Is Biologic Control of Marasmius

Fairy rings are common natural phenomena in woodlands, grasslands, and other plant covers all over the world (24,25,27). Superstition associated the occurrence of rings with the supernatural activities of witches, goblins and fairies, hence the name "fairy rings" or "witches' rings" (18). Soil and litter fungi are the common, although not the only, causes. The annular development of fungal fairy rings results from the apical growth habit of fungal hyphae. Eventually, the fungus may produce conspicuous fruiting bodies associated with one or more concentric ribbons or rings of stimulated plant growth and perhaps a zone of suppressed herbage (Figs. 1 and 2). Fruiting may not take place every year (31), and, in some years and at different times of the year, one or more zones may be absent. Sometimes only a circle or arc of fungal fruits occurs.

The rings or ribbons of stimulated and suppressed plant growth are usually most noticeable in those species with a definite mycelial zone in the soil. This occurs in *Marasmius oreades* (Bolt. ex Fr.) Fr., common in temperate to subboreal grasslands. Mature rings of this species have an inner zone of stimulated herbage resulting from microbial breakdown of nitrogenous compounds in the fungal thallus as it dies out centripetally (23). An outer lush green ring is often seen and may be caused by an increased uptake of nutrients from humus degraded by the advancing fairy ring mycelium (13).

In rings caused by *M. oreades* and some *Psalliota* spp., the soil mycelium may be abundant enough to interfere with the penetration of water. The grass plants then suffer from drought and may die, resulting in a bare zone sandwiched between two lush zones. In *M. oreades*, tan-colored fruits are usually found, from summer to autumn, at the junction of the bare and outer lush zone. *M. oreades* is capable of parasitizing grass roots (2,7),

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and some isolates produce hydrogen cyanide, a potent biocide (7,11). The significance of these findings in ring formation and plant death is still controversial (6,8,18,24).

Why Control M. oreades?

M. oreades fairy rings may cause considerable damage to agricultural grassland and amenity turf (Fig. 3) in many parts of the world, though not always (21,25). Particularly during dry summers, fairy rings are often conspicuous in light soils of low fertility and inadequate moisture, as, for example, in the light brown and brown soils of the Canadian prairies and the sandy soils of golf links in eastern England and Scotland. In light soils, the mycelium may often be found to a depth of 30 cm. In heavy clay soils, the fungal hyphae are usually in the top 5 cm, that is, in the thatch of dead and decaying plant material (Fig. 4). M. oreades rings appear to be less prevalent in high rainfall areas, as in western Norway, where only one record, at Levanger in Nord Trondelag, has been made of the fungus (G. Gulden and A. Gjervein, personal communications). Yet M. oreades is quite common in pastures and amenity turf in eastern Norway, which is much drier (26; J. D. Smith, unpublished).

M. oreades rings cause pasture deterioration by increasing the proportion of bare ground, thereby allowing invasion by weed species (8). Their effect on herbage yield and quality is difficult to estimate because the reduction in yield where bare zones occur may be partly offset by increased growth and nutrient content of herbage in the stimulated zones(1). However, Hardwick and Heard (8) noted that in some cases herbage yield was halved by M. oreades rings.

Damage to amenity turf is through disfigurement of a uniform green appearance of lawns and playing greens. Stimulated and bare zones may also affect the trueness of the playing surface, especially on golf and bowling greens. Rings are prevalent on dry or lightly watered golf course fairways but much

less frequent on well-irrigated and fertilized greens.

