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Species of the three groups of fungi characterized here on the basis of their energy source acquisition have differing potentials for becoming problem organisms following introduction as alien fungi new to Iowa.

The decomposer group of fungi that obtain an energy supply by action of extracellular enzyme activity on dead plant tissues typically have perennial mycelium, are cosmopolitan in distribution, and are unlikely to become problems even if established. The second group, the mycorrhizal/lichen group are highly specific in their relationships. The mycorrhizal fungus group have a potential for being introduced as mycorrhiza already established with the roots of particular vascular plants. Their potential for survival and establishment would be linked with that of their vascular plant associate. The third large and diverse group of plant parasitic fungi holds great potential for becoming destructive problem fungi on susceptible native plant species. In Iowa, the development of the white pine blister rust fungus *Cronartium ribicola* Fischer on *Pinus strobus* L. and *Ophiostoma ulmae* (Buisman) Nannf. and *Ophiostoma novo-ulmae* Brasier on elms, particularly on *Ulmus americana* L., are classic examples of the destruction of native plant species by introduced fungi.

INDEX DESCRIPTORS: alien fungi, fungal plant pathogens, diseases caused by introduced fungi, white pine blister rust, elm wilt.

The fungi have often been labeled "a treacherous and mutable tribe". That harsh description does indeed apply to many of the fungi from a human viewpoint, but is not appropriate as a characterization of the many fungi that we deem useful. Before we consider the diverse ways introduced fungi can have an impact on and change an area, in this discussion focused on Iowa, it may be useful to consider some of the basic information about fungi and their interactions with other organisms.

The vegetative structures of the fungi are typically microscopic, thus not readily seen or considered where a field area is being studied and characterized. Most fungi have filaments, like fine threads, called hyphae or mycelium, as their vegetative structure. These grow and branch from the tips of the hyphae. Sometimes parallel aggregates of hyphae do become large enough to be visible as cord-like threads (Alexopoulos et al. 1996). Typically however, awareness of the presence of these fungi occurs only when they develop characteristic macroscopic spore producing structures which are called mushrooms, boletes, morels, puffballs, etc., or when their food obtaining activities result in destruction or modification of another living organism. Our attention is alerted particularly when the changes are counter to our interests.

Fungi are heterotrophs, thus they rely on pre-fixed energy sources as do animals, and like them, fungi lack the independence of green plants. Many fungi are dependent on dead plant residues as an energy source (Frankland et al. 1982). Digestive enzymes produced in the living fungal protoplast move outside the hyphae and act upon appropriate components of the substrate in which the fungus is growing. Soluble digestion products are absorbed back into the hyphae and utilized for maintenance and growth of the fungus. The results of these activities are the decomposition of organic residues [e.g., the decay of logs, twigs and leaves on the forest floor, the conversion of litter on the soil in a grassland, the modification of plant parts in the soil, with the release of residue components and availability of these materials to be utilized again by other organisms (Frankland et al. 1982)]. These decomposer fungi occasionally produce fruiting bodies on or in which specific kinds of spores, the reproductive units of the fungi, develop, are released and disseminated. Some of these fungi form fruiting bodies at specific seasons, but not necessarily every year as environmental factors vary. Also, these fungi are perennial in an area because their vegetative hyphae can persist through unfavorable environmental situations, resuming growth with the return of favorable conditions.

A second large group of fungi are able to utilize the photosynthetic products of specific living plants by establishing a unique system with an advantage to both the fungus and the associated green plant. One system involves fungal hyphae becoming established between the cells of the plant roots connected to a mantle of hyphae around the root with branches growing far out into the surrounding soil. The benefits are food for the fungus and minerals and water for the green plant. The two form a mycorrhiza, a fungus root (Smith and Read 1997). As new roots are initiated, the fungus grows from old roots to the new one and thus can perpetuate the relationship indefinitely. Some mycorrhizal relationships are very specific, involving a single species of tree and a particular fungus. Usually relationships are not so limiting, with several fungal associates and a given plant species or a fungus capable of a mycorrhizal relationship with several plant species (Smith and Read 1997). Fungus fruiting bodies which form spores, the disseminative units of the fungi, may develop on the soil in the canopy zone of the plant associate but are not necessary for maintenance of the relationship.

