Know-how for Horticulture

Review of downy mildews on nursery plants

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VIC Department of Primary Industries

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Downy mildews on nursery plants **is a synopsis designed for nursery managers as part of the final report for the Horticultural Research and Development Corporation Project NY406**

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CONTENTS

INTRODUCTION

Downy mildew diseases cause enormously significant problems in nursery seedlings, if not controlled. They are prevalent in cool wet months, but can occur all year around. The diseases generally don't kill the plant; they make it look ill, uncared for and therefore unsaleable. Downy mildew diseases are found on many nursery seedling lines e.g. stock, brassicas, viola, anemone, onion and lettuce.

The diseases are estimated to cause economic losses of 10-12% in production of ornamental and vegetable seedlings in nurseries, which are valued at $60 million nationally (32 million punnets). Crop loss estimates, made by growers suggest that losses due to downy mildews account for about $4 million in retail sales nationally.

SYMPTOMS

Downy mildews produce a 'downy' mass of spores (sporulates) on the under leaf surface Symptoms of flecking, speckling and blotching appear on the upper leaf surfaces and heavily infected leaves may yellow, prematurely wither and then die. In contrast, **powdery mildews produce a 'powdery' mass of white spores on the upper leaf surface.** Leaves may eventually yellow but they tend to persist on the plant.

THE DOWNY MILDEW FUNGI

The fungi which cause downy mildew diseases are classified in the Order Phycomycetes and Class Oomycetes and are distantly related to the phytophthoras and pythiums. Downy mildews grow only in living plant tissues; they are obligate parasites. They cannot be grown on agar culture plates. Although the brassica downy mildew has been grown sparsely on tissue cultured callus, spore production was atypical.

The vegetative body of the fungus consists of hyphae (filaments) which lack cross-walls. When grouped together hyphae form a mycelium. The fungus grows between cells in the leaf. Knobs of hyphae (haustoria) penetrate through walls of plant cells, but not into the adjacent cell membranes. The fungus drains nutrients from plant cells, stressing the leaf and causing premature leaf death. The 'down' on the undersurface of the leaf consists of the asexual sporing structures of the fungus. They look like little trees (sporangiophores) with fruits (sporangiosporesi.e. spores) on the ends of the branches (Fig 1).

- The fungus is mainly located within the leaf tissue.
- Contact fungicides often don't reach it, because they remain on the leaf surface.
- Contact fungicides may give little control once the disease is established within the leaf.

INFECTION

Cycle of infection (Fig. 1)

A. A vegetative spore on the surface of a leaf has produced a germtube and at its tip an appressorium (knob) has formed, below which the fungus penetrates the cuticle and enters the leaf e.g. brassica downy mildew. The fungus causing onion downy mildew enters the leaf via the stomata.

B. After the fungus has entered the leaf, a hypha (thread-like body of a fungus) grows between the leaf cells). Hyphae of the fungus penetrate into leaf cells and enlarge into knob-like structures (haustoria). It is through these structures that the fungus obtains its nutrition from the host tissue.

C. The fungus grows through the leaf tissue for 5-7 days (brassica downy mildew), too small and too concealed for us to see. Vegetative spore producing structures (sporangiophores) emerge through stomates on the undersurfaces of leaves at night. By morning, vegetative spores are fully formed on their tips and appear as a 'downy' mass on the under surface of the leaf.

D. As the sun rises in the morning and the air dries out, the sporangiaphores twist back and forth, flinging the spores into space.

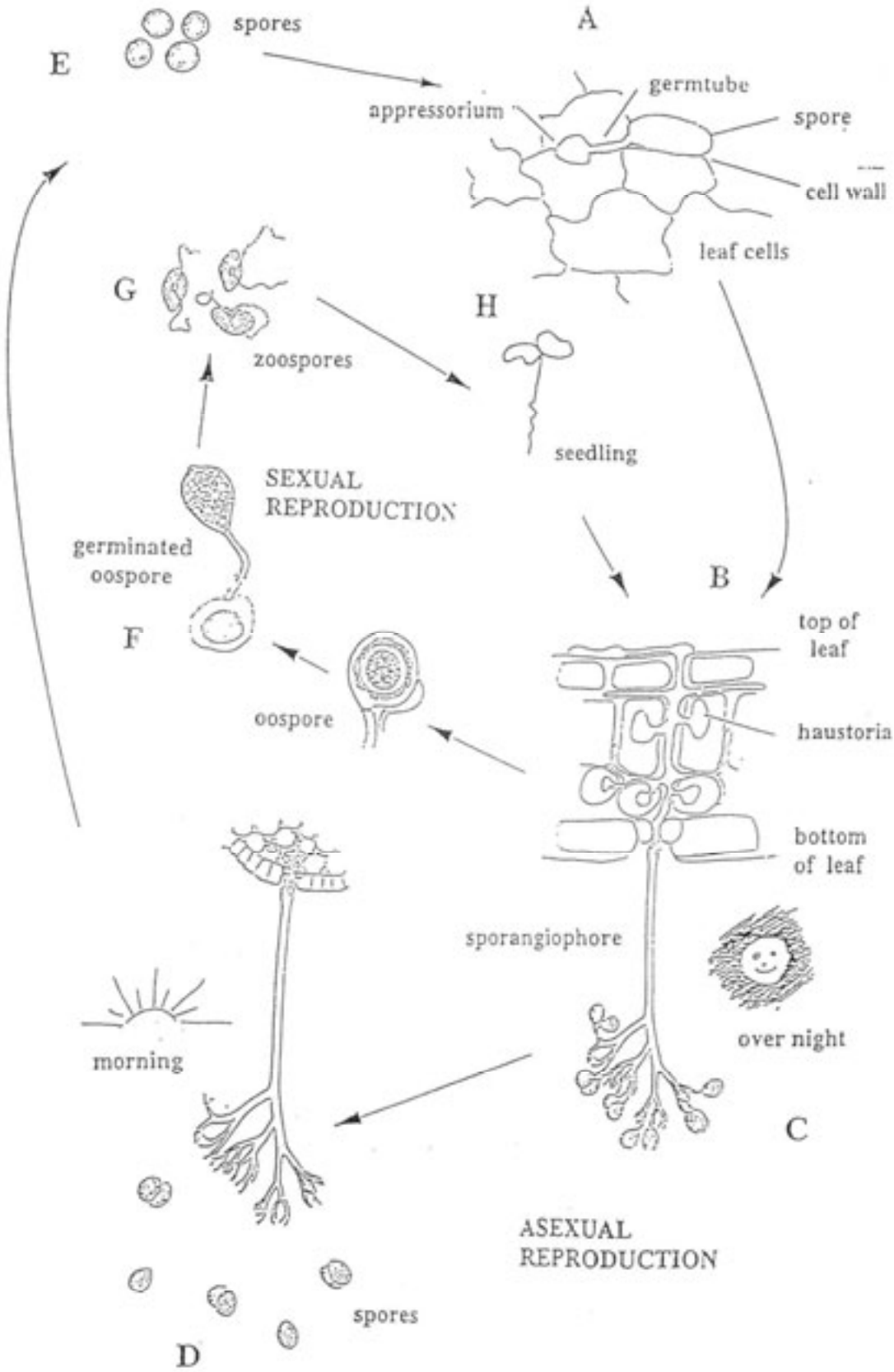
E. Spores are dispersed by wind currents.