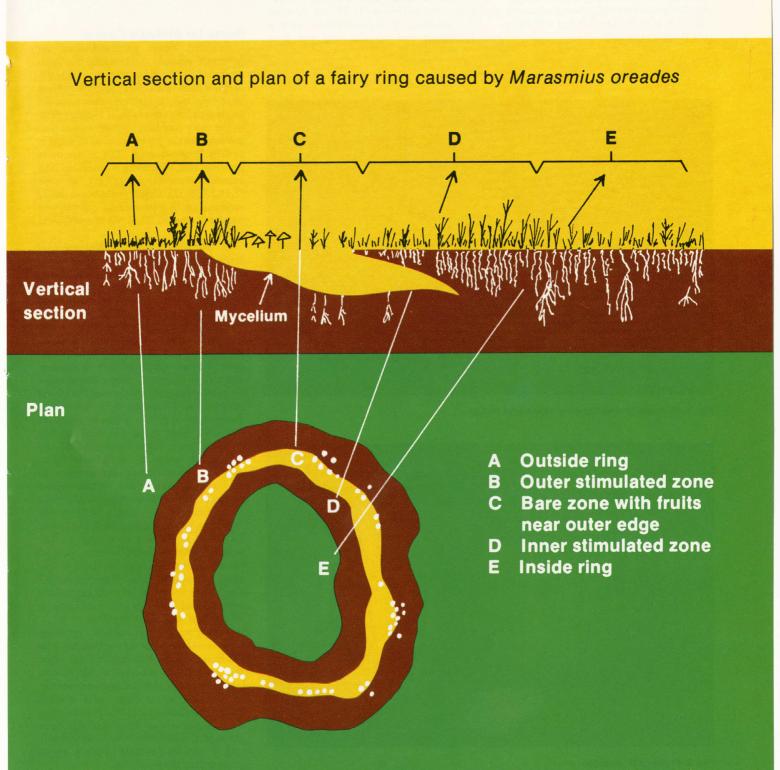
The lush green rings of grass in stimulated zones may persist through fall into winter. This unseasonable growth is susceptible to late autumn attacks by Fusarium nivale (Fr.) Ces., which are often seen after snowmelt (26). Recovery of this damaged grass may result in a stimulated zone not originating directly from the activity of M. oreades mycelium.

Failure of Fungicides and Soil Amendments

Methods tried for the control of M. oreades have been reviewed extensively (22-24,27). I have tested many previously suggested and some untested soil amendments, fungicides, and physical methods (23). With fungicides, the difficulty lies not in finding a material that will kill the fungus without damaging the plants (22) but in delivering the material where fungicidal action is required. The abundant soil mycelium is hydrophobic, as is the soil it pervades. Even pricking or spiking such soil rarely assures perfusion with water solutions or suspensions of fungicides. Because ring symptoms, including fruit production, vary in intensity from year to year (22,31), depending on climatic conditions, reports of effective materials and treatments should be viewed with caution unless the effect persists over several seasons and the number of untreated controls is adequate.

I noted that several fungicides applied in water to spiked rings partially controlled or temporarily suppressed symptoms (23). Soil amendments had little effect. Recently, systemic fungicides effective against basidiomycetes have been field-tested against M. oreades rings. Symptoms were effectively suppressed for 2 yr by carboxin at 7.5 g/a.i./m² applied in water to spiked rings, almost completely suppressed for 2 yr by oxycarboxin at 11.25 g/a.i./m^2 , and partially suppressed by benodanil at 7.5 g/a.i./m² (5). Roediger (20) found that benodanil at 2.5 g/a.i./m² was very effective in preventing the appearance of

preades Fairy Rings Possible?



rings, but the effect lasted for only one growing season.

Fumigation and Soil Disturbance

The failure of wet chemical treatments and soil amendments led to investigation of other soil treatments. Although *M. oreades* and other fungal fairy rings may be eliminated by careful excavation and complete removal of mycelium-infested soil, preferably followed by fumigation of the excavation with a volatile fungicide (23), this is very laborious when rings are abundant and large. Also, soil imported to fill the excavation, unless taken from a regularly cultivated area such as a vegetable plot, may be infested with fairy ring fungus mycelium.

Cunningham (4) used a solution of 0.125% formaldehyde in water to control fairy rings in New Zealand. In an attempt to overcome the hydrophobic property of the soil, this material was either poured down holes punched inside and outside the outer stimulated zone or applied to the thoroughly cultivated soil of the ring from which the turf had been stripped. The treated site was covered to seal in the fumigant and was eventually resown or returfed. I found that elimination using formaldehyde fumigation necessitated removal of infested turf plus an uninfested border and thorough cultivation of the soil below (23,27). An aqueous 2% solution of formaldehyde with a surfactant was applied and the area



Fig. 1. M. oreades ring showing zones and fruits.



