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# A Multiple Component Analysis of the Take-all Disease of Cereals

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"Take-all" root, crown, and foot rot caused by the ubiquitous soilborne fungus *Gaeumannomyces graminis* (Sacc.) Arx & D. Olivier var. *tritici* J. Walker (syn. *Ophiobolus graminis* Sacc.) is the most damaging root disease of wheat (*Triticum aestivum* L.) worldwide (3,8,17). Early symptoms of take-all are subtle and easily overlooked. Dark brown "runner" hyphae (ectotrophic growth) of the fungus may or may not be observed on the root surface, because *G. graminis* frequently penetrates young roots and grows between the cortex and stele (38). The absence or presence of runner hyphae is not a good diagnostic character of disease because the fungus grows epiphytically over the cortex of resistant rye and oat roots without causing disease.

Plants can be infected in all stages of growth when environmental conditions are favorable. Light to dark brown or black lesions and necrotic tips are characteristic root symptoms (Fig. 1). Severe infection blackens and extensively destroys the root system. A black mycelial mat of the fungus may form on the basal stem or "foot" area of the plant, and most of the roots are heavily melanized. On young plants, above-ground symptoms are characteristic of a general nutrient stress (Fig. 2) and are frequently misdiagnosed as nitrogen deficiency. A misdiagnosis of magnesium deficiency in highly weathered soils, and application of dolomitic lime (calcium and magnesium carbonates) as a source of magnesium, increases the severity of take-all and exacerbates the nutrient deficiency.

Grain losses of 10–15% from reduced root absorptive capacity and killed or aborted tillers may go undetected in the field. Wheat fields severely infected with the take-all fungus may have an uneven appearance in height by heading, although significant levels of infection frequently go undetected (3,17,38). Whiteheads, i.e., prematurely ripened, poorly filled, or empty seed heads, produced on severely infected plants may be scattered throughout the plant population (Fig. 3) or occur in circular to irregularly shaped areas in the field. With adequate moisture, heads of prematurely killed plants are generally higher in soluble carbohydrates and are readily colonized by various saprophytic fungi; they have a blackened appearance by harvest time. Yield losses vary by soil type, management, and climate for the major wheat-producing areas of the world, with estimates from 1 to 50% of the potential yield and from 0.2 to 0.5 kg/ha of wheat grain for each 1% of the plant population affected (3,8,17). Estimated losses in Indiana over a 10-year period (1972–1981) ranged from 4 to 25% of the potential wheat yield (20).

The absence of genetic resistance and effective chemical controls for take-all imposes many constraints on management practices and has given this disease a notorious reputation among cereal growers. Extensive research since the initial description of take-all 150 years ago in Australia has provided a wealth of information on all aspects of the disease (3,17) and has made it an important model for studying other soilborne diseases. As with many soilborne diseases, however, the vast pool of information on take-all has frequently created a greater frustration at its elusive control. Various hypotheses of the effects of cultural practices on survival, pathogenicity, and susceptibility have been promoted to explain the many anomalies of this disease.

Take-all is primarily controlled by cultural and management practices such as crop sequence, pH adjustment (acidifi-

cation), and tillage, all of which have a pronounced influence on the form and abundance of essential plant nutrients in the soil. Few diseases respond as dramatically to nutrition as take-all, and disease severity is increased by a deficiency of any of the essential mineral nutrients (3,12,14,19,22–24,39,40). Until recently, major emphasis has been on the effect of nitrogen, and a sufficiency of nitrogen has been a standard recommendation for many years to reduce the severity of take-all. Specific forms of nitrogen have different effects on take-all (27,30,50); nitrate nitrogen increases, and ammonium nitrogen decreases, severity of take-all. There is a striking positive correlation between the effect of various cultural practices on nitrification and the severity of take-all (Table 1). The use of a nitrification inhibitor with ammonium and those conditions and crop sequences that inhibit nitrification also reduce take-all (21,22), and vice versa. However, some practices, such as planting oats before wheat in rotation, have little apparent effect on nitrification but provide some of the most effective control of take-all (3,12,22). This suggests that the form of nitrogen, as influenced by the rate of nitrification, may act indirectly or with other factors to influence the severity of take-all.

Five years into an intensive study on the natural biological control of take-all with continuous wheat monocropping (48), a fortuitous event caused us to focus our attention on manganese. One of our farmer-cooperators direct-drilled (double-cropped) soybeans across our study area shortly after we harvested the wheat. Soybeans in the most severe take-all areas showed slow growth and interveinal chlorosis characteristic of severe manganese deficiency, whereas plants in adjacent plants appeared normal (16). Tissue analysis of the soybeans verified the deficiency of manganese only in plants grown in areas of the field where wheat was severely infected by take-all; a manganese sulfate foliar spray allevi-



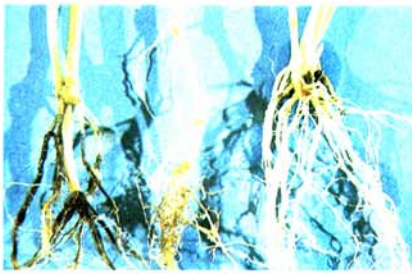


Fig. 1. Wheat roots showing (left) dark brown to black and (middle) light brown lesions caused by infection with *Gaeumannomyces graminis* var. *tritici*; (right) noninfected roots.