F. Oospores (sexually produced spores) form in senescing leaves which later fall to the ground. Oospores germinate in the soil to produce a sporangium containing flagellated zoospores.

G. Flagellated zoospores are dispersed by water.

H. Zoospores infect young seedlings through hypercotyls, cotyledons, stems and leaves to cause systemic infections.

Fig 1 Infection cycle of downy mildew
(Parts of this figure are from Ingold, C. T. 1973. The Biology of Fungi. Hutchinson Educational, Great Brittan.)



Asexually Produced Spores (Sporangiospores)

Asexual spores are the major means of fungal spread. The higher the spore load the higher the intensity of the infection. Older plants are less susceptible to infection, requiring more spores for symptoms to develop. Scientists have shown that a single spore was able to initiate infection in kohlrabi.

In experiments with detached cabbage cotyledons, the infection process was shown to take place within 3 hours.

- Cabbage cotyledons were inoculated at time zero with spores.
- The cotyledons were then sprayed with zineb (a contact fungicide) at time zero, at one hour, 2 hours, 3 hours, 4 hours and 5 hours after inoculation.
- Symptoms of downy mildew developed predominantly when zineb was applied 3, 4 and 5 hours after spore deposition.
- These results suggest that the fungicide was no longer effective when applied at 3, 4 and 5 hours after the spores. The infection process must have taken place within 3 hours!

Sexually Produced Spores (Oospores)

Oospores are thick walled and so able to survive unfavorable conditions. They probably survive in or on rotting plant debris in the field. Survival in irrigation water has not been demonstrated. Oospores are considered to be the main means of carry over of the fungus and the cause of primary infection on field grown crops of e.g. broccoli, cabbage and cauliflower. Overseas the fungus is considered to over-winter on perennial plants, winter annuals or plant debris. The latter are probably not applicable to the nursery situation as seedlings are grown in sterile non-soil mixes.

REPRODUCTION

Asexual or Vegetative

Asexual or vegetative reproduction in downy mildew is the production of genetically identical spores (sporangiospores), without any sexual processes. In downy mildews the asexual spores are produced on the tips of microscopic tree-like structures (sporangiophores). These structures emerge through the stomates on the undersurfaces of leaves, at night. In the early morning they appear as a fluffy white mass on the undersurface of cotyledons and leaves. For brassica downy mildew, it takes approximately 4-7 hours for the structures to emerge and for the spores, which are microscopic, egg shaped and range in size from 24-27 jam long to 12-22 um wide, to form on their tips.

Sexual

Sexual reproduction leads to variation or genetic differences in the offspring which is an advantage for survival of the species, especially under changing environmental conditions. There is evidence for both self-fertilizing (homothallic) and cross-fertilizing (heterothallic) forms in *Peronospora parasitica* and *Bremia lactucae,* although the latter is considered to be the more common. The products of sexual reproduction are the oospores. Their formation is favored by factors causing normal senescence of host tissue. Consequently they are abundant in yellowing and dying leaves and senescing cotyledons. They are rare in green tissue.

CARRY-OVER/SPREAD

Debris

Oospores (sexually produced spores) of the fungus form in dying leaves. The thick walls of oospores makes them resistant to desiccation and attack from other organisms when leaves fall to the ground as debris and rot. In this way they survive unfavorable conditions and carryover the disease from one season to the next or from one crop to the next.

Old seedlings

Old seedlings, past their use-by date, often carry a few downy mildew lesions which may have the capacity to produce a few spores (vegetative sporangiospores). If seedlings are not discarded, they have the potential to produce inoculum (spores) to infect the next generation of seedlings. In this way the disease can cycle around a nursery from old seedlings to young seedlings. This is the most likely cause of the problem and appropriate hygiene measures, such as roguing, are required.

Seed

Of the downy mildews considered in this report, only the downy mildew on brassicas (P. *parasitica),* poppies (P. *arborescens)* and marigolds (P. *farinosa)* are reportedly seedborne. Survival of P. *parasitica* in brassica seed has been detected in Russia, China and India. Heat treatment of seed at 48°C-50°C for 20 minutes reduced disease incidence from 42.5% to 2.5% in Russia. Downy mildew on cabbage in Russia was shown to be internally located as removal of the seed coat did not reduce disease incidence. On radish in India, downy mildew was shown to enter the stigma and ovary leading to embryo and pericarp infection producing infected seedlings. Mycelium of P. *parasitica* has been found contaminating seed coats of Chinese cabbage in China but infection of seedling was not consistent.

No evidence has been found to suggest that seed sold in Australia is contaminated.

Soil

Soil-borne oospores are the major source of infection in field grown Chinese cabbage in China and of cabbage seedlings in the USA. It is, however, difficult to induce oospores to germinate or to cause plant infection. The production of seedlings in a sterilized non-soil mix, suggests that oospore contamination of the mix is highly unlikely in the nursery situation.

Weeds

Weedy species of Cruciferae or Brassicaceae are considered to be able to carry the downy mildew disease without expressing symptoms. Although the production of spores may be sparse, it is considered to be sufficient to infect cultivated brassicas and cause the disease. A similar situation probably exists for lettuce.

Water

Although vegetative spores need water to germinate, the survival of oopores in irrigation water is unknown.

