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Downy Mildew of Pearl Millet

Pearl millet (*Pennisetum glaucum* (L.) R. Br.) is known by various names in different languages: pearl, bulrush, cattail, or spiked millet in English; bajra in Hindi; dukhn in Arabic; and mil a chandelles in French. In India, Arabia, and Africa, pearl millet has been cultivated as a forage or cereal crop for at least 3,000 years. Pearl millet originated in Africa and was subsequently introduced into India. Some researchers believe that millets were the first cultivated crops to be used for human food in prehistoric times (10). The world area cropped to pearl millet is about 26 million hectares. The crop is grown on the poorest soils and under harsh climatic conditions where no other crop can grow. Therefore, pearl millet is the food of the poorest of the poor. Although the crop is quite hardy, it still suffers from various biotic stresses. One of the major biotic yield-reducing factors is the disease downy mildew, caused by *Sclerospora graminicola* (Sacc.) J. Schröt. The disease is of great economic importance in India and in many countries in Africa, including Senegal, Mali, Burkina Faso, Niger, Nigeria, Togo, Chad, Tanzania, Zambia, and Mozambique. The pathogen has been reported in more than 20 countries (23).

History of Downy Mildew Disease in India

The downy mildew pathogen was first reported on pearl millet in India in 1907 (5). Although the disease was established in most of the pearl millet growing areas, high disease incidence and yield losses were reported only in poorly drained, low-lying areas (7). Because of the use of local cultivars and traditional cultivation methods, the disease remained sporadic until 1970. Yields were low but stable.

To meet the growing demand for food, the Indian Council of Agricultural Research (ICAR) established "All India Coordinated Projects" for crop improvement in 1957. A coordinated project for the improvement of sorghum (*Sorghum bicolor* (L.) Moench) and pearl millet was established in 1960. The objectives of these projects were to produce short, early-maturing, and high input responsive cultivars (24). The discovery of cytoplasmic-genic male sterility in pearl millet (4) encouraged breeders in India to produce F_1 hybrids for increasing grain yield. Tift 23A, a male-sterile line bred in Georgia, USA, was imported and a hybrid program began.

The first pearl millet hybrid, HB1 (Tift 23A × Bil 3B), was released for commercial cultivation in India in 1965, closely followed by HB2 and HB3. The cultivation of these hybrids resulted in a quantum jump in yield. In 1970–71, when HB3 was grown on less than 20% of the area, India harvested a record grain yield of 8.2 million metric tons. In the following year, a severe and widespread epidemic of downy mildew occurred that reduced the total grain yield to about 4.6 million metric tons (Fig. 1).

The parent line, Tift 23A, was bred in Georgia, where downy mildew does not occur. Unfortunately, the line was not tested for its reaction to downy mildew after its introduction into India, primarily because downy mildew was at that time a sporadic disease and high yield was the first criterion—the host was emphasized over the pathogen. Downy mildew appeared on Tift 23A and on all its hybrids as early as 1965, but it was ignored because of the improvement in grain yield and low disease levels. Widespread cultivation of uniformly susceptible F_1 hybrids for several consecutive years increased oospore inoculum in the soil, and environmental conditions favorable to the disease resulted in epidemics in 1971–72. These high-yielding cultivars were grown for several years despite their known susceptibility to downy mildew (9). Following these epidemics, several newer downy mildew resistant cultivars were grown widely; however, total grain yield never again reached the record level of 1970–71. The growing of susceptible hybrids produced such high densities of oospores of the downy mildew pathogen in the soil that even the local (land race) cultivars, which normally were not damaged, became seriously diseased.

Symptomatology

Two types of symptoms, downy mildew and green ear, are produced. Downy mildew symptoms may appear on the first leaf, but generally on the second and third leaves in the form of chlorosis of the leaf lamina beginning at the base of the infected leaf. The chlorosis progresses to successively higher leaves, covering the entire lamina on the third or fourth leaf. Under high humidity (>95% RH) and moderate temperature (20 to 25°C), chlorotic areas on leaves produce abundant asexual sporulation, generally on the abaxial surface of leaves, giving them a downy appearance. Severely infected plants remain stunted and do not produce panicles. The half-leaf symptom, shown by a distinct margin between the diseased (basal) portion and the nondiseased areas toward the tip, is a characteristic symptom of the disease (Fig. 2). After leaf symptoms develop, all the subsequent leaves and the panicle have symptoms due to the systemic nature of the disease, except in the case of recovery resistance, where plants outgrow the disease (21). Green ear symptoms appear on panicles due to the transformation of floral parts into leafy structures (Fig. 3). Sometimes symptoms may appear as local lesions on the leaves under west African conditions.

Pathogen

S. graminicola produces both asexual spores (sporangia, zoospores) and sexual spores (oospores). Sporangia are hyaline, thin-walled, ellipsoid, and papillate, with dimensions of 15 to 22 × 12 to 21 µm. In nature, sporangia are produced during the night between 0100 and 0400. Optimum sporangial production occurs at 20 to 25°C and 95 to 100% RH. Sporangia are ephemeral. They germinate directly by germ tubes and by releasing 1 to 12 zoospores. However, germination by zoospore release is most common. Zoospores germinate by germ tubes and retain their infectivity for about 4 hours at 30°C and for a longer time at lower temperatures (18,20). Oospores are thick-walled resting spores produced in infected leaves. A mature oospore is brownish yellow and spherical, and measures 32 µm (22 to 35 µm) in diameter. The pathogen is heterothallic, but homothallism also occurs (6). Recently, a repeatable method of oo-

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spore germination was developed (8) (Fig. 4.)

The pathogen was first reported on *Setaria viridis* (L.) P. Beauv. by Farlow in 1884, and later on pearl millet and other hosts (3). Isolates from different hosts are highly host-specific but morphologically similar (S. D. Singh, *unpublished*). Considerable variability occurs in the pearl millet pathogen. For example, HB3, which was highly resistant to downy mildew at Mysore, was highly susceptible at other places in India (3). The International Pearl Millet Downy Mildew Nursery (IPMDMN), conducted annually since 1976, showed that certain entries were consistently more susceptible at some locations in western Africa, particularly at Kano in Nigeria, than at locations in India. These differences in the reactions of entries to downy mildew in IPMDMN tests were confirmed to be genetic (1,16).

Recently, differences in virulence were demonstrated in a downy mildew infected plot at Durgapura, Rajasthan, India, where HB3 was last sown in 1977 and was susceptible. However, when it was sown again in 1980, after a gap of 3 years, it showed very high resistance. Under controlled conditions in the greenhouse, HB3 was highly resistant to the Durgapura isolate but highly susceptible to a Patancheru isolate (26). When grown repeatedly, HB3 became susceptible to downy mildew at Durgapura. Similar results were obtained with another hybrid cultivar in Maharashtra state of India (2,23). It appears that the pathogen develops a host-specific population(s), and that this population(s) survives as long as the particular host is grown but dies out when the host is withdrawn. This phenomenon may serve as a means of cultural control of downy mildew through gene deployment over time if it can be demonstrated true with other cultivars and at other locations (13).

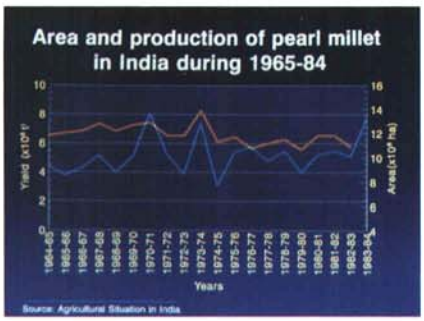

Fig. 1. Area and production of pearl millet in India from 1965 to 1984. Source: Agricultural Situation in India.

Fig. 2. Pearl millet leaf showing a typical half-leaf symptom.

Disease Control

Several control measures, including the use of resistant cultivars, fungicides, and cultural practices, have been suggested. However, only a few control measures are being utilized.

Seed sanitation. Seed infested with oospores is a primary source of overwintering inoculum and is also important in dissemination of the pathogen from one region/country to another. To stop this spread, a seed treatment procedure has been jointly developed by ICAR and ICRISAT. Seed are surface-sterilized with 0.1% $HgCl_2$ for 10 minutes, followed by washing in several changes of distilled water; they are then heated to 55°C for 12 minutes to inactivate seedborne internal mycelium, dried under shade, and treated with metalaxyl at 2 g a.i. kg^{-1} of seed. Although this treatment is routinely used by the Indian Plant Quarantine Department for the importation of all pearl millet seed into India, it is not practical for treating large seed quantities.

Chemical Control of Seed, Soil, and Airborne Inoculum. Metalaxyl, a systemic fungicide, has been highly effective in controlling downy mildew. As a seed treatment at 2 g a.i. kg^{-1} of seed, it protects against soil and seedborne inoculum and is also absorbed by seedlings, protecting them from sporangial inoculum. This treatment protects all the basal tillers. However, because of loss of fungicide over time, secondary tillers developing 30 days after sowing may become diseased if inoculum is present. Therefore, the crop should also be sprayed with metalaxyl at least once about 25 days after sowing, particularly when the crop is intended for seed production, where a total absence of the disease is desired. This treatment also reduces the buildup of inoculum. Spraying is not necessary for commercial production, as secondary tillers do not contribute greatly to yield (25). Metalaxyl spray can also arrest further development of symptoms in systemically infected plants, regardless of their age, but the panicle length is reduced if diseased plants are sprayed after panicle development (19). This results from infected panicles becoming green ears during development (S. D. Singh, *unpublished*).

Host-plant resistance. Downy mildew epidemics in India came suddenly and became so frequent and widespread that the Indian National Program faced a difficult situation in the seventies. At that time, reliable resistance-screening techniques and sources of resistance were not available. Therefore, ICRISAT placed major emphasis on downy mildew research, in collaboration with the All India Coordinated Pearl Millet Improvement Project (AICPMIP). Studies on disease epidemiology and pathogen biology were conducted (28), which helped in developing screening techniques and in identifying genetically resistant germ plasm.

Field screening techniques. An ideal field screening technique should provide uniform distribution of inoculum, allow natural inoculation at the susceptible stage of the crop, minimize escapes, and utilize both types of inocula (oospore and sporangia), while allowing breeding activities to be conducted in the same field. The infector-row technique (23,30) fulfills these criteria. This technique involves the sowing of infector rows (every fifth or ninth row) with a susceptible cultivar(s) 3 weeks before sowing test material. These rows are inoculated with sporangia at emergence, followed by frequent furrow-irrigation during the first 15 days after

Fig. 3. Disease-free and malformed earheads (green ears) of pearl millet. Note the different types of malformation that can occur.

sowing to promote high humidity, followed by normal irrigations. Test material is sown when infector rows develop 40 to 50% disease. Disease evaluation is conducted initially at the seedling stage and later at the soft dough stage. This technique is routinely used at National Agricultural Research System (NARS) locations globally (Fig. 5).

Laboratory screening techniques. Laboratory screening techniques are useful for precise pathological studies, for mass screening of breeding material in greenhouse/laboratory conditions, and for detection of escapes from field screenings. An ideal technique must allow natural inoculation at the most susceptible stage of crop development with an appropriate inoculum concentration and the development of host and pathogen under optimum conditions (temperature and humidity). The procedure must not overemphasize either the host or the pathogen. The technique developed at the ICRISAT Asia Center (IAC) involves inoculation of potted seedlings in the coleoptile-to-one-leaf stage using a microsyringe (Fig. 6) (17). Alternatively, the seedling at this stage can be spray-inoculated. This method is being used for mass inoculation of breeding material (Fig. 7) (23), because it allows mass screening in a very small space (30 to 40 seedlings per 10-cm-diameter pot) and in a short time (about 20 days from sowing to evaluation). There has been a good correlation between the results of field and greenhouse screenings. Due to its routine use for mass screening at IAC, the level of resistance in our breeding material has increased substantially, and the size of our field nursery has also decreased considerably, resulting in substantial cost reduction.

Sources of resistance. The process of resistance identification is long and includes preliminary evaluation of germ plasm and breeding material at IAC (12), and testing of promising material (with less than 5% downy mildew) multilocationally at highly infested locations worldwide. Three types of resistance have been identified.

Sources of stable resistance: Several western African accessions showed high levels of resistance at several hot-spot locations in India and western Africa and over several years of tests. These include ICML 12, ICML 13, ICML 14, ICML 15, and ICML 16 (22); and P310-17 and P1449 (S. D. Singh, *unpublished*).

Sources of recovery resistance: Recovery resistance is a phenomenon in which systemically infected plants outgrow the disease and produce healthy panicles (Fig. 8). Genotypes possessing this trait do not interfere with the pathogen in spore germination, penetration, development of disease symptoms, or sporulation, thus allowing the pathogen to complete its life cycle. This trait allows the host and the pathogen to coexist without affecting the yield. The trait is heritable. The unique feature of the cultivars possessing recovery resistance is that if they become diseased, they quickly recover from it and behave as resistant cultivars.

The recovery resistance mechanism has been discovered in many accessions and breeding lines, but only a few accessions had high levels of this type of resistance. Through pedigree breeding, the level of

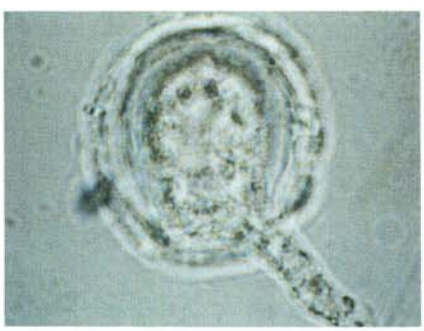

Fig. 4. Germinating oospore of *Sclerospora graminicola* (×330).

Fig. 5. Downy mildew field screening nursery at ICRISAT Center. The taller rows running across the field are infector rows. The younger crop sown between the infector rows is the test material. Note the presence of susceptible indicator rows among the test material. In the background is the pearl millet breeding nursery.

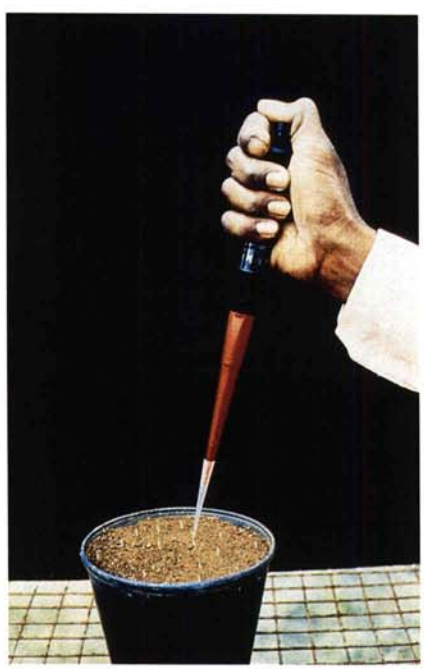

Fig. 6. A seedling inoculation technique: a precise method of inoculation of seedlings with sporangia. Each seedling is inoculated with a known volume of inoculum.

Fig. 7. A method of mass inoculation of seedlings with sporangia. This method is now being used routinely to screen large amounts of breeding material under greenhouse conditions.

Fig. 8. Natural remission of downy mildew symptoms (recovery) after the development of systemic infection. Plant showing recovery on the same shoot. Note the presence of asexual growth on several infected leaves.

recovery resistance was increased to more than 95% in a male-sterile line, 1CMA1, which is being used to produce commercial hybrids in India (S. D. Singh and B. S. Talukdar, *unpublished*). Other recovery resistance sources include SDN-503, P1449, and ICMA 841.

Sources of complete resistance: Recently, accessions were identified that show 100% resistance in the most stringent in-greenhouse inoculation tests against major pathotypes in India, and also to several field populations of *S. graminicola* in field disease nurseries in India and western Africa. These are IP 18292 and IP 18298. Five others, IP 18293, IP 18294, IP 18295, IP 18296, and IP 18297, showed a few infected plants at one or more locations. A significant feature of these sources is that they possess morphological markers (e.g., white leaf sheath, no midrib, purple leaves, etc.) (Fig. 9A and B). These traits will be highly useful in maintaining the genetic purity of these lines. Complete resistance coupled with marker traits make them unique sources of resistance.

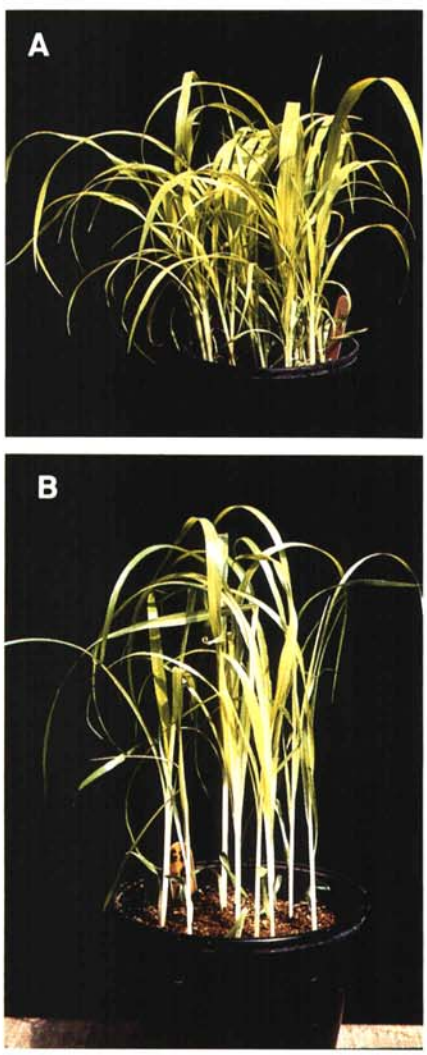

Fig. 9. Two of the seven newly identified sources of resistance to downy mildew: (A) yellow seedlings, and (B) seedlings with white leaf sheath.

Development of resistance based on residual variability: Pearl millet is a highly heterogeneous crop. Therefore, 100% resistance or susceptibility is not common in nature. Because of this, resistant cultivars have a proportion of susceptible plants and susceptible cultivars a proportion of resistant ones. To test whether the resistance level in a susceptible cultivar can be increased by selection, a highly susceptible land race from Chad, 7042, was chosen. By selecting resistant plants and carrying their progenies for five generations following pedigree selection in a disease nursery, ICML 22, a line that showed greater than 95% resistance against the most aggressive populations of downy mildew present in India, was selected (29). The line also tested as photoperiod insensitive (14). ICML 22 is being used extensively in breeding programs. ICML 11, a line resistant to rust (*Puccinia penniseti* Zimm.), was selected from the same land race, which was also susceptible to rust (15).

Using the above methodology, a downy mildew resistant male-sterile line, ICMA 841, was selected from a susceptible male-sterile line, 5141 A (27). ICMA 841 is a leading male-sterile line in India, and its hybrids have been grown on more than 1 million hectares for the last several years.

This research demonstrated that susceptible cultivars can be revived if residual variability for resistance exists. Such cultivars not only are inexpensive and faster to develop, but also will be well-adapted and accepted by farmers. This method should be regarded as a routine cultivar-maintenance operation for increasing the useful life of commercial cultivars. The exercise will ensure full exploitation of the high-yield potential of released cultivars. Cultivars would be changed only when higher yielding cultivars with additional useful traits are available, and not only because of their susceptibility to downy mildew, as has happened in the past.

Utilization of resistance. At IAC and at the NARS in India and Africa, resistance sources are used to breed pollinators, male-sterile lines, and cultivars. These include ICML 12, ICML 13, ICML 15, ICML 16, P1449, IP 18292, and IP 18293. By routine screening in the disease nursery and greenhouse, resistance in the progenies of composites has reached such a high level that incorporation of resistance from other sources is not needed. At ICRISAT Sahelian Center, Niger, progenies of populations are tested in a downy mildew nursery at Bengou and Sadore for increasing resistance. Since the level of resistance in the original populations is high, incorporation of resistance from other sources is not considered necessary at this time.

Fig. 10. Two NHB 3 plots grown with and without seed treatment with metalaxyl. The untreated NHB 3 hardly produced any heads under severe disease pressure.

Use of resistant cultivars. Two types of cultivars have been developed, open-pollinated varieties and F_1 hybrids. Among the open-pollinated varieties, WC-C75 and ICTP 8203 became popular. WC-C75 has been grown in India on an estimated 1 million hectares for the last decade without any report of its being susceptible to downy mildew. Downy mildew resistant hybrids ICMH 451 and Pusa 23 are being grown on 1 million hectares each for the last several years. Many hybrids produced by public sectors are also being grown. In western Africa, ICRISAT has developed some downy mildew resistant cultivars, including ICMV1 and ICMV2 (Senegal) and IKMP2, IKMP3, and IKMV 8201 (Burkina Faso). These are being grown on a considerable area in western Africa (23).

A new concept in the production of hybrids is the development of topcross hybrids. In these hybrids, the pollen parent is a genetically diverse population instead of an inbred line. The genetic heterogeneity of the pollen parent provides a broad genetic base to the hybrid, which may make its resistance more stable than that of the single-cross hybrids. ICRISAT has produced a topcross hybrid, ICMH 88088, which possesses a high level of downy mildew resistance and outyields all the available cultivars. This hybrid is becoming popular with many farmers (B. S. Talukdar, *personal communication*).

Inheritance of resistance. Although resistance was found to be dominant over susceptibility and is controlled by one or more dominant genes with some modifiers, a true picture of inheritance is not yet clear (23). With the availability of precise inoculation techniques, and highly homozygous resistance and susceptibility sources, precise information on the genetics of resistance will soon become available.

Fluctuation in disease control. By 1981–82, several downy mildew resistant cultivars became available and were grown by farmers. Still, disease epidemics occurred in 1983 and 1984, and again in 1986 to 1988, in some parts of India. The reason for these epidemics was the cultivation of a single, genetically uniform genotype on a given area for several successive years (11) despite the availability of other resistant cultivars. This enabled the pathogen to adapt to the host and mul-

tiply. Several reasons, including the farmers' preference for the cultivars, nonavailability of seed of other resistant cultivars, and lack of extension education and proper planning were the primary factors involved. Such factors sometimes are difficult to control and indirectly contribute to disease epidemics.

Management Strategies

The availability of many resistant cultivars with diverse genetic backgrounds, produced through different breeding approaches, and an effective systemic fungicide provide ample opportunities for the long-term control of this disease.

Diversification of cultivars. Epiphytotics occurred in the past due to the development and buildup of host-specific pathogen populations (26). Therefore, repetitive cultivation of a hybrid in a given area should be avoided. Instead, several hybrids should be grown on a given area. Deployment of different cultivars over time, based on the principle of host-specificity, is another alternative approach. Because the pathogen is highly host-specific, the virulence will gradually shift to fit the cultivar grown in a given area over a long period. Host-specific oospore populations may die out in 2 to 3 years after the specific host is withdrawn from cultivation. Consequently, a cultivar that has been withdrawn can be reintroduced after a gap of 3 or 4 years (13). However, for this approach to work, a number of adapted hybrids are needed. A coordinated effort by research programs, extension services, and seed production, distribution, and sales agencies is necessary.

Topcross hybrids may be particularly appropriate for African conditions, where the downy mildew pathogen is more variable and aggressive, and also in countries where seed production laws do not require uniformity in growth and maturity. Open-pollinated varieties that are populations containing large genetic differences among plants are valuable for keeping the disease under control. They will have a buffering effect against shifts in pathogen virulence. Such cultivars are not disease free, but epidemics are unlikely to develop on them for several years.

Use of metalaxyl. Metalaxyl should not be used on a regular basis to completely protect the crop from the disease, nor should it be used to encourage planting of susceptible cultivars (Fig. 10). These two practices will increase the chances for stepwise buildup of resistance in the pathogen resulting in the ineffectiveness of the fungicide. The fungicide could, however, be used for 1 or 2 years if a known popular cultivar has become susceptible and alternative resistant cultivars are not immediately available. The fungicide should also be used periodically in disease-endemic seed-producing areas to reduce oospore build-up and also to produce a disease-free crop (25).

Cultural practices. Of the several cultural practices, roguing of infected plants soon after their detection is the only method that should be routinely used (23). This method will reduce the spread of the disease (by decreasing sporangial production in the same season and by reducing oospore production for the following season) and will also allow time for the surrounding plants to compensate for yield through increase in tillering.

In summary, downy mildew disease will continue to be a threat to pearl millet. Resistant cultivars that have been successful in India will remain the most economical and feasible method of control of this disease, both in India and in Africa. However, shifts in the pathogen population must continuously be monitored in order to replace commercial cultivars as they become susceptible to downy mildew. Also, strategies for efficient utilization of resistance genes that include pyramiding several genes in single cultivars, combining major genes with incomplete resistance, and deploying different genes over time will have to be developed. Such strategies will restrict the development of virulent populations for a longer time and provide durable control of the disease. Metalaxyl is recommended as a seed treatment in both India and Africa, but it should be used judiciously.

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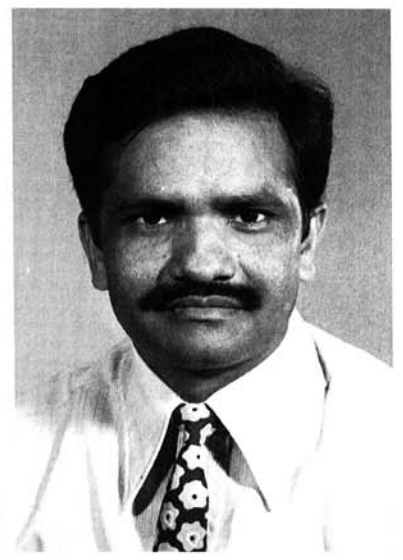

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