Fig. 2. Symptoms of nutrient deficiency on young winter wheat plants severely infected by *Gaeumannomyces graminis* var. *tritici*.

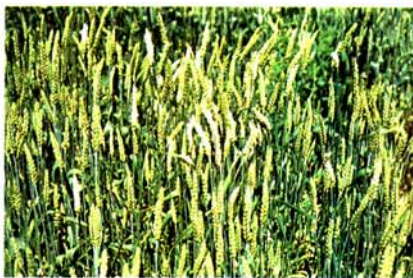


Fig. 3. Whiteheads (prematurely ripened, poorly filled, or empty seed heads) are signs of severe take-all infection and may be scattered throughout a wheat field or occur in clumps. Wheat stems are frequently stunted and gray-green before whiteheads develop, giving the field an uneven, rough appearance.

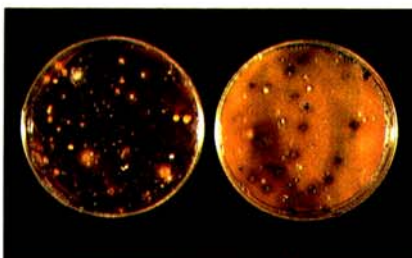


Fig. 4. When plated on Gerretsen's medium (52), rhizospheres of severely infected plants (left) have a much larger population of manganese-oxidizing organisms than do rhizospheres of adjacent, less severely diseased plants (right). Dark brown colonies are manganese oxidizers, white colonies are manganese reducers, and brown colonies surrounded by a clear area produce organic acids that reduce manganese even though the organisms are manganese oxidizers.

ated the deficiency symptoms. Soil tests indicated an adequacy of manganese, and there was no difference in manganese concentrations in soil of areas where the soybeans were severely deficient and of adjacent areas where soybean growth appeared normal. Soils in the area are regularly limed to prevent manganese toxicity to melons.

Because the availability of manganese may be greatly influenced by the activity of rhizosphere organisms (26,32,37, 52-54) between a pH of 5.2 and 7.8, we assayed the population of manganese-oxidizing and manganese-reducing organisms in the rhizosphere of symptomatic deficient soybean plants and nearby normal ones. Deficient plants consistently had a 10-fold higher population of manganese-oxidizing organisms in their rhizosphere than non-deficient plants (26). The following year, similar findings were obtained with comparative assays of severely diseased individual wheat plants and nearby, less diseased plants growing in commercial fields in various locations in Indiana (Fig. 4). Although take-all had previously been reported to be more severe on manganese-deficient plants in hydroponic culture (32,39,40), similar effects have been reported for many other nutrients (22,23,39). This field observation indicated the dynamic role of biological components in influencing manganese availability and focused our attention on the interactive role of manganese in take-all. At the same time, Graham (12) in Australia independently arrived at a similar conclusion based on the correlation of environmental conditions influencing take-all with those influencing manganese availability.

Those conditions that increase manganese availability generally reduce the severity of take-all, while those that reduce manganese availability generally increase the severity (Table 1).

We have somewhat systematically evaluated the various conditions influencing take-all with their effect on manganese availability over the past 15 years. It is in this context that we make a "multiple component" analysis of take-all by discussing the effect of the individual conditions for each part of the "host-parasite-environment-time pyramid" (4) on the relative availability of manganese and then assimilate them into a whole to more clearly understand disease escape and avoidance, biological control, tolerance, resistance, virulence, and suppressive soils. It is our experience that the multiple component approach facilitates the organization of additional information that leads to more effective management of this serious soilborne disease of wheat and other cereals. The multiple component approach "provides the mechanism for conceptually dissecting" the favorable and unfavorable environments that each host and pathogen brings to the relationship over time (4). In the *G. graminis*-wheat-environment interaction, the sum, balance, and interaction of all potential components contribute to the intensity of the relationship and determine whether the interaction is parasitic, mutualistic, or commensalistic (Fig. 5). It should be clear that some of the components defined by research over the past 150 years are of greater importance than others. Thus, although take-all results only when all conditions are favorable, disease severity is determined by the

Table 1. Effects of conditions that influence take-all on nitrification and manganese availability

Condition	Nitrification	Manganese availability	Take-all
Liming	Increase	Decrease	Increase
Manure	Increase	Decrease	Increase
Loose seedbed	Increase	Decrease	Increase
Soybean crop prior to wheat	Increase	Decrease	Increase
Alfalfa crop prior to wheat	Increase	Decrease	Increase
Nitrate nitrogen	... <sup>2</sup>	Decrease	Increase
Short monocropping	...	Decrease	Increase
Plant stress	...	Decrease	Increase
Early seeding of winter wheat	...	Decrease	Increase
High moisture	Increase	Decrease	Increase
Alkaline pH soils	Increase	Decrease	Increase
Nitrification inhibitors	Decrease	Increase	Decrease
Acid pH soils	Decrease	Increase	Decrease
Oat crop prior to wheat	...	Increase	Decrease
Ammonium nitrogen	...	Increase	Decrease
Tolerant cultivars	...	Increase	Decrease
Late seeding of winter wheat	...	Increase	Decrease
Lupin crop prior to wheat	Decrease	Increase	Decrease
Chloride fertilization	Decrease	Increase	Decrease
Firm seedbed	Decrease	Increase	Decrease

<sup>2</sup>Unknown or effect depends on environmental conditions.