Fig. 2. Fruits of M. oreades.

covered, followed with a vapor seal. The site was resodded or reseeded after the fumigant dispersed.

Like many other soil sterilization treatments, only partial sterilization results from formaldehyde fumigation. After treatment, the surface of the soil lumps may become colonized by *Penicillium* spp., some of which are probably antagonistic to *M. oreades*. Other volatile biocides, such as methyl bromide and chloropicrin, have been used successfully by professional operators in place of formaldehyde (27).

Bases for Biologic Control

Irrigated, fertile grassland does not generally provide a favorable environment for the development of typical *M. oreades* fairy rings. The reason for this is uncertain, but, under such conditions, the existence of microflora highly antagonistic to the fairy ring fungus is probable. Soil moisture in the mycelial zone of rings is usually lower than in other zones or in nonring soil, especially in summer and autumn when fungal growth is rapid (7,14,23,29,31). This is probably of major importance in determining species and numbers of microflora in the different zones.

In Suffolk, England, Warcup (31) made fungal counts in soil profiles of the mycelial zones of M. oreades in autumn and compared these with counts from nonring soil. The mycelial zone contained a restricted population of fungi, with fewer species and colonies than the surrounding soil. Ascomycetes, such as Arachniotus sp., Gymnoascus subumbrinus, Cladosporium herbarum, and a Penicillium sp., were isolated more frequently from mycelial zones than from normal soil. I counted more colonies of Penicillium spp. on dilution plates of Czapek's agar from the soil of the mycelial zone than from that of the stimulated zones of from soil taken outside a ring during the summer in northern England (23). Much higher bacterial counts were obtained from the inner stimulated zone, where old mycelium was being degraded, than from elsewhere in the ring or outside it. The usually higher bacterial count in the top 8 cm of normal soil was reversed in the outer stimulated zone, where the count was higher at depths of 8-15 cm. In the outer stimulated zone, the mycelium of M. oreades was in the top 8 cm.

I suggested that, when growing actively, M. oreades was antagonistic to soil bacteria (23). Antibiotics from other Marasmius spp. are known (23), but so far these have not been demonstrated in M. oreades other than as a mutual inhibitor or inhibitors (29). The chemical characterization of these has not been attempted. Since they seem to be stable in soil, it may be possible to use them to prevent ring development.

Dilution plate counts were made in the three zones of six *M. oreades* rings at two locations at Saskatoon in spring 1977 (29). No species or group of fungal species other than *M. oreades* was found to be characteristic of any of the zones. Bacterial counts for the three zones varied from ring to ring. Only one of the six rings did not have a lower moisture content in the bare zone than in other zones. Many fungi isolated from the three zones of *M. oreades* rings showed antagonism toward isolates of the latter in vitro, but apparently *M. oreades* was not antagonistic to these fungi (29).

In an *M. oreades* ring, the normal soil microflora is influenced by the acropetal advance of the fungal mycelium, which at first is on the soil surface. In a centripetal direction, the mycelium becomes more deeply seated in the bare zone and more mature. Finally, the staled mycelium is degraded in the inner stimulated zone. This creates a soil ecological research problem of considerable complexity. Profile studies at different seasons for many years are needed to obtain a clearer understanding of microfloral interactions.

Lebeau and Hawn (12) developed a simple biologic control of *M. oreades* by pricking the ring and soaking the infested turf with water every second day for a month. This method depended on destruction of the *M. oreades* mycelium by increased bacterial and fungal activity resulting from extremely wet soil conditions that overcame the hydrophobic properties of the fungus. Although intensive watering combined with adequate fertilization will alleviate ring symptoms, the complete water-soaking needed for ring fungus eradication is often difficult to achieve.

Regularly cultivated plots of soil act as biologic and/or physical barriers to growth of M. oreades mycelium, and cultivation in the path of an advancing ring in turf has been suggested as a control (27). Soraurer (30) and Ritzema Bos (19) noted that digging up rings killed the fungus, and they ascribed this to drying out of the soil and fungus. Soil disturbance physically interferes with plant and soil colonization by the ring fungus and mixes active with less active or moribund mycelium and substrate. Probably, the substrate contains selfinhibitory staling substances and is deficient in nutrients.

Examination of soil profiles indicates that *M. oreades* mycelium progresses in grassland by first colonizing dead plant material at the base of the sward before moving into the thatch and deeper soil layers. The fungus was capable of crossing triple cordons sanitaires of 2% mercurous chloride in sawdust by growing over their surface in the litter layer (23). Cultivated soil has no fresh litter layer, and the soil moisture regimen and probably also the microflora are different than under grass. This may result in unfavorable growing conditions



Fig. 3. Severe damage by *M. oreades* rings to the turf of a memorial garden. Many of the rings are broken downslope.



Fig. 4. Mycelium of *M. oreades* intesting thatch and plant roots in the upper 5 cm of heavy soil. Mycelium is on the soil surface of the outer lush zone of the ring.



Fig. 5. M. oreades rings obliterating each other.



Fig. 6. Mutual antagonism between two dikaryotic isolates of M. oreades in culture.



Fig. 7. (Right) Half of a lawn heavily infested with *M. oreades* treated by soil mixing and (left) temporary control plot (April 1974).

for the ring fungus.

M. oreades rings on slopes are nearly always incomplete on the downhill side (26). Coville (3) suggested that decomposition products of fungal growth washed down from above are harmful to the growth of the fungus lower down. Bayliss (2) produced some evidence that a toxin from the fungus is self-inhibitory. I noted that very young rings on slopes are often complete circles (26) and suggested that water flowing downslope over the waterrepellent bare zone in a ring collects in the center of the ring and is held against an arc of impervious mycelium downslope. This moisture produces favorable conditions for development of an antagonistic microflora. Eventually, the mycelial zone dam gives way and the ring is breached. Both a self-inhibiting metabolite and an antagonistic microflora may be involved in ring breaking.

Two rings of *M. oreades* that meet almost invariably obliterate each other (Fig. 5). Among other species, mutual elimination also is common when rings of the same species meet (2,16,18,21,25, 26,32). Two main explanations have been given for this. Wollaston (32) was the first to suggest that when two rings meet "the exhaustion of a particular 'pabulum' occasioned by each, obstructs the progress of the other, and both are starved."

The chemical composition of ring and nonring soil differ considerably, especially in the form of soil nitrogen (9,14,15,23). With the passage of the fungus, total nitrogen is changed little; total carbon declines but probably recovers rapidly as the bare zone is recolonized. Changes in the form of the humus are considerable, however. For example, growth of *M. oreades* through the thatch in turf causes visible changes. Utilized thatch takes on a characteristic reddish-brown, fretted appearance.

Mathur (13) showed that the fungus could chemically degrade soil humus in vitro. The first suggestion of a self-inhibitory metabolite in *M. oreades* was by Coville (3). This was further indicated by Bayliss's studies (2) and shown to occur in vitro in dikaryotic isolates (29) (Fig. 6). Mutual inhibition of dikaryotic isolates of the same fungal species has also been shown to occur in other turfgrass pathogens, namely, the low-temperature basidiomycete (LTB) snow mold, *Typhula incarnata* Lasch ex Fr., and *T. ishikariensis* Imai (10,28).

The two factors—exhausted nutrient and self-inhibition—may explain the long delay in recolonization of used soil by *M. oreades* and also why one *M. oreades* ring is seldom found inside another. Exceptions to this are sometimes noted. Rings may occur in the downslope gap of larger rings on slopes without mycelium. Rarely, small, poorly developed rings may be found inside much larger incomplete rings; presumably, the depleted soil eventually recovers after the

passage of the fungus and the inhibitor is degraded.

Practical Biologic Control

Field surveys in high incidence regions indicated that "mutual obliteration" or "growing out" against cultivated soil or physical barriers were the main reasons for the decline in incidence of *M. oreades* rings in amenity turf (25,26). An immunization technique for turf with attenuated isolates, which had been suggested as a means of control (25), has not yet been attempted because of difficulties in establishing the fungus by soil inoculation (25,27).

An empirical method involving the mixing of so-called normal soil with infested soil was developed before mutual inhibition between *M. oreades* isolates or antagonism between fungi of the soil microflora and the fairy ring fungus in vitro had been demonstrated. The procedure, intended for lawn-type turf highly infested with *M. oreades* (27), is done as follows:

The turf is stripped from the lawn and composted off the site, or the grass is killed in situ with a nonresidual total herbicide such as glyphosate. The soil (or the soil with dead turf in place) is then cultivated repeatedly in different directions with a heavy-duty rotary cultivator to break up and mix the mycelium-infested soil with nonring soil. Any dry areas, particularly bare zones, should be soaked with water at this time. A surfactant may assist water penetration to any mycelium below cultivation depth. In regions with winter snow or rain, the cultivated land could be left rough to allow deep penetration of water. The area is then prepared for sodding or seeding, preferably the latter, since the risk of introducing further infestation in imported soil is minimized. When the turf is established, the chances of reinfestation appear to be reduced by good management, particularly good irrigation. As a general guide, enough water should be applied to wet the soil to a depth of 12.5-15 cm. The turf surface should be allowed to dry between waterings. Inadequate, shallow irrigation keeps the turf surface moist and encourages spongy thatch development, which may favor spore germination and superficial growth of M. oreades.

This technique was first applied in the autumn of 1973 to half of a home lawn very heavily infested with *M. oreades*. Reseeding was done in the spring of 1974 (Fig. 7). The other half of the lawn served as a temporary control plot and was treated and resodded in 1976. Neither plot has shown fairy rings since (Fig. 8). Two other infested home lawns were treated in 1977 and 1978 and resown. Adjacent infested lawns served as controls. No rings have appeared on the treated lawns. Another infested lawn was treated in 1977 and resodded the same

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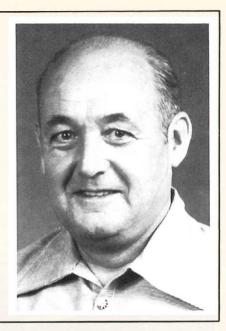




Fig. 8. Same lawn as shown in Fig. 7 after treatment of both sides and eradication of rings (June 1977).

year. Again, adjacent lawns served as controls. Sod from an uninfested portion of the lawn was used for part of the resodding. Two pieces of 10-yr-old, imported, mycelium-infested turf were used along one border. These showed two fragmented rings with typical *M. oreades* fruits 18 mo after sodding, but the remainder of the lawn is still free from rings.

The described method of eradication is promising, but further testing is needed to prove its effectiveness. Studies on ring initiation are required before adequate methods of preventing turf infestation can be developed.

Compared with rotary cultivation, digging or plowing is probably inadequate to effect eradication. Persoon (17) noted that after a ring of *M. oreades* was dug up

several times for 1 or 2 yr, the fungus reappeared but was sparse. Shantz and Piemeisel (21) reported that rings of Agaricus tabularis Peck (Psalliota arvensis Sch.) persisted for at least 7 yr without apparent injury after plowing and fruited as well in cultivated cereal fields as in native grassland. However, because its mycelium is often 5-8 cm below the soil surface and may go 10 cm deeper, some would be undisturbed by shallow cultivations. The mycelium of M. oreades is usually more superficial. Hardwick and Heard (8) suggested that control of M. oreades in pasture might be possible by plowing and rotation of crops. However, M. oreades rings in a pasture in Sussex persisted after plowing for two wheat crops until March of the next year but could not be found in August in a maize

crop grown after the wheat (A. J. Heard, personal communications).

The effect of different types of cultivation on the persistence of *M. oreades* and other fairy ring fungi requires further study.

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