, provided a real breakthrough for the control of downy mildews. The fungicide is absorbed through the leaves, stem and roots and inhibits protein synthesis in the fungus. It has various formulations, and can be applied as a seed treatment or foliar spray.

3.7.1. Seed treatment

Fungicidal seed treatment followed by a foliar spray is a common practice to control downy mildews when deemed economical. Metalaxyl seed treatment (0.25–0.6 ai kg^{-1} seed) has been reported to control downy mildews in pearl millet (Singh and Shetty, 1990), sorghum (Anahosur, 1986; Lakshmanan, 1992), maize-*Peronospora sorghi* (Figueiredo and Anahosur, 1993), maize- *P. sacchari*, the sugarcane downy mildew (Singh and Lal, 1985), rapeseed mustard (Kolte, 1985; Saharan, 1992), sunflower (Patil et al., 1991), soybean (Singh and Pandey, 1998) and cucurbits (Maharishi and Siradhana, 1990). Seed treatment with Apron SD 35 (metalaxyl 2 g ai kg^{-1} seed) followed by two foliar applications of Ridomil MZ-72 at 30-day intervals provided the best control of downy mildew of mustard and increased the yield substantially (Mehta et al., 1996; Puzari and Saikia, 1997). The best control of onion downy mildew was obtained by seed treatment with metalaxyl at 2 g ai kg^{-1} seed followed by dry heat at 40°C for 8 h (Mir and Dhar, 1988).

In opium poppy seed treatment with *Azotobactor* reduced the downy mildew incidence as well as N-requirement of the crop (Chakrabarti and Yadav, 1991). Dithiocarbamates were highly effective in controlling primary infection and secondary spread in Rajasthan. Seed treatment with Dithane Flowable (0.6%) decreased primary infection by 40% (Cheema et al., 1990). Various fungicides, metalaxyl, fosetyl, mancozeb and copper oxychloride, either alone or in combinations have been used to control grape downy mildew (Jamadar et al., 1998; Sapkal et al., 2000).

3.7.2. Foliar spray

Prior to 1970 control of downy mildews on crucifers and other cash crops relied on frequent application of sprays and dusts of fungicides like chloranil, copper-based fungicides and zineb. These were subsequently replaced by other non-systemic fungicides: captafol, daconil, propineb, and mancozeb (Butler and Jones, 1949; Saharan, 1992). A number of fungicides, such as captafol, mancozeb, difolatan, copper oxychloride, propineb and metalaxyl, have shown good efficacy in controlling downy mildews on various crops, including crucifers (Saharan, 1992; Verma et al., 1994).

Downy mildew of mustard has been controlled successfully by difolatan, mancozeb and metalaxyl. Three sprays of Ridomil MZ-72 (metalaxyl and mancozeb @0.25%) at 20-day intervals beginning 40 days after sowing provided maximum disease control (82%) and increased yield by 49% (Saharan et al., 1997). In other downy mildews, seed treatment followed by one-two sprays have been found effective (Anahosur and Patil, 1983; Singh and Shetty, 1990). More recently, foliar spray of phosphonic acid compounds significantly controlled downy mildew of maize (*P. sorghi*) and increased the yield substantially (Panicker and Gangadharan, 1999).

Development of metalaxyl-resistant strains in oomycetes is well known (Georgopoulos and Grigoriu, 1981; Crute et al., 1985; Davidse, 1985; Georgopoulos and Skylakakis, 1986), and this is attributed mainly to genetic uniformity of the host cultivar and genetic variability in the pathogen. The risk of development of a fungicide-resistant strain in downy mildew pathogens in India appear very low because of several reasons, including varietal diversity of the crop, use of mixture of fungicides (systemic and non-systemic), mixed cropping system, and small farm holding.

3.8. Biocontrol

Garlic juice extract is reported to be toxic to *P. parasitica* on radish (Saharan et al., 1997). Parasitism of pearl millet downy mildew pathogen by *Fusarium semitectum* Berk. and Rav. was reported by Rao and Pavgi (1976), but its effective use has not been demonstrated. Seed treatment of opium poppy with *Azotobactor* species reduced the downy mildew incidence and also the N-requirement of the crop (Chakrabarti and Yadav, 1991). This, however, needs further investigation to enhance the efficacy of *Azotobactor*. Potential of biocontrol agents for controlling downy mildews seems very limited as compared with seedling and root diseases.

3.9. Integrated disease management

Cultural, chemical, and biological control, and HPR are the components of integrated disease management. Cultural control methods have been partially successful in most cases to reduce the primary inoculum. Metalaxyl is an effective fungicide for all downy mildews, but development of metalaxyl-resistant strains in some downy mildew pathogens, including *P. parasitica* (Crute et al., 1985) has posed a limitation on its widespread use. Biological control of downy mildews has so far been limited to experiments and it will require substantial research efforts to achieve any success. HPR offers the best opportunity to manage the downy mildews.

4. Epilogue

Research on downy mildews has been relatively neglected in comparison with other biotrophs, such as

rusts and powdery mildews. The past decade has, however, seen a considerable increase in research activities, linked to an increased perception of economic importance, and improved understanding of life cycles and genetics of host-pathogen interaction. At present, only lettuce downy mildew (*Bremia lactucae*), is among the genetically best characterized fungal pathosystems (Crute, 1992; Michelmore, 1995).

Several new technologies have the potential to contribute significantly to the improvement of HPR to the downy mildews. These include somaclonal variants arising from tissue culture, in vitro selection, genetic transformation, dihaploid production from cultured anthers, and the use of saturated genetic linkage maps for MAS. The first two of these areas will require reliable systems for plantlet regeneration from cultures of protoplasts, cells, or callus. Genetic transformation may also rely upon tissue culture systems, but other approaches are also available.

In the Indian context, there is an urgent need for strategic research planning to effectively manage various downy mildews. This literature survey indicates large gaps in the knowledge of most downy mildews, except those of pearl millet, sorghum and maize, which have been researched intensively by international agricultural research centers. In other crops the lack of systematic research planning and execution to cover areas of distribution, pathogen biology, population structure, epidemiology, control methods, and genetics and mechanism of resistance prevents the development of an effective integrated disease management system. A multidisciplinary approach with good teamwork is needed to achieve this. A Working Group on the downy mildews organized at the national level is needed to manage the research portfolio and make use of modern advances in various disciplines. Advances in molecular techniques have provided a new set of tools for analyzing genomic variation and host-pathogen interactions (Michelmore, 1995). DNA polymorphisms are a rich source of molecular markers for genetic analysis and are also of potential value as diagnostic characters discriminating between species or pathotypes. An alternative approach for identifying DNA markers is to use RAPDs. One significant advantage of this technique with non-culturable pathogens such as downy mildews is that fingerprints can be generated from small amounts of DNA obtained form spores and mycelium. These molecular approaches promise to answer or at least clarify many of the unresolved questions concerning downy mildews. DNA probes detecting repetitive sequences are powerful tools for population studies and have already proved invaluable for analyzing diversity in other fungal pathogens, for example, *Magnaporthe grisea* (rice blast) (Levy et al., 1991) and *Phytophthora infestans* (Drenth et al., 1993). Not only these tools have value in research, but also for applied use. Yao et al. (1990, 1991) used a radiolabeled probe prepared from genomic DNA of *P. sorghi* to detect the presence of the pathogen in sorghum seeds.

Understanding of the host specificity of downy mildews requires genetic and molecular analysis in both the host plant and the pathogen. Methods for identifying and mapping host genes determining specificity are advancing rapidly; bulk segregant analysis to identify molecular markers linked to resistance genes should accelerate isolation and cloning of these genes (Michelmore, 1995).

For pearl millet a saturated genetic linkage map based upon molecular markers has been developed, and markers are being identified to assist breeders in selecting individual plants carrying specific resistance alleles of interest (Jones et al., 1995). Molecular markers are also being used to characterize populations of the pearl millet downy mildew pathogen (Sastry et al., 1995).

The future research efforts on downy mildews in India should focus on:

1. distribution and mapping in various crops;
2. the role of weather factors on disease development and spread;
3. the relative roles of asexual and sexual spores in infection and disease spread;
4. oospore survival under field conditions and the influence of various cultural practices on their survival and disease causing potential;
5. the importance of seed transmission and interstate quarantine regulation;
6. the genetics and mechanism of resistance; characterization of resistance sources for genetic makeup;
7. monitoring and characterization of pathogen populations within India;
8. the use of molecular tools to better understand genetics of host-pathogen interaction; and
9. integration of control methods to develop an effective and economic disease management package.

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