A basically similar balanced situation between either a single celled or short filamentous green alga and a fungus, or a filamentous blue-green cyanobacterium and a fungus results in a plant called a lichen (Ahmadjian 1993).

The third large and diverse group of fungi that are plant parasites obtain their food utilizing a green plant as a host and may affect their host plants in a variety of ways (Agrios 1988). Some plant parasitic fungi produce compounds that kill host plant cells and then digest the dead cells. Some fungi colonize specific tissues in the host plant such as the water conducting cells of the xylem, plugging them

until they can no longer function. Other fungi, the obligate parasites, can establish a relationship only with living host cells in which there is a transfer of food materials into their hyphae with no immediate visible damage to the host cells (Alexopoulos et al. 1996). However, by using photosynthate that would normally be utilized by the host plant in growth and development they affect the ability of the plant to grow and compete effectively for survival and/or limit plant reproduction. Fungal species with parasitic capabilities have the most potential for being undesirable new arrivals in an area as well as the most obvious.

The potential for introduction and establishment of alien fungi into Iowa varies greatly in the three groups of fungi just characterized on the basis of energy source acquisition. The saprobic fungi that use dead organic materials, principally plant residues, are least likely to be affected by introduced fungi. Many are already cosmopolitan in their distribution and also opportunistic in their colonization. The saprobes that produce macroscopic spore-producing structures, some mushrooms, puffballs, hard puffballs, morels, false morels, that are potentially edible by man have been reasonably well documented in "mushroom" books with local or regional applications such as the Iowa based book by Huffman et al. (1989). However, mycologists in the United States have seldom been careful recorders of distribution information even for the macrofungi or perhaps have not worked to make the information generally available. When detailed studies have been done, documentary material from such studies are typically deposited in herbaria and are available for future study and interpretation. More commonly, there are neither herbarium reference materials nor lists of fungal species for particular sites.

For Iowa, the most comprehensive listing of fleshy fungi is of the Basidiomycetes, and this report is limited to members of that group with one-celled basidia (Gardner 1947). It does provide valuable presence/absence information about distribution at that time, but its use is limited. The lack of predictability of formation of fruiting structures by which the fungi can be identified and the ability of these fungi to be perennial vegetatively are confounding factors (Tiffany et al. 1998). A given saprobic species may be well established in a particular site and grow vegetatively for years without forming an identifiable fruiting structure, thus no evidence of its presence would exist to be recorded. A species seemingly new to an area could be indeed introduced into the area via plant materials, soil, or by various human activities, or it could be simply a well established member of the saprobic fungus community that is at last apparent. A further complicating factor is the ephemeral nature of most mushrooms and other fleshy fungi. Even the saprobic fungi that have the potential to develop anytime during the growing season may emerge and decay quickly. Thus their presence might not be recorded unless an observer happened to be present at that exact time (Tiffany et al. 1998).

The Gardner (1947) list, incomplete as it probably is, is our most valuable information to aid in interpreting the presence of a "new" species. If a fungus is indeed an introduced species not previously established in the area, how does its presence impact the known fungus population? How do we follow its progress, either to successful establishment, thus limiting the native species by competition for resources, or resulting in exclusion because the new species cannot effectively compete? These and other questions are challenges when considering the effect of introduced fungi of this capability.

The second fungal group, characterized as the mycorrhizal associate group, would be dispersed to new areas most probably on young transplants with mycorrhiza already established in their roots. Thus, potted plants, such as those small conifers sold as potted Christmas trees and destined to be later planted outside could introduce new fungi. These plants should have been associated with mycorrhizal fungi in the seedling beds and mycorrhiza developed. Because of their special association, such fungi would probably not be competitive with the native fungi. They might, however, become well adapted if their plant mycorrhizal associate is successful.

The most obvious fungi with a potential to establish in a new site are the plant parasitic fungi. Several interesting scenarios may develop with these fungi. The crop plants that are the basis of Iowa's farming economy are introduced plants, of which soybeans are the most recent introduction to be planted in large acreages. In Gilman and Archer's 1929 publication on fungal parasites on plants in Iowa and in the first supplementary list in 1932, soybeans were not mentioned (Gilman and Arthur 1929, Gilman 1932). However, in the second supplementary list (Gilman 1949) soybean and soybean parasites were recognized. In the introductory comments accompanying this latest list, Gilman (1949) listed the reasons for the number of new species reports. He stated, "The other fact was the reporting of seven fungi on soybeans, an instance of the introduction of a new crop gradually becoming attacked by an increasing number of parasites as the time of exposure and the population both increased." No doubt the highly specialized parasites that have established a food acquiring relationship with living soybean cells were travelers that came with soybeans when they were introduced into the United States as a crop plant. They could have been carried in or on the seeds or on plant residues contaminating the seed lots. The highly specific obligatory parasitic fungi are less likely to pose a threat to native plants, but the new plants may be colonized and utilized by native fungi that are less discriminating about their hosts. For example, the obligate parasitic downy mildew fungus of soybeans would not be likely to be a threat to native legume species. Interestingly, less discriminating root rot fungi in the soil such as species of *Pythium* or *Phytophthora* (Alexopoulos et al. 1996), could potentially utilize soybean roots as an additional substrate to be colonized. However, such opportunistic development of native fungal species is not an item for this discussion.

The introduced fungi that are much more likely to be problems are those with a potential for disease development in plants native to the area. Native plants would have had no previous exposure to the introduced potentially parasitic fungus and could be completely susceptible. The classic example of destruction of a host species throughout its range by an introduced fungus, chestnut blight caused by the ascomycete *Cryphonectria parasitica* (Murr.) Barr, was developing in the eastern United States in the early 1900s (Anagnostakis 1987). However, the deciduous forests of eastern Iowa did not include chestnut, *Castanea dentata* (Marsh.) Borkh., thus this tragic destruction of a native species was not a factor in the forests of Iowa.

The first well documented occurrence of significant development in Iowa of an introduced parasitic fungus on a native plant is the development of the white pine blister rust fungus, *Cronartium ribicola* Fischer, on eastern white pine, *Pinus strobus* L. (Boyce 1961). The rust fungi are obligate parasites, establishing a feeding relationship with living host cells. These fungi also have a complex life cycle, commonly utilizing two different plant hosts, usually in different plant genera, to complete their life cycle. In the case of white pine blister rust, the two hosts involved are five-needled pines and *Ribes* spp., currants and gooseberry (Darrow and Detweiler 1934). Thus two susceptible host species must be present in an area if the rust fungus is to become successfully established. On the white pine host, elongate swollen areas develop on branches or on the main trunk. Eventually the stems are girdled and the distal portions die, usually after a period of several years (Boyce 1961). Each year spores are produced that cannot establish and grow on the white pine, but do colonize leaves of *Ribes* spp. There the fungus has little effect on the leaves but two kinds of spores are developed, one in dry pustules that are dispersed in the wind to colonize other *Ribes* leaves and a

second kind in columns that produce spores that can only grow on white pine needles. The fungus grows from the needles into stems, completing the cycle (Alexopoulos et al. 1996). For the fungus to be successful, susceptible species of each host plant must occur in a reasonably close proximity in the field as the spores produced on the *Ribes* that are invasive on the white pine are thin walled and not adapted for long distance dissemination. As a result of the infections, older pine trees are prone to wind damage and are killed eventually, seedling trees die after a few years and white pine stands are not maintained. The potentially productive white pine forests are totally changed.

Cronartium ribicola is thought to be native originally to Asia on Swiss stone pine and is presumed to have spread gradually in Europe on that host. The rust fungus seems able to infest all five-needled pines. Eastern white pines from North America had been introduced into Europe after 1705 and grown extensively. The rust was not reported in Europe until 1854 when it was observed on both white pine and *Ribes*. At that time it was not known that the spore stages on these plants were actually different growth stages of the same fungus. By 1900 white pine blister rust was widespread on both hosts over northern and most of western Europe. The rust was known to have been in the northeastern states of the United States by 1898, but was first officially recorded on *Ribes* in the state of New York in 1906 and in 1909 on eastern white pines (Boyce 1961). It was later documented that low priced, infected three-year old white pine seedlings from a German nursery had been widely distributed and planted throughout the northeastern United States. In 1910, trees imported from several French nurseries were also identified as diseased. The rust has eventually spread throughout the eastern range of white pine west into Minnesota and Iowa and south into North Carolina (Maloy 1997).

In British Columbia, the rust fungus was introduced in 1910 on a single shipment of one thousand eastern white pine transplants from a nursery in France. From these diseased plants, the rust spread throughout Washington and Oregon into northern California, where it occurs on sugar pine, and throughout northeastern Washington, northern Idaho and western Montana on western white pine trees (Peterson and Jewell 1968). Potentially, all five-needled pines in the western United States are in danger. Different species of susceptible *Ribes* hosts occur in western United States, so again, both hosts are available and the rust survives. The rust has even successfully colonized whitebark pine, a slow growing and long-lived tree of western high elevation forests (Baskin 1998).

In Iowa, by the 1920s the rust was present in the native eastern white pine stands in the northeastern region of the state (Spaulding 1922, Gilman and Archer 1929). It was officially recorded on *Ribes* sp. in that area in 1929 (Gilman 1932). While loss of white pines in Iowa obviously has not had the economic impact that occurred in the lake states and the white pine lumber producing areas in northeastern United States and later in the western five-needled pine forests (Maloy 1997), it has limited the presence of this stately pine in its native range in Iowa. The fungus is still present here and active on both hosts.

Documentation exists for two other less spectacular introductions of rust fungi into Iowa on seedling pine stocks (McNabb and Shurtleff 1957), emphasizing the potential for introduction of fungal parasites established in nursery stock. *Cronartium comptoniae* Arth., sweet fern blister rust, was found on Mugho pine seedlings in a nursery near Mason City in the summers of 1955 and 1956. The seedlings had been obtained from a wholesale nursery at Fryburg, Maine in 1953 and were no doubt infected before shipment to Iowa. The other host in this rust's life cycle, sweet ferns *Myrica asplenifolia* L. and *M. gale* L., do not occur in Iowa (Arthur 1934). The lack of this necessary host limited development of the rust to plants that were already diseased as spores produced on the pine could only establish new colonies on the sweet fern host. The rust did not become established in Iowa, but did cause the loss of already diseased nursery stock.

The other well-documented introduction on nursery stock was on ponderosa pine (*Pinus ponderosa* Lass.) planted in a windbreak two miles north of Atlantic. The seedlings were obtained from the State Forest Nursery at Keosauqua in 1940 and by 1950 showed signs of disease. In 1957 when the diseased trees were examined (McNabb and Shurtleff 1957), galls were common. Diseased trees develop round perennial woody galls, usually on branches, with production each year of spores that can directly infect other ponderosa pines. Some trees had many galls, others only a few. Several years of below normal rainfall had occurred before the planting was examined, an additional stress for the diseased trees. Unlike the two rusts discussed previously, the ponderosa pine gall rust, *Endocronartium harknessii* (J.P. Moore) Y. Hirat, is a short cycle rust developing only on ponderosa pine (Hiratsuka 1969, Ziller 1974). Unless diseased trees are destroyed, the rust becomes established on other ponderosa pines, a situation that may well have been responsible for the many young diseased trees in the planting discussed here.

Other parasitic fungi may have been similarly introduced on nursery stock, but their arrival and success or failure is not documented. However, the introduced fungus that has had the most significant impact on the Iowa flora is an ascomycete, *Ophiostoma ulmi* (Buisman) Nannf. (May 1931, McKenzie & Becker 1991) and later *Ophiostoma novo-ulmi* Brasier (Brasier 1991). They are the causal agents of elm wilt or Dutch elm disease, often labeled as one of the most widely known and destructive plant diseases of the twentieth century.

Initial symptoms of the disease are the wilting and curling of the leaves at the tips of small branches in the upper canopy of the tree (Anonymous 1961). These leaves may turn yellow or become a dull green before finally becoming brown and dying. If the bark is peeled from a diseased branch, brown streaks are visible in the sapwood indicating the presence of the fungus plugging the xylem and interfering with normal water movement to the leaves (May and Gravatt 1931). Development of the disease and ultimate death of the elm host varies with species of elm, the time of year, the general condition of the tree and the weather (May 1931). The disease is potentially lethal to species of native American elms, with American elm, *Ulmus americana* L., the principal and most susceptible host.

O. ulmi produces two kinds of spores during its life cycle, both capable of causing disease, although the asexual spores are more commonly involved. These may be produced in a mucilaginous matrix from hyphae growing in the wood of diseased trees, developing abundantly along tunnels carved by the bark beetles (Alexopoulos et al. 1996). Transmission of the fungus is directly related to the distribution of the bark beetle vectors.

Diseased trees are more likely to be utilized as breeding sites by bark beetles, the young adults then being in an optimum position to be contaminated by spores of the fungus when they emerge and fly to young elm twigs to begin feeding. The combination of bark beetles as a vector transmitting a virulent fungus to a susceptible host was a tragic combination.

Elm wilt was first observed in the Netherlands in 1919, and by the time the fungus was isolated and identified as the causal agent, thousands of elms were diseased and dying. The fungus is presumed to have been brought to Europe on Asiatic elm stocks that are generally quite resistant (Brasier 1990). The disease was reported in England in 1927 and was found in North America at Cleveland, Ohio in 1930 (May 1931). Shipments of diseased elm logs containing both the fungus and one species of European bark beetle were carried from Atlantic seaports via railroad to veneer mills. By 1934 four disease sites in the United States had been identified (May

1934). Unfortunately, warnings that elm logs should not be imported had been ignored. One species of European bark beetle had been present in the United States since 1909, and several species of native bark beetles were readily available as vectors of the introduced fungus.

In 1957, McNabb observed wilted diseased American elms at Fort Madison in southeastern Iowa along the Mississippi River and later that summer in the vicinity of Davenport (Anonymous 1961, Sinclair and Campana 1978). The fungus spread quickly across the state, reducing the population of American elm, the most susceptible of the native elm species, from a favorite landscape tree to a scattered population of a few mature floodplain and lawn trees and seedling elms along fence rows and in river bottom lands.

A second wave of elm wilt disease development was recorded in Britain in the early 1970s (Gibbs and Howell 1972) and also soon after in midwestern North America (Mitchell and Brasier 1994). The more virulent fungus involved with this second disease outbreak was interpreted by Brasier to involve a new strain of the fungus that he labeled *Ophiostoma novo-ulmi* Brasier (Brasier 1991). Some of the mature trees that survived the earlier exposure and a number of young trees have become victims of *O. novo-ulmi*. Both the fungus and its bark beetle vectors are still well established and active, a deadly combination for the American elm.

Not only did this introduced fungus cause the loss of elms lining city boulevards with branches making a green arch over the roads in the summer and of single stately lawn trees, the cost of removing the trees and replacing them with a variety of other species was a severe financial problem for individual home owners and municipalities.

Modern rapid travel facilities make global distribution of fungus spores and diseased plant parts a constant threat of new destruction. The successful establishment of an introduced fungus and the potential for severely limiting or eliminating a host plant species is well documented by the history of elm wilt. The potential for destruction is always there; continuing constant awareness is necessary to prevent yet other destructive situations. These parasitic fungi are indeed "a treacherous and mutable tribe".

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