ENVIRONMENTAL CONDITIONS AFFECTING INFECTION

Dew

This is the formation of minute specks of water on the leaf surface as the air cools at night.

> **Watering seedlings in the presence of dew will increase the period of time that leaves are wet in the morning which is when spore release occurs.**

For this reason watering of seedlings in the presence of dew should be avoided. The dew period can be shortened with the placement of covers over seedlings.

Fertilizer

Maintain a balanced program of nutrition. A deficiency of potash increases the susceptibility of cauliflowers to brassica downy mildew. Deficiencies of sulphur and excesses or deficiencies of nitrogen, phosphorus or potash have no direct effect on downy mildew development in brassicas. High nitrogen fertilization programs make lettuce seedlings more susceptible to downy mildew *(B. lactucae).*

Humidity

Spores (asexual) are released in the morning as the air dries out, by the twisting and untwisting of the spore producing bodies (sporangiophores). High humidity encourages spore formation, spore germination and spore infection. It is difficult to control downy mildew when persistent high humidity occurs throughout the day.

Irrigation

Watering seedlings in the morning, especially after a dew, lengthens the period of time leaves are wet which is when spore release and infection take place. Over-head sprinklers wet leaf surfaces, wash off chemicals and increase humidity thus enhancing the development of downy mildew. One short, heavy watering is best as it reduces the length of time leaf surfaces are wet and thus susceptible to infection. Timing and duration of irrigation is probably less critical in hot dry weather as water will evaporate quickly from leaf surfaces.

Light

Vegetative spores are produced during darkness e.g. *P. parasitica, P. violae* and *Bremia lactucae,* and released during the following morning. Spores of *P. parasitica* take approximately 7 hours to form and fully mature in the dark. Low light intensities can promote sporulation whilst high ones can be inhibitory. This may account for symptoms being more common on lower seedling leaves and lower leaves of field grown brassicas.

Blue wave lengths of light or periods of white light during the night have been shown to inhibit spore production in curcubit downy mildew *(Pseudoperonosporacubensis)* at 24°C, to significantly reduced it at 23°C, to have no effect at 15°C and promoted spore production at 10°C. In Israel blue igloo covers are used to hinder sporulation of downy mildew on curcubits.

Rain

Downy mildew of brassicas is more severe in the field when rainfall exceeded 750-1000 mm/yr. Rain has the effect of washing spores out of the air thus depositing them onto leaf surfaces. Morning rains can extend the length of time leaves are wet after a dew thus providing ideal conditions for infection. Keeping leaves dry, especially in the morning when spores are released will help to reduce infection.

Temperature

Downy mildews tend to be associated with cool weather. See specific downy mildew diseases for their optimum temperatures of activity. Raising the glasshouse temperature, without raising the relative humidity, dries leaves off quickly and reduces the opportunity for spores to germinate and infect. Unfortunately this option is often expensive.

Ventilation

A good movement of air around and through a nursery is necessary to speed up the drying of soil and plant surfaces in order to reduce infection periods. Excessively dense foliage, crowded seedlings or structures which interfere with air circulation (e.g. hedges) should be avoided. Any nursery practices which reduce the time leaf tissue remains wet will help to inhibit the development of downy mildews.

Water

Wet surfaces of leaves (leaf wetness) are essential for downy mildew infections because spores need water to germinate. Wet leaf surfaces can result from dew, irrigation or rain.

Wind

Spores are basically wind dispersed, however, wind also has a drying effect by reducing the humidity around seedling and the moisture on leaves and cotyledons.

DISTRIBUTION

In Australia downy mildews are considered to be a problem in all states except the Northern Teritory. In Victoria, they are prevalent on brassicas, viola, stocks and lettuce seedlings. They cause major problems on brassicas, stock, lettuces and roses in New South Wales. Brassicas, onions and roses are severely affected in Queensland. Whilst in Western Australia the disease is only a problem on brassicas in the wetter areas.

HOST RANGE

Downy mildew diseases occurring on different genera of host plants are caused by different genera or species of fungi (Table 1). These fungi are all host specific, consequently the fungus causing downy mildew of lettuce will not cause downy mildew on brassicas. The fungi infect ornamentals, vegetables and weeds which can act as reservoirs for the carry-over of the fungus from one season to the next.

i

Table 1 List of host plants for various downy mildews

Host Plant	Downy Mildew Fungus	Recorded
Allium (onion)	*Peronospora destructor*	Q, N, S, T, V
Anemone	*Peronospora anemones*	N
	Plasmopara pygmaea	-
Antirrhinum (snapdragon)	*Peronospora antirrhini*	N, Q
Arctotis	*Peronospora halstedii*	N
Aster	*Basidiophor entospora*	-
Brassica	*Peronospora parasitica*	N, Q, S, T, V, W
Campanula	*Peronospora corollae*	-
Centaurea (cornflower)	*Bremia lactucae*	N, V
Cheiranthus (wallflower)	*Peronospora parasitica*	N, V
Chrysanthemum	*Bremia lactucae*	-
	Peronospora radii	-
Clarkia elegans	*Peronospora arthuri*	-
Dianthus (carnation)	*Peronospora caryophyllus*	-
Dianthus	*Peronospora dianthicola*	N, V
Eustoma (lisianthus)	*Peronospora chlorae*	N, Q, S, V
Geum	*Peronospora gei*	N, S, V
Hebe	*Peronospora grisea*	N
Helichrysum	*Bremia lactucae*	-
Helianthermum	*Peronospora leptoclada*	-
Helianthus (sun flower)	*Peronospora halstedii*	N, Q, S, T, V
Helleborus	*Peronospora pulveracea*	N, Q, T, V
Lactuca (lettuce)	*Bremia lactucae*	N, Q, S. V
Lobularia (alyssum)	*Peronospora parasitica*	N, V
Matthiola (stock)	*Peronospora parasitica*	-
Mesembryanthemum	*Peronospora mesembryanthemi*	-
Mimulus (monkey flowers)	*Peronospora jacksonii*	-
Myosotis (forget-me-not)	*Peronospora myosstidis*	N, Q, V
Nicotiana (tobacco)	*Peronospora tabacini*	N, Q, T, V
Papaver (poppy)	*Peronospora arborescens*	-
Primula	*Peronospora oerteliana*	N, Q
Ranunculus	*Peronospora anemonse (P. ficarie)*	N, Q, V
Rosa (rose)	*Peronospora sparsa*	-
Senecio (cineraria)	*Peronospora halstedii*	N, V, W
Viola (pansy)	*Peronospora violae*	-
	Bremiella megasperma	

N, New South Wales, Q, Queensland, S, South Australia, V, Victoria, W, Western Australia, -, not recorded in Australia.

Allium (Onion) downy mildew

Downy mildew of onions can be caused by systemic infections of bulbs or from infections of leaves by airborne spores. Systemic bulb infections dwarf plants and cause distorted pale-green leaves which bend markedly downward. Leaf infections first appear as pale, oval to elongate spots. In humid weather greyish spores appear on leaves and spots. Leaves shrivel, collapse and die. Severe leaf damage causes 'bottle-neck' symptoms and hinders bulb development.

Spore production is stimulated by a relative humidity of 95% or more and free water on the leaf surface. The optimum temperature for spore production is 10°C-13°C with a range of 1°C-18°C. Spores are released due to changes in relative humidity. They are dispersed by wind during the day, especially from 1000-1200 hours and have been recorded at 1500 feet (450 m) above onion fields. They can remain viable for several days.

Spores infect leaves after long periods of leaf wetness over a temperature range of 3.5°C-25°C with an optimum of 13°C. They germinate in 2-2.5 hours and infection takes about 3 hours. Symptoms develop 10-17 days after infection but take longer to develop (18°C-20°C days) at higher temperatures of 25°C to 30°C.

There is no evidence of seed transmission of *Peronospora destructor* which causes downy mildew of onions, although the fungus has been found in flower parts. The aerially dispersed spores (asexual sporangiospores) produce local infections on leaves and flower stalks and inconjunction with moisture, temperature and the size of onion fields are responsible for the rapid build up of the disease (epidemics). Oospores (sexually produced spores) form in plant parts and after leaf fall they can contaminate the soil for up to 25 years. The fungus can survive from season to season in systemically infected bulbs or as oospores in the soil. A model has been developed to predict outbreaks of onion downy mildew on field crops.

The fungus responsible for onion downy mildew *{Peronospora destructor)* attacks both cultivated and wild species in the genus *Allium.* Host plants are *A. albidum, A. alataviense, A. altaicum, A. ascalonicum, A. cepa, A. fistulosum, A. flavum, A. galanthum, A. obliquum, A. ochroleucum, A. oschaninii, A. pskemense, A. schoenoprasum,* and *A. tuberosum.*

Management strategies to control the disease include heat treatment of bulbs, removal of infected plant debris, eradication of volunteer plants and the avoidance of sprinkler irrigation.

Anemone and Ranunculus downy mildew

Two downy mildews infect anemones *(Peronospora anemones* and *Plasmopara pygmaea). Peronospora anemones* produces a dull green to grey colouration on leaves, which often curl downward. Pink to purple shades of colour appear on leaves as the disease progresses, followed

by patches of dead brown tissue on older foliage. Masses of whitish grey spores form on the undersurface of infected leaves and also on bracts and petioles. Spore production, however, may be sparse. These spores are dispersed by rain and harvesting but not by wind.

Late in the season oospores form in petioles and peduncles. When infected leaves die and become plant debris in soil, the oospores contaminate soil for subsequent crops. A crop rotation of 5 or more years has been suggested to reduce incidence of the disease. Germination of oospores in soil is encouraged by regular and prolonged rainfall. The *P. anemones* which attacks *A. coronana* and *A. globosa* doesn't infect ranunculus, whilst the *P. anemones (P. ficarie)* which infects ranunculus doesn't infect anemones.

Plasmoparapygmaea causes blackening of foliage and produces masses of white spores on the undersurfaces of leaves.

It is very rare and has not been recorded in Australia.

Antirrhinum (Snapdragon) downy mildew

Downy mildew on snapdragons is generally confined to seedlings and young plants where it causes stunting of the entire plant, a rosette of small leaves forms on plant tips and foliage turns a pale yellow green colour. Leaves droop downward and curl inwards. If the shoot is killed,, plants can resprout from basal buds. The fungus, *Peronospora antirrhini*, which causes the disease is systemic within the plant. White to purple spores form on the undersurfaces of leaves, but with heavy infections spores may form on both leaf surfaces and stems. These vegetatively produced spores give rise to secondary infections. On older plants the disease causes pale yellowish spots on leaves.

The disease is promoted by high relative humidity and low temperatures. Reducing relative humidity has been shown to control the disease. The fungus produces spores over the temperature range of 7°C - 22°C with optimum production at 13°C. Spores will only germinate in water. Oospores (sexually produced spores) form in leaves, stems and roots, which later fall to the ground resulting in oospore contamination of the soil. Contaminated seed is suspected to disperse the disease, however, this has never been proven. Reports of varietal resistance to the disease are contradictory. Breeding snapdragons for resistance to downy mildew was unsuccessful in California.

Brassica downy mildew

Spores generally land on leaves in the morning and need wet leaf surfaces to germinate. The biochemical processes for infection are set up within 3 hours whilst the physical process of the fungus entering the leaf may takes up to 24 hours. The fungus grows through the leaf tissue for 5-7 days, unobserved by the human eye. Spores are produced overnight on the under leaf surface. As the air dries out in the mornings spores are released and dispersed by air currents. Downy mildew on broccoli, Brussels sprouts, cabbage and cauliflower first appears on the undersurface of cotyledons, as a fluffy, white mass of spores and spore producing structures (Fig. 2). This can only be detected by turning the cotyledon over as there are no visible symptoms on the upper surface of the cotyledon. Later, the disease appears as a black-gray speckling on the upper surface of cotyledons (Fig. 3). On purple cabbage, symptoms are associated with a pronounced greening of the cotyledons. Symptoms initially appear on one cotyledon only, then shortly after on the other.

The fungus sporulates predominantly on the lower surface of the leaf, opposite the black speckling, and on the hypocotyl by producing a white carpet of spores. The cotyledons turn yellow (Fig 4), sporulation continues and the leaf prematurely shrivels and dies. At this stage the fungus becomes systemic, surviving in the vascular tissue of the host plant. Under extremely humid conditions sporulation also occurs sparsely on the upper leaf surface. On the first true seedling leaves symptoms appear as irregular black blotches. Sporulation occurs on the undersurface and the leaf yellows within and beyond the lesion. As seedlings mature and produce leaves, symptoms decline and eventually the seedlings appear to outgrow the disease.