“relative” favorableness of the individual components as a part of the whole system.

## Components of the Plant That Influence Take-all

Manganese, unlike other essential minor elements such as copper, zinc, iron, and molybdenum that are generally only integral components of enzymes, also functions as an activator for a wide variety of enzyme-catalyzed reactions (5,6,14,32). Manganese interacts with nitrogen metabolism and is intimately involved in respiration, photosynthesis, hormone metabolism, and the synthesis of secondary metabolites associated with the defense of plants against pathogens (Fig. 6). The activity of manganese as a cofactor in the shikimic acid pathway (deoxy-D-arabinoheptulosonate-7-phosphate synthase, phenylalanine ammonia lyase, indoleacetic acid lyase, and lignin synthesis enzymes) is probably a critical aspect of its involvement in the plant's resistance to take-all because resistance is associated with lignification (lignitubers) and the production of toxic phenolic compounds (3,6,49). The involvement of ammonium in the formation of amino acid intermediates and products of the shikimic acid pathway associated with disease resistance could explain the observation that ammonium, as well as manganese, reduces the incidence and severity of take-all. In addition, root development is positively correlated with the availability of manganese (22) and is stimulated by ammonium forms of nitrogen. Enhanced root growth could constitute a mechanism for disease escape, and siderophores exuded from plant roots are important in manganese uptake (38). Thus, under manganese-deficient conditions, photosynthesis is reduced, nitrogen is inefficiently metabolized, and defense reactions are severely limited.

*G. graminis* has a wide host range on Poaceae (Gramineae) and is an economically debilitating pathogen on wheat, barley, and many turfgrasses (3,17,38). High levels of resistance to take-all are not present in commercial wheat lines, although a limited range of tolerance does exist. In a 3-year study (Huber, unpublished), the yields of older cultivars of hard red winter wheat (Itana [CI 12933], Centurk [CI 15075], and Ridit [CI 6703]) grown in naturally infested field soil in southeastern Idaho were reduced proportionately much less than the yields of high-yielding soft white winter wheat cultivars (Gaines [CI 13448] and Nugaines [CI 13968]), even though the extent of root necrosis appeared comparable. This difference in yield loss between the two types of wheat with similar levels of disease probably reflected the lower nutrient requirement (27) and greater efficiency of partitioning

vegetatively stored nutrients by the hard red winter wheats, in contrast to the longer requirement for nutrient uptake to fulfill needs of the developing kernels (55) by the high-yielding soft white wheats. We have found that nutrient uptake generally is required for a longer period during grain fill in higher yielding winter wheats and that recently developed, higher yielding winter wheats under nutrient-deficient conditions are more susceptible to take-all. Soft red winter wheat cultivars also differ from each other in susceptibility to take-all. This difference in susceptibility appears to reflect increased nutrient efficiency during early growth, a more prolific root system, and/or the ability to accumulate relatively high levels of manganese in the seed.

Plants grown from seed containing high levels of manganese had increased seedling vigor, a more extensive root system, less severe disease, and consistently higher yields than the same cultivars grown from seed with lower manganese content (36,44). Application of manganese as a seed treatment reduced take-all and increased yields (14). We found a similar benefit from manganese seed treatment with some cultivars (Fig. 7), but results were not as consistent as with seed selected for a higher manganese content. Several wheat cultivars accumulated similar amounts of manganese in the endosperm regardless of the relative nutrient content of the soil in which they were grown. Thus, the favorable and unfavorable components of wheat influencing take-all include the length of required nutrient uptake to meet the kernel demands, nutrient uptake and partitioning efficiency, and ability to accumulate manganese in seed as a benefit for subsequent seedling growth (Table 2). Plants under stress frequently have higher populations of manganese-oxidizing organisms in their rhizospheres and are more susceptible to take-all than nonstressed plants (3,26).

Rye, oats, and some triticale are resistant to take-all despite epiphytial growth of *G. g. tritici*. Although quite resistant to take-all, neither rye nor

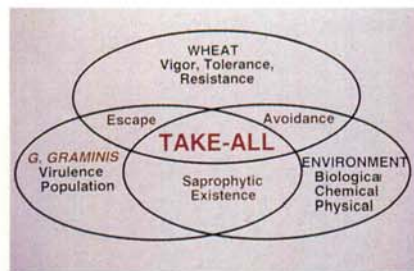


Fig. 5. In the *Gaeumannomyces graminis*-wheat-environment interaction, the sum, balance, and interaction of all potential components (favorable and unfavorable) determine whether the interaction is parasitic, mutualistic, or commensalistic.