Overseas the fungus is considered to overwinter on perennial plants, winter annuals or plant debris. The latter are probably not applicable to the nursery situation as seedlings are grown in a sterile non-soil mixes.

Outbreaks of the downy mildew disease on brassicas are favored by temperatures in the range of 10°C-16°C as both spore production and infection takes place. The optimum temperature for specific fungal activities has been well documented. Sporangia formation peaks at 8°C-10°C, asexual spore germination is best at 8°C-12°C and spore release is optimum at 8°C-16°C. Infection from asexual spores is pronounced at 16°C. Haustoria formation and lesion expansion are optimum at 20°C-24°C and 20°C, respectively.

The fungus *Peronospora parasitica* can display varying degrees of virulence or specificity in its host requirements. This specialization may be shown at the host genus level, at the host species level and even at the cultivar level (Table 2). Basically this means that:

1) The fungus parasitising one genus of plant, may or may not be restricted to that plant genera, e.g. downy mildew on stocks will only infect stocks *(Matthiola* sp.) but will not infect *Brassica* spp. However, downy mildew on radish and wild radish *(Raphanus* spp.) can infect *Brassica* spp. Consequently some weedy species of plants can act as reservoirs for carry over of spores to the next season and infection of commercial crops.

2) Similarly, the fungus parasitising a species of plant within a genus, may or may not be able to attack other species of plant within that genus, e.g. downy mildew on winter oil seed rape *(B. napus)* can also infect *B. oleracea* (cabbages and cauliflowers etc). So growers in the UK cannot grow these to crops together

3) The ability of the fungus to parasitise a particular cultivar can vary from one part of a country to another. For example, the fungus isolated from the cabbage cultivar Golden Acres at Winsconsin (USA) and at Arizona (USA) were shown to have different pathogenicities on a "Differential Set of Host Cultivars". This type of specialisation within a cultivar grown at different localities is referred to as geographic specialization.

Table 2.
Host list of the *Brassica* downy mildew, *Peronospora parasitica* (Pers. ex Fr.)Fr.

Botanical name	Common name
Armoracia rusticana	horseradish
Aubretia sp.	aubretia
Brassica alboglabra	Chinese kale
B. campestris subsp. *pekinensis*	Chinese cabbage
B. campestris subsp. *rapifera*	turnip
B. chinensis	Pak-choi (chinese mustard)
B. fruticulosa	twiggy turnip
B. juncea	Indian mustard
B. napus var. *napus* f. *annua*	rape
B. napus var. *napus* f. *biennis*	colza
B. napus var. *napus oleifera*	oil seed rape
B. napus var. *napobrassica*	swede
B. nigra	black mustard
B. oleracea var. *acephala*	kale
B. oleracea var. *acephala* sub-var. *medullosa*	marrow-stem kale
B. oleracea var. *botrytis* sub-var. *cauliflora*	cauliflower
B. oleracea var. *botrytis* sub-var. *cymosa*	Chinese broccoli
B. oleracea var. *botrytis* sub-var. *italica*	broccoli
B. oleracea var. *capitata*	cabbage
B. oleracea var. *gemmifera*	Brussels sprouts
B. oleracea var. *gongyloides*	kohlrabi
B. tournefortii	Mediterranean turnip
Camelina sativa	false flax
Capsella bursa-pastoris	shepherds purse
Cheiranthus allioni	wallflower
C. cheiri	English wallflower
Coronopus didymus	lesser swine cress
C. squamatus	swine cress
Crambe maritima	sea kale
Diplotaxix muralis	wall rocket
Eruca sativa	purple-veined rocket
Lepidium graminifolium	pepper cress
Malcolmia africana	African stock
Matthiola incana	stock
Nasturtium officinale	watercress
Raphanus raphanistrum	wild radish
R. sativus	radish
Rhynchosynapis monensis	Isle of Man cabbage
Sinapis alba	white mustard
S. arvensis	charlock

4) To date 5 formae speciales have been recognized for *P. parasitica.* When *P. parasitica* obtained from one genus of plant has been shown to only infect that one genus, then that *P. parasitica* is termed a formae speciales (f. sp.) of P. *parasitica.* The *P. parasitica* isolated from stock will only infect stock and not *Brassica* spp. The 5 formae speciales are:-

P. parasitica var./formae speciales *brassica* on *Brassica* spp. *P. parasitica* var./formae speciales *capsellae* on *Capsella* spp. *P. parasitica* var./formae speciales *matthiola* on *Matthiola* spp. *P. parasitica* var./formae speciales *raphani* on *Raphanus* spp. *P. parasitica* var./formae speciales *sinapidis* on *Sinapsis* spp.

There are, however, always exceptions, see 1) above.

5) To date 3 races of the fungus have been identified within the variety *B. oleracea* var. *botrytis* on the basis of their ability to infect various "US Plant Introductions" of *B. oleracea* var. *botrytis.* These races have been referred to as race 1, 2, and 3. Experiments have indicated that host plants can have resistance to races 1, 2, 3 and 1 6 2 of the fungus. It is major or dominant gene resistance. Interestingly, although disease resistance and waxiness of foliage were inherited independently, cultivars with heavy foliar wax were more resistant to downy mildew compared with those with none or only light deposits of wax.

Dianthus (carnation) downy mildew

Downy mildew of carnation *(Dianthus caryophyllus)* is caused by *Peronospora dianthicola,* whilst the disease on annual *Dianthus* is caused by *Peronospora dianthi.*

Downy mildew on carnation leaves causes pale green to yellow bands on leaves, which may bend at these lesions. Shoot infections result in the development of axillary buds, giving infected plants a bushy appearance. Infected plants are stunted and wither. Yellow flowering varieties are very susceptible to the disease. Oospores form abundantly in leaves during autumn and eventually fall and become plant debris. They can carry the fungus over the winter to spring where they can initiate disease.

The fungus causing downy mildew on annual *Dianthus* is systemic within the plant. The foliage of infected plants turns pale green then yellow and eventually withers. White downy spores form abundantly on lower leaf surfaces and sometimes on the upper surfaces. Heavily infected plants are stunted and appear bushy due to the development of axillary buds. Oospores form abundantly in diseased tissues and probably function similarly to those of P. *dianthicola.*

Hebe downy mildew (shrubby veronica)

The fungus *Peronospora grisea* causes downy mildew on Hebe (Fig. 5). Large brown lesions develop on leaves and disfigure plants. Downy greyish spores form on the under surfaces of lesions. Young infected shoots dry out, wither and die. Densely packed cuttings are very

susceptible to the disease compared with older plants. Varietal susceptibility has been observed by the author.

Lactucae (lettuce) downy mildew

The fungus *Bremia lactucae* causes downy mildew on lettuce (Fig. 6), globe artichokes, endive, chicory and on ornamental and wild species of Compositae. Shoots and roots, but not flowers are infected, often systemically. Cotyledons of seedlings are very susceptible to the fungus. The fungus produces spores on both leaf surfaces of infected cotyledons. They turn yellow and stop growing, causing stunting and plant death. Seedlings become less susceptible to the disease with age.

On mature plants, symptoms are worst on the lower leaves. Spores are formed on the undersurface of leaves, followed by the development of light green to yellow spots, which may later turn brown. Spots have an angular appearance because they are limited by veins. Spores formed on the under surfaces of leaves are dispersed by wind over long distances. They are the main means of spreading the disease and are viable for 60 days at low temperatures and high relative humidities.

The disease occurs following prolonged cool wet or humid weather in spring or autumn. Spores require free water to germinate as they contain a water soluble germination inhibitor. Germination of spores occurs over a wide temperature range from 0°C-20°C and takes 1-2 hours, while the fungus can penetrate the leaf surface in 3-4 hours. At higher temperatures the percentage of spores germinating declines. At high relative humidity the incubation period is 5-6 days at 19°C-22°C, but 28 days at 6°C. Spore production requires free water on the leaf over a temperature range of 4°C-24°C with the optimum at 10°C-12°C. Spore production over lettuce crops peaks between 1000 and 1200 hours and they remain viable for several days.

Dispersal of the fungus is unlikely by seed. Mature leaves bearing oospores, which later fall to the ground as plant debris are incorporated into soil and probably carry the fungus over from season to season and crop to crop. Alternative hosts such as *Lactuca saligna, L. virosa* and *L. serriola* are infected by the race of *Brema lactucae* which also infects cultivated lettuce. The asexually produced spores on the undersurfaces of leaves are primarily responsible for causing epidemics of downy mildew.

There are a number of physiological races which are restricted to species within the genus Lactucae. Extensive breeding programs have resulted in the development of cultivars with tolerance to the fungus. A predictive model for lettuce downy mildew has been developed in the United States.

Lobularia (alyssum) downy mildew

The fungus *Peronospora parasitica* causes downy mildew on alyssum (Lobularia maritima). This fungus is thought to be a host specialized form of P. *parasitica.* Symptoms (Fig. 7) are gall-like blisters, which are atypical for downy mildews. Salt toxicity in alyssum produces similar symptoms, but without the blisters.

Matthiola (stock) downy mildew

Light green patches form on the upper leaf surface (Fig. 8) while masses of downy white spores are produced directly below, on the lower leaf surface. Infected leaves turn yellow then brown and prematurely fall. Only *Matthiola incana* and *M. bicornis* are susceptible. None of the cultivated stocks are resistant, although some cultivars support less sporulation than others. The fungus causing downy mildew on stocks is *Peronospora parasitica,* however, it is a different race to the *P. parasitica* causing downy mildew on brassicas. The fungus causing downy mildew on stocks will not infect brassicas and vice versa. The optimum temperature range for infection to take place and for spore formation (vegetative spores - sporangiospores) is 15.5°C-21 °C, whilst the range in 4.5°C-27°C. The fungus is not active at temperatures outside this range. After infections have occurred, symptoms take 5-7 days to develop at the optimum temperature range.

Papaver (poppy) downy mildew

Light green to yellow blotches or patches appear on the upper leaf surface (Fig. 9). Leaves appear distorted and eventually turn brown. Masses of fluffy grey spores develop on the lower leaf surface. The optimum temperature for spore (vegetative) germination is 19°C, whilst the range is 2°C-23°C. Beyond this range germination is delayed. The fungus, *Peronospora arborescens,* is reported to be seedborne on *Meconopsis* spp. (Chinese poppy) and *Papaver* spp. (poppies), especially in the Middle East. Oospores (sexually produced spores) form prolifically in leaves and contaminate soil after leaf fall, thus carrying the fungus over to subsequent crops. The disease is favoured by heavy potting mixes, wet and humid weather.

Rosa (rose) downy mildew

Rose downy mildew (Fig. 10), is caused by the fungus *Peronospora sparsa.* Red to purple to brown blotches form on leaves, which readily fall off on touch. Infected flowers and buds are deformed whilst infected stems may die. The fungus can survive over winter in plant parts, such as stems. The optimum conditions for disease development are relative humidities above 90% and low temperatures. Spores take up to 4 hours to germinate in water over a temperature range of 4°C-27°C, with an optimum of 18°C. After the fungus has infected a plant, it can produce spores in 3 days. Some control of the disease in obtained by ventilating glasshouses to reduce humidities to less than 90% and by raising temperatures above 27°C. Roses grown at less than 85% RH are not infected. Varietal differences in susceptibility to *P. sparsa* have been reported. Fungicides have been evaluated for the control of the diseases.

Senecio (cineraria and Compositae) downy mildew

The two downy mildews which attack cinerarias and other Compositaes (e.g. *Centaurea, Gallardia* and *Helichrysum)* are *Plasmopara halstedii* and *Bremia lactucae.* On *Senecio cruentus, P. halstedii* causes leaf spots up to 3 cm in diameter, which are white on the upper surface and brownish on the lower surface. *B. lactucae* on cinerarias causes irregular leaf spots which are yellow to red in colour and leads to withering and defoliation.

Viola (pansy) downy mildew

Downy mildew on violas is caused by *Peronospora violae* in Europe, Asia and Australia, whilst in America it is caused by *Bremia megasperma*. Symptoms consist of light green to yellow patches which appear on the upper leaf surface (Fig. 11). Masses of mauve coloured spores form directly below on the under leaf surface. There are no reports of the disease being seedborne, however, this may be because nobody has checked. In France cultivars were evaluated for their susceptibility to the disease. The white, clear blue and yellow flowering varieties are more susceptible to the disease than the variegated ones. Spectacular epidemics have been reported after sprinkler watering in dry autumn weather. Project NY406 trapped spores of *P. violae* in the mornings, suggesting that the fungus is similar to *P. parasitica* in releasing its spores in the mornings.

FUNGICIDES

Fungicides for the control of downy mildews

Some chemicals currently registered for the control of downy mildew on brassicas, ornamental or vegetable seedlings are given in Table 3. Some of the failures of fungicides to control the disease are attributable to late application or inappropriate choice of chemical.

Principles of chemical control

1. Read the label

Before using a chemical or following any chemical recommendation the user should **ALWAYS** check the uses described on the label of the product. If this product has not been recently purchased, contact the place of purchase or the local reseller to check that the product and its uses are still registered. Users should note that the directions on the currently registered label should **ALWAYS** be followed.

2. Choice of fungicide

Choose a fungicide which is suited to the biology of the fungus. For fungi on leaf surfaces a contact fungicide is appropriate. For fungi developing internally within a plant a systemic fungicide is required. Downy mildew has both an external (germination of spores on leaf surfaces) and internal (hyphal growth) phase on the host.

3. Application

Foliar fungicides should be applied with a hollow cone nozzle, under high pressure (greater than 100 KPa). Nozzles should be regularly calibrated and discs checked for wear. When using booms, each nozzle on the boom should be calibrated to deliver no more than a 5% difference in volume.

4. Preventing fungicide resistance developing

It is good practice to rotate the use of different types of fungicides (Table 3) in order to reduce the likelihood of fungi developing resistance to a particular fungicide. The ideal situation is to include a "site-specific" and a "multi-site" chemical, but both must be effective and their mixing must be safe. Half rates of chemicals should not be used as this can lead to the stepwise development of resistance in the fungal population. The regular application of the same site-specific fungicide must be avoided .

Fungicide resistance

Fungi develop insensitivity, tolerance or resistance to fungicides usually by the repeated use of the same chemical. This can happen by mutation, by sexual reproduction or by movement of pathogen populations. If in a population of a pathogen a few individuals arise which are tolerant to a particular chemical, then repeated use of that chemical actively selects for these few individuals. Consequently they multiply and eventually outnumber those individuals which cannot tolerate the chemical. Thus the bulk of the fungal population becomes tolerant to the fungicide and it no longer controls the disease. Once resistance develops in a population of a fungus it is not rapidly lost.

Mode of action of fungicide

Contact fungicides The "contact" fungicides protect plants from potential attack. They prevent the fungus from infecting the plant. They must be constantly present on the foliage when spores are deposited and must be in direct contact with the fungus. Consequently contacts must be applied routinely or when disease is expected. The contacts generally prevent spores from germinating or affect germtube growth. The method by which they do this depends on the type of fungicide. They do not penetrate into the plant tissue but remain on the surface and so are exposed to rainfall and weathering thus requiring repeated applications.

Eradicants These fungicides eliminate, cure or remove the fungus after infection has taken place, e.g. Foli-R-Fos is an eradicant for downy mildew on grape vine.

Locally Systemic Fungicides whose target site is restricted to the initial stages of infection or penetration of the fungus into the leaf. e.g. cymoxanil

Protectants Term to describe application or activity of a contact fungicide. Protectant fungicides are preventatives, i.e. they defend, shield or screen a plant from infection. The fungicide should be applied before the fungus or spores are present, e.g. contact fungicides.

Single-site and multi-site fungicides Site specific chemicals act on one biochemical reaction only, where as multi-site chemicals have a more general effect and so act on a broad range of biochemical reactions. The regular use of the same site-specific chemicals should be avoided as this has led to the selection of chemically resistant fungi, whereas the use of multi-site fungicides has led to few cases of resistant fungi developing.

Synergism A fungicide mixture consisting of 2 separate chemicals giving better control as a mixture than when applied separately, e.g. mixtures of phenylamides with contact fungicides.

Systemic fungicides "Systemic" fungicides act by eradicating a pathogen which has already become established within the plant i.e. they have a curative action. They move to a certain extent within the plant. With some, movement is predominantly in the upward direction in the transpiration stream eventually accumulating at the leaf margins. Others can move both up and down within a plant.

Table 3 Function and action of some common types of fungicides which are currently registered for control of various downy mildew diseases.

Function	Action	Type	Common Name	Example of Trade Name	Selected Registration Details
Contact	multi-site	Copper	copper oxychloride	Melpat coppox	ornamentals (A*)
			copper hydroxide	Kocide	onions (QSVW)
	multi-site	Dithiocarba-mates	mancozeb	Dithane	lettuce, onions, cauliflower, Brussels sprouts, cabbage, broccoli (A)
			metriram	Polyram	lettuce (A)
			propineb	Antracoil	onions (A), lettuce (TVW)
			zineb	Zineb	roses, stocks, zinnias, onion, crucifers (A)
Systemic	multi-site	Phosphonates	phosphonic acid	-	pending
	single-site	Phenylamides	furalaxyl	Fongarid	seedlings, roses, established plants (A)
			metalaxyl	-	-
			oxadixyl	-	-
	single-site	Morpholine	dimethomorph	-	-
Combination			propineb + oxadixyl	Fruvit	lettuce, onions (A)
			mancozeb + oxadixyl	Recoil	lettuce, onions (A)
			mancozeb + dimethomorph	Acrobat	lettuce, onions (A)
			metalaxyl + mancozeb	Ridomil 720	lettuce, onions (A)

*, Letters refer to States of Australia where the fungicide is registered for use: A, all states of Australia; Q, Queensland; S, South Australia; T, Tasmania; V, Victoria; W, Western Australia. Information was obtained from the Chemical Standards Branch database of DNRE during 1996.

CONTACT FUNGICIDES

Copper compounds

e.g. copper hydroxide

copper oxychloride The toxic agent is the copper ion (Cu) which forms in the presence of water. The Ci/* penetrates into spores of the fungus and interferes with fungal enzymes. These compounds present few hazards to humans or the environment. They can, however, be phytotoxic to plants causing reduced growth, burning and hardening of foliage. The copper based sprays were the first available for downy mildew control, with copper oxychloride being produced in the early 1900's. Several copper based sprays are currently registered for control of downy mildews. Copper is often marketed in mixtures with other fungicides.

Dithiocarbamates

e.g. mancozeb (Dithane)
metiram (Polyram)
propineb (Antracol)

zineb (Curit) These compounds are broad spectrum contact fungicides which interfere with fungal metabolism. All are currently registered to control various downy mildews. Climatic conditions do not interfere with the fungicide action, but they readily wash off foliage with rain. They tend to improve the appearance of foliage. They are toxic to plant cells but are not taken up by them. This suggests that they should not be applied if plant tissue is damaged, i.e. if there is insect damage to the foliage.

Mancozeb

Mancozeb is registered for downy mildew control on a variety of plants. Although there are incidences of mancozeb foliar sprays not controlling downy mildew on cabbage seedlings or on seed producing cauliflowers, this may be associated with lateness of application. Mancozeb appears to be most effective in combination with systemic fungicides.

Metiram (Polyram)

Metiram was introduced around about 1963. It has been used to control downy mildew on grapevines, hops and lettuce.

Propineb (Antracol)

Propineb, introduced in 1963, has a long residual activity. It has some inhibitory action on powdery mildews and red spider mite. It was shown to reduce early infections and increase size and dry weight of seedlings. Applications to mature plants, where the disease is established, were ineffective. A mixture of propineb + oxadixyl (Fruvit) is used to control downy mildew on onions and lettuce.

Zineb

Zineb was first reported in 1943. It is registered for control of downy mildew on a variety ot plants. It tends to get little mileage in the literature these days as preference is given to the use of mancozeb, a related dithiocarbamate,and to systemic fungicides.

SYSTEMIC FUNGICIDES

Phosphonates

Phosphonic acid

e.g. Phosphonic acid (Agrifos)

Phosphonates are broad spectrum, systemic fungicides used for the control of root, stem and foliar diseases. They move both up and down within a plant, so when applied to foliage they will move down the plant to protect the roots. They are toxic to fungi which are growing internally within the plant. Although phosphonates were initially thought to stimulate the hosts' natural defence mechanisms, this is largely a byproduct of their fungitoxicity. The mode of action of Agrifos remains unresolved.

Phosphonic acid is applied as a drench or foliar spray, but, in high concentrations, has a reputation for stunting plant growth. When applied to field grown plants as a foliar spray it reduced disease incidence by a half and increased head weight in broccoli. It has also been successful in controlling post-harvest development of downy mildew in cauliflower curds. It has a post-infection curative activity on grape vine downy mildew.

Phenylamides

e.g. furalaxyl (Fongarid)
metal axyl oxadixyl

The phenylamide group of fungicides have a protective and curative activity against the downy mildews (Peronosporales). They are easily absorbed by roots, green stems and leaves. Being systemic they are readily translocated to shoots in the water conducting tissues. Biochemically, they reduce protein synthesis by the fungus. Unfortunately the prolific application of the metalaxyl and furalaxyl has produced resistant strains of downy mildews. Where field resistance of downy mildews is suspected a different type of chemical should be applied or they should be mixed with a protectant and the number of applications of the phenylamide should not exceed 2 per season. This slows down the build up of resistant strains.

Furalaxyl (Fongarid)

Furalaxyl, a "single site" fungicide, was introduced in 1977. It is closely related to metalaxyl and has both curative and protective activity. It is currently registered to control downy mildew on ornamental seedlings, roses, and established plants.

Metalaxyl

Metalaxyl, a "single site" fungicide was introduced in 1977 by Ciba-Geigy. Metalaxyl acts internally within the plant to inhibit mycelium growth and fungal sporulation, once the fungus has entered the host. It has been successfully used as a seed treatment, a compost amendment and a foliar spray for seedlings and field grown plants to control *P. parasitica.*

Initially it was the wonder fungicide for controlling downy mildew, but in recent years the foliage sprays have fallen from favour due to the rapid development of resistant fungal strains. Strains of *P. parasitica* resistant to metalaxyl have been recorded in the UK. The resistant strains are spreading and still prevalent in areas where metalaxyl sprays have been discontinued. Metalaxyl resistant and susceptible isolates were, however, both found to be susceptible to propamocarb. It is often mixed with protectants as an anti-resistance strategy and to broaden its spectrum. There are cases of metalaxyl + mancozeb no longer controlling downy mildew in seedling. It is currently not registered for brassicas crops, but is registered for lettuce and onions. Metalaxyl resistant strains of *P. destructor*, which causes downy mildew on onions, have been reported from the Lockyer Valley in Queensland.

Oxadixyl

Oxadixyl, introduced in 1983, controls foliar, stem and root diseases. Synergistic effects have been found between oxadixyl and contact fungicides. It is often used in combination with contact fungicides to increase the range of pathogens controlled and to reduce the selection of resistant fungal strains. Oxiadixyl, by itself, did not control downy mildew on cabbage seedlings, however, a mixture of oxiadixyl + mancozeb (Recoil) is registered for control of downy mildew on lettuce and onions.

Morpholines

e.g. dimethomorph (Acrobat)

The activity of these fungicides is confined to the group of fungi known as the Oomycetes to which the downy mildews belong. They hinder fungal sporulation and mycelial growth by interfering with fungal cell wall formation. They have both fungicidal and fungistatic activity, although the mode of action of the fungicide is unknown. Acrobat has recently been registered to control downy mildew on lettuce and onions.

CONTROL STRATEGIES FOR DOWNY MILDEWS

To control downy mildew on seedlings and in nurseries, integrate management strategies and fungicide sprays.

1. **Hygiene**
   Keep all areas clean and weed free. Rogue out heavily infected seedlings as these provide a source of spores for subsequent infections.

2. **Irrigation**
   Avoid watering seedlings in the mornings, when spores are released and available for infection.

3. **Ventilation**
   Space trays of seedlings to improve ventilation. This will dry leaf surfaces off quickly to reduce leaf wetness and thus infection.

4. **Nutrition**
   Maintain a balanced program of nutrition as a deficiency of potassium (K) will make seedlings (cauliflowers) more susceptible to the disease.

5. **Fungicides**
   Apply fungicide protocols developed by Projects NY406 and NY97011 or maintain a fungicide spray program consisting of registered fungicides when the downy mildew disease is expected.

6. **Monitor**
   Monitor seedlings on a regular basis to detect downy mildew (at least once a week).

7. **Quarantine**
   Isolate stock plants, especially when first introduced into the nursery.