triticale provides protection for a subsequent wheat crop (17,46). Rye is the most efficient commercially grown cereal for minor element uptake (9), and triticale lines that contain the rye chromosome conditioning nutrient efficiency are as resistant to take-all as rye; however, lines that do not contain this segment of the rye chromosome are as susceptible to take-all as wheat. In contrast to the failure of rye and triticale to reduce the severity of take-all in a subsequent wheat crop, a previous crop of oats provides consistent control of take-all of wheat. Oats are generally considered resistant to some strains of *G. graminis* (vars. *tritici* and *graminis*) but susceptible to *G. g. avenae* (3). Production of avenacin, a triterpenoglycoside compound with general antifungal activity, in root cortex tissues of oats has been associated with resistance to take-all (2). Synthesis of avenacin may be independent of the suppression of manganese-oxidizing organisms by root exudates in the rhizosphere but may be influenced by manganese. Isolates producing avenacinase have been designated *G. g. avenae* because of their virulence on oats, which are otherwise considered resistant to *G. graminis*. Resistance of oats to take-all also is correlated with resistance to gray speck disease (manganese deficiency) as a result of root exudates that are toxic to manganese-oxidizing organisms in the rhizosphere (22,52-54). In some of our trials, oat lines susceptible to gray speck were susceptible to take-all and failed to provide significant protection to a subsequent wheat crop. Take-all of oats, once relatively

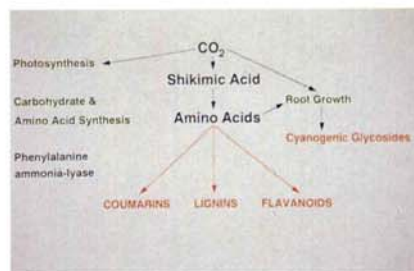


Fig. 6. Potential roles for manganese in disease resistance.



Fig. 7. (Right) Take-all is less severe in plants grown from seed treated with 0.5 kg/ha of manganese (as manganese sulfate) than in (left) plants grown from nontreated seed.



common, generally has been quite rare since cultivars resistant to gray speck (resistant to manganese deficiency) have been available. Take-all of oats occurs only in areas where levels of soil manganese are well below concentrations required for physiologic sufficiency, regardless of biological activity in the rhizosphere (3,17). Susceptibility of oats to take-all in Western Australia soils characteristically low in manganese (17) may be due to the requirement for manganese in the production of avenacin or to the lack of enough manganese to meet general plant requirements even though manganese-oxidizing organisms are suppressed in the rhizosphere.

### Components of the Pathogen That Influence Take-all

*G. graminis* is an amazingly well-adapted soilborne fungus that can grow at a pH ranging from 3.2 to 11.0 and a temperature ranging from 4 to 30 C. The fungus grows at very wide C:N ratios and persists indefinitely once introduced into temperate soils (3). Components that are favorable or unfavorable for disease include virulence (manganese oxidation, production of avenacinase), population, and sensitivity to microbial antagonists (Table 2).

Discriminating between heritable variation of the pathogen and variation from interactions with the environment is

difficult. Differences in virulence are common among isolates of *G. graminis*, and virulence may be lost with subculturing, although some isolates are very stable. Graham (14) correlated virulence with the manganese-oxidizing ability of the pathogen. *G. graminis* isolates that failed to oxidize manganese were nonpathogenic or only weakly virulent, and those that oxidized manganese readily were highly virulent. In evaluating the relationship of manganese-oxidizing potential with virulence, Roseman et al (42) found that some isolates of *G. g. tritici* were sensitive to temperature for both manganese oxidation and virulence, whereas others were insensitive to temperature for both characteristics across a range of 8 to 30 C. Isolates that were highly virulent (and oxidized manganese) only at high temperatures (25 or 30 C) were coinoculated with isolates that were virulent (and oxidized manganese) only at low temperatures (8 or 15 C) to see if cross-protection could be observed. In both combinations and with a number of different isolates, coinoculation resulted in either increased disease severity or disease severity consistent with the most virulent isolate at the particular incubation temperature. This study was further confounded by the observation that the disease was more severe in inoculated nonsterile, disease-conducive field soil (heavily populated by manganese-oxidizing microorganisms) than in the same soil sterilized and reinfested with *G. g. tritici*. This indicates a synergistic effect similar to that observed with some potential biological control bacteria that can oxidize as well as reduce manganese in soil. Some isolates of *G. g. graminis* have been reported to reduce take-all severity, yet most of those we have examined (virulent isolates from turf) are manganese oxidizers in culture but only weakly virulent or nonpathogenic on wheat.

Dispersive X-ray microanalysis with a scanning electron microscope comparing manganese oxidation by *G. g. graminis* with that by *G. g. tritici* indicated that manganese oxidation occurred only around the lobed hyphopodia (appressoria) and related infection structures of *G. g. graminis*. In contrast, highly virulent *G. g. tritici* isolates oxidized manganese at a distance from the mycelium (Fig. 8). Manganese oxide deposits were observed in cortical cells and root hairs of plants infected with *G. g. tritici* as well as along runner hyphae of the fungus. Dispersive X-ray microanalysis confirmed the precipitate as manganese oxide. This difference between *G. g. graminis* and *G. g. tritici* in manganese oxidation could be important in pathogenesis because the physiological immobilization of manganese around the infection court in advance of *G. g. tritici* hyphae could compromise the plant's

**Table 2.** Components of the wheat plant, the pathogen (*Gaeumannomyces graminis*), the biotic environment, and the abiotic environment that are favorable and unfavorable for take-all

Favorable for disease	Unfavorable for disease
<b>Wheat plant</b>	
Nutrient deficiency	Nutrient sufficiency
Nutrient-inefficient (especially manganese)	Nutrient-efficient (especially manganese)
Susceptible	Tolerant or resistant
Low seed manganese	Manganese accumulation in seed
Slow root growth	Fast (extensive) root growth
High yield potential	Low yield potential
Limited siderophore production	High siderophore production
Stimulation of manganese oxidation	Suppression of manganese oxidation
Limited root exudation	High root exudation
No production of toxic root exudates (especially avenacin)	Production of avenacin (and other inhibitors)
High plant population	Low plant population
Stress-sensitive	Stress-tolerant
Nitrate nutrition	Ammonium nutrition
<b><i>G. graminis</i></b>	
Highly virulent	Nonpathogenic
Large population	Absent or small population
Fast growth rate	Slow growth rate
Oxidizes manganese	Unable to oxidize manganese
Produces avenacinase (for oats)	Unable to produce avenacinase
Insensitive to soil antagonists	Sensitive to soil antagonists
Insensitive to temperature	Sensitive to temperature
Nitrate nutrition	Ammonium nutrition
<b>Biotic environment</b>	
Large population of manganese oxidizers	Small population of manganese oxidizers
Low population of manganese reducers	High population of manganese reducers
Fast rate of nitrification	Slow rate of nitrification
Low general microbial activity	High general microbial activity
<b>Abiotic environment</b>	
Nitrate nitrogen	Ammonium nitrogen
Alkaline soil pH	Acid soil pH
Organic fertilization (animal manure)	Inhibition of nitrification
Imbalanced nutrients	Balanced nutrients
Optimum temperature for manganese oxidation	Temperature for manganese reduction
High soil moisture	Low soil moisture
Conductive soil	Suppressive soil
Soybean or alfalfa prior crop	Oat or lupin prior crop
Loose seedbed	Firm seedbed
High plant population	Low plant population
Plant stress	Manganese, chloride fertilization
Short monocropping	Long monocropping (take-all decline)
Early seeding	Late seeding
Application of lime (calcium carbonate)	Application of "acid" fertilizers



resistance mechanisms (lignin development, secondary metabolism, etc.) (49) more effectively than the more localized immobilization around *G. g. graminis* hyphopodia.

The manganese oxidation of nonpathogenic *G. g. graminis* isolates in culture points up the need to understand all the potential interacting factors in nature that influence manganese oxidation as a mechanism of virulence. Manganese oxidation appears to be a component of virulence where manganese is oxidized in advance of the infective hyphae of *G. g. tritici* (1,14,42,58). We have also found (*unpublished*) that the frequency of bacteria isolated from wheat rhizospheres that were capable of inhibiting manganese oxidation was higher with *G. g. graminis* than with *G. g. tritici*. When manganese oxidation was inhibited by an associated soil bacterium, whether or not growth rate of the fungus was affected, the fungus was nonpathogenic on seedling wheat plants. Although growth rate in field soil could be important in making initial root contact, neither growth rate, pigmentation, nor cellulase activity of isolates differing in these characteristics has been correlated with disease severity in the laboratory (3).

Reduced disease severity with certain crop rotations has been attributed to poor survival of *G. graminis*. This reduction, however, probably reflects the lack of techniques to evaluate populations in the field, since assays based on infection of a "trap crop" are selective for highly virulent isolates and a susceptible host. The rapid buildup of take-all in a field and the ability of the fungus to colonize many plants epiphytically suggest that reduced virulence of the pathogen could account for reduced disease without a significant change in the pathogen's population. Several manganese-reducing bacteria selected for their biological control potential against *G. g. tritici* were able to prevent manganese oxidation of the fungus as well as infection of a wheat seedling placed on the combined culture without restricting growth rate of the fungus across an agar medium. However, several combinations of manganese-reducing bacteria with *G. g. tritici* that inhibited manganese oxidation in agar culture failed to inhibit oxidation on the root surface or pathogenesis under these highly conducive conditions. In contrast, manganese-oxidizing bacteria generally resulted in more severe disease both in agar tests and in naturally infested field soil (Fig. 9).

### Components of the Environment That Influence Take-all

Components of the soil environment that are favorable and unfavorable for disease have been extensively recorded throughout the 150 years this disease has been studied (3,17). Although many of

these components are correlated with nitrification, they are more consistently correlated with manganese availability (Table 1), and the dynamics of the biological soil environment must be considered as well as the abiotic environment if this disease is to be understood and managed.

**The biological environment.** Component interactions of the biological environment with take-all may be both direct (by suppressing or enhancing growth and/or virulence of the pathogen) and indirect (by increasing or reducing plant resistance) (Table 2). Evidence of a role for microorganisms in suppressing take-all has included the greater general microbial activity and lower incidence of disease in loamy and take-all suppressive soils and with take-all decline than in sandy and take-all conducive soils (3,17,48). Garrett (11) postulated that high CO<sub>2</sub> levels from high microbial activity in soil were inhibitory to *G. graminis*. The direct effect of many soil microorganisms on manganese availability appears especially critical because manganese availability may be largely determined by the activity of manganese-oxidizing or manganese-reducing organisms between a pH of 5.2 and 7.8 (32). Microbes also are sensitive to pH, moisture, temperature, and nutrient elements in the physical environment. We have found that severely diseased plants frequently have a higher population of manganese-oxidizing organisms in their rhizospheres than adjacent, less severely diseased plants (Fig. 4). The take-all tolerant cultivar Auburn (CI 17898) had a significantly lower population of manganese oxidizers in its rhizosphere than the more susceptible cultivar Beau (CI 17420).

Disease severity has been markedly increased by seed bacterization with various strains of manganese-oxidizing organisms and lessened by bacterization with some manganese-reducing organisms (Fig. 9). Seed bacterization with *Bacillus subtilis* strain A-13 or *Pseudomonas aureofaciens* 2-79, organisms that can oxidize as well as reduce soil manganese, increased take-all unless nitrification was inhibited to prevent the bac-



Fig. 8. Highly virulent isolates of *Gaeumannomyces graminis* var. *tritici* oxidize manganese (brown deposits in the MnSO<sub>4</sub>-amended PDA) at a distance from the mycelium. (Courtesy H. J. Arnott)

terium's oxidative potential and reduced take-all when nitrification of applied ammonium nitrogen was inhibited with a nitrification inhibitor or by soil fumigation (24,25,54,56,57). This effect of the form of nitrogen on the manganese-oxidizing ability of the potential biological control organism may explain the reports of these and similar organisms reducing take-all in inoculated fumigated soils (which are toxic to the *Nitrosomonas* spp. responsible for nitrification) but their frequent failure to reduce disease severity—or even increasing severity—in many natural field soils (17,25). We also have observed synergistic interactions of manganese-oxidizing soil microbes with *G. graminis*. Take-all is frequently more severe in growth chamber studies in inoculated, conducive field soils with a high population of manganese-oxidizing organisms than in the same soil that has been sterilized and reinfested with the pathogen. This synergistic effect of the soil microbiota with *G. graminis* also can be reproduced in growth chambers or the field with specific manganese-oxidizing organisms such as *Agrobacterium radiobacter* that are common in wheat rhizospheres (Fig. 9).

The biological environment also includes the effects of weeds on the soil microflora or as competitors for essential nutrients. Take-all is generally more severe where quackgrass (*Agropyron repens*) has been a problem in previous crops, especially if treated with the herbicide glyphosate (17). Weed competition for nutrients is one factor involved in the

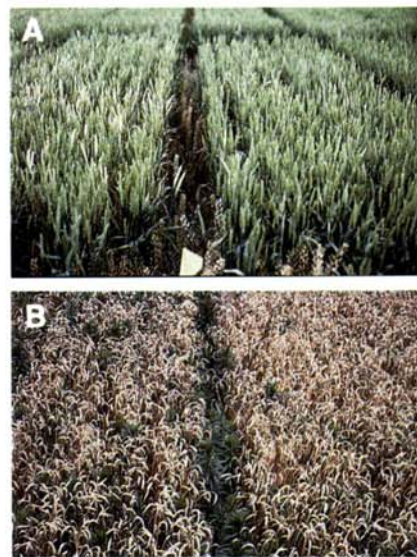


Fig. 9. (A) Take-all is less severe in (right) wheat grown from seed inoculated with *Bacillus cereus*, a manganese-reducer common in wheat rhizospheres, than in (left) wheat grown from seed inoculated with *Agrobacterium radiobacter*, a manganese-oxidizer also common in wheat rhizospheres. (B) The same plots 4 weeks later.



increased severity of take-all and may explain our observations of the more severe disease with downy brome (*Bromus tectorum*), an early-season grass competitor, than with quackgrass, a late-season competitor. The effect of glyphosate is especially interesting because this foliage-applied herbicide inhibits 5-enolpyruvylshikimate-3-phosphate and, thus, the shikimic acid pathway in plants; take-all increases in the season after the application of the herbicide, however. The effect of glyphosate on take-all is probably indirect, since the average half-life of glyphosate in soil is less than 60 days (33). Glyphosate is considered a nonpersistent herbicide in soil, and most crops can be planted or seeded directly into treated areas after application because uptake via the root system is precluded by soil inactivation on clay particles through complexing with metal ions. Thus, predisposition to take-all by glyphosate may be the result of modification of the soil microflora directly (51) or during decomposition of the herbicide-killed plant tissues, i.e., stimulation of manganese-oxidizing organisms, or by complexing with soil manganese to reduce its availability for plant uptake. Another explanation for the effect of grassy weeds and glyphosate on take-all could be the increased inoculum potential of the pathogen as it parasitizes the grasses and the weakened resistance of the grasses after application of glyphosate, which could allow the fungus to colonize the tissue more completely than normally possible.

Wheat—and many other plants—can use either ammonium or nitrate equally well for growth. However, the biological oxidation of ammonium to nitrate nitrogen (nitrification) has a definite influence on take-all through its effect on stability of the form of nitrogen in the soil and the availability of a specific form of nitrogen for plant uptake (Fig. 10). Nitrogen applied in the ammonium form is rapidly converted (1–3 weeks) to the nitrate form in most cultivated soils (23,28). The *Nitrosomonas* and *Nitrobacter* spp. responsible for nitrification

are inhibited at acid pH and anaerobic soil conditions. Ammonium nitrogen is primarily metabolized to amino acids in the root system before translocation to other parts of the plant. The rhizosphere becomes more acidic as ammonium nitrogen is absorbed (28,50), and root exudates contain a large number of organic compounds that are available and stimulatory to rhizosphere microorganisms. In contrast, nitrate nitrogen is translocated to leaves and other aboveground plant tissues, where it is reduced to amino nitrogen and metabolized to amino acids with only limited modification of the rhizosphere microflora. Nitrite and nitrate reductase are both very sensitive to heat and moisture stress conditions, common to severe take-all losses, so that adsorbed nitrate, even though plentiful, may not be physiologically available to the plant. The reducing environment promoted by ammonium uptake suppresses manganese-oxidizing organisms, stimulates manganese-reducing organisms, and increases manganese uptake by the plant. Phosphate and zinc uptake also are increased by ammonium nutrition but not by nitrate. Nitrification, although strongly inhibited in climactic ecological systems, is generally rapid in most cultivated soils, and the response of take-all to different forms of nitrogen applied in the field may be limited unless nitrification is inhibited (22,28).

One of the deterrents to more effective utilization of animal manures for cereal production has been the recognition of increased take-all (but reduced *Rhizoctonia*) after manuring. Manure stimulates nitrification and other microbial processes so there is a greater proportion of nitrate nitrogen available in the soil, and the response is similar to nitrate nitrogen. Inhibiting nitrification of organic manures has removed the predisposing effects of these materials on take-all and increased their value for crop production by stabilizing nitrogen in the ammonium form (22–24).

**The abiotic environment.** Take-all is typically described as a disease that is prevalent on alkaline, low-fertility soils (3,17)—conditions characteristic of

immobilized manganese and manganese deficiency (12–15,22,32). Soil suppressive to take-all has a high level of available manganese and high biological activity (reducing) to maintain the manganese in an available form for plant uptake. The limited number of laboratory reports of an association of manganese with take-all reflects the difficulty in establishing manganese deficiency under pot culture conditions and the dynamic interactions of season, soil, and biological conditions on manganese availability. Even though substantial amounts of manganese may be present in the soil at alkaline pHs, its availability is limited by chemical oxidation and microbial activity. Take-all is severe on soils characteristically low in manganese so that neither soil condition nor microbial activity can increase the level to full sufficiency for resistance or plant growth. This may account for the susceptibility of oats to *G. g. tritici* in Western Australia and the infrequent occurrence of take-all on oats resistant to gray speck, as mentioned previously. Direct manganese amendment of these soils has been demonstrated to reduce take-all (47). All of the conditions influencing take-all are correlated with their effect on manganese availability (Table 2), and recommendations to decrease take-all severity encompass practices that specifically increase manganese availability. In contrast, take-all is increased by practices that reduce manganese availability (such as liming acid soil), by a loose seedbed, by applying nitrate nitrogen, and by certain preceding crops in the rotation.

**Lime.** Lime (calcium carbonate) is routinely applied to cultivated soil to adjust pH to levels optimum for plant growth. Increased take-all commonly observed after applications of lime is attributed to changes in soil pH and redox potential (7,40,50). However, liming also increases the population of manganese-oxidizing organisms, suppresses the population of manganese reducers (32,41), and stimulates nitrification, all of which reduce the availability of manganese for plant uptake. An acidic soil pH and acid-forming fertilizers generally favor the reduced form of manganese.

**Seedbed.** A firm seedbed has been a standard recommendation to reduce take-all for many years (3,17). A loose seedbed increases soil aeration and manganese-oxidation, whereas a firm seedbed has more anaerobic reducing sites and manganese-reducing organisms, although soil compaction increases the loss of nitrate nitrogen through denitrification and may restrict root growth and the accessibility of soil manganese. Use of press wheels on our grain drill to firm the soil after seeding increased manganese tissue concentrations from 11 to 17 ppm and markedly reduced take-all (Fig. 11).



**Fig. 10.** Wheat planted in soil naturally infested with *Gaeumannomyces graminis*: (Right) Effect of inhibiting nitrification of preplant fall-applied anhydrous ammonia fertilizer and (left) effect of non-stabilized anhydrous ammonia, applied at the same rate, on take-all.



**Fig. 11.** (Right) The four rows of wheat planted in soil firmed by press wheels on the grain drill have less take-all than (left) the four rows of wheat planted in loose soil.



**Nitrogen.** Nitrogen application has been a standard recommendation for reducing take-all for years. It is often difficult, however, to relate nitrogen sufficiency levels to disease severity because of the dynamic interactions that occur when nitrogen fertilizer is added to the soil. Also, response to the form of nitrogen, i.e., ammonium or nitrate, metabolized by the plant differs dramatically. Take-all severity is generally increased by nitrate nitrogen and decreased by ammonium nitrogen. Grain yield losses from take-all usually decrease as the rate of nitrogen increases, even though the severity of infection, as measured by root necrosis, may increase with nitrate sources of nitrogen. Yield loss is reduced because the increased availability of nitrogen offsets the impaired absorptive capacity of the infected tissues. Stimulation of root growth by nitrogen and increased availability of nitrogen both function as disease escape mechanisms.

Many of the differences in disease severity observed with the two forms of nitrogen are related to differences in their metabolism. Most of the nitrate nitrogen absorbed is translocated to leaves, where it is reduced to amino nitrogen for amino acid synthesis. In contrast, ammonium nitrogen is primarily metabolized in the root tissues, and the amino acids formed (glutamic acid, glutamine, asparagine) are then translocated to other parts of the plant (22,28). The roots serve as a carbohydrate "sink" with ammonium for the formation of amino acids, so that excessive levels of ammonium may induce a carbohydrate deficiency (ammonium toxicity) in other parts of a small seedling or may stimulate photosynthesis in an older plant by removing feedback inhibition. Another effect of ammonium metabolism in the root is the availability and exudation of a variety of nutrients so that the rhizosphere flora is stimulated significantly. Control of take-all with ammonium is generally enhanced with a nitrification inhibitor (Fig. 10) to stabilize nitrogen in the ammonium form for a longer period of time (22,28) (Table 3). Because ammonium nitrogen is rapidly converted to nitrate nitrogen in most soils, little difference in effect on disease severity may be observed with the two forms unless nitrification is inhibited.

Two mechanisms appear to be responsible for the increased manganese availability and plant uptake observed after application of ammonium nitrogen (34). The first is a general suppression of manganese-oxidizing activity and an increase in the population of manganese-reducing organisms in the soil (32,38), and the second is an increase in soil acidity in the rhizosphere (50), which also may account for the increased zinc and phosphate uptake observed with ammonium applications. Nitrate, on the other hand, increases the activity of organisms that oxidize manganese to

nonavailable forms. An exception to the general situation observed in the field is the reduced take-all with nitrate nitrogen (more than with ammonium nitrogen) in glasshouse soil that has been heavily leached, a process that removes soluble manganese from the profile (18).

**Crop sequence.** The effect of specific crop sequences on take-all is a combination of altered manganese availability and nitrification, which also affects manganese availability (22,29,31). These, in turn, influence the inoculum potential of the pathogen. As previously discussed, oats, in contrast to rye, appear to reduce take-all by inducing changes in the soil microflora that increase the availability of manganese (22,53,54). In addition to inhibiting nitrification, lupins (*Lupinus* spp.) accumulate manganese, which is later released during mineralization. The reduction in take-all following lupins may reflect both increased availability of manganese during biomineralization of residues and reduced nitrification (30). In contrast, alfalfa, which provides an amount of residual nitrogen similar to that provided by lupin, increases nitrification, manganese oxidation, and take-all (22,30-32). The population of manganese-oxidizing organisms in wheat rhizospheres increases under short (two to five consecutive crops) monocropping but decreases to levels similar to those of a climax ecosystem under long monocropping conditions.

Manure amendment supplies both carbon and nitrogen for soil microorganisms and thus stimulates nitrification. Although the nitrogen in manure is initially in the ammonium form, it is rapidly nitrified (30,31) and has an effect similar to nitrate nitrogen unless nitrification is inhibited with nitrapyrin. The effects with manure observed after inhibition of nitrification are similar to those observed with inorganic ammonium nitrogen. Plant residues such as straw may stimulate manganese-oxidizing organisms (53) or, as peat, act as a nutrient "sink" to immobilize manganese in the soil (25,45).

**Other abiotic factors.** Other abiotic factors influencing take-all also are correlated with manganese availability. High rates of band-applied chloride fertilizers increase manganese availability, suppress nitrification, and reduce take-all (7,24). Increased nutrient stress is common with a high plant population that competes for manganese reserves and increases take-all. Late-seeded winter wheat plants have a lower need for manganese because of limited growth before winter dormancy, and manganese-oxidizing organisms are less active in the rhizosphere so that infection is delayed or reduced. In contrast to winter wheat, late-seeded spring wheat plants may be under more manganese stress because of drier soils or higher activity of manganese-oxidizing organisms in the warmer soils. Wet soils can leach soluble manganese from the root zone and increase the activity of manganese-oxidizing and nitrifying organisms.

### Understanding the Outcome of the Interacting Factors

The take-all disease occurs only when favorable conditions of the three factors of plant, pathogen, and environment overlap (Fig. 5). The severity of disease reflects the extent of influence the various factors have on manganese availability and its interaction with the physiology and resistance of the plant. Severity of disease depends on the combination of factors present and increases as manganese availability is reduced. Disease occurs only when the combination of pathogen, environment, and microbes induces a manganese deficiency in the plant sufficient to reduce resistance. Disease resistance occurs only when manganese and other factors are maintained near sufficiency for the plant. The physiological availability of manganese must counter the manganese-oxidizing potential of the pathogen in the infection court and result in active defensive responses on a localized basis (ligni-

**Table 3.** Effect of nitrogen rate and nitrification inhibition on wheat grain yield and take-all in three naturally infested field soils

Nitrogen <sup>a</sup>		Sand		Loamy sand		Silt loam	
Rate (kg/ha)	Nitrapyrin	Yield (kg/ha)	Take-all <sup>b</sup>	Yield (kg/ha)	Take-all	Yield (kg/ha)	Take-all
0	0	1,320 a <sup>c</sup>	30 a	1,188 a	50 a	2,508 a	8 a
44	0	1,584 ab	26 a	2,442 b	23 b	3,102 b	3 b
	+	1,980 b	16 b	3,234 c	11 c	3,828 c	2 b
88	0	1,787 b	18 b	3,300 c	19 b	4,158 c	1 b
	+	2,838 c	9 c	4,422 d	7 c	4,620 d	1 b
132	0	2,640 c	12 bc	3,366 c	20 b	4,620 d	1 b
	+	3,232 d	3 c	4,950 e	6 c	4,752 d	1 b

<sup>a</sup>Fall-applied as anhydrous ammonia preplant with injection knives on 6-cm centers.

+ = Anhydrous ammonia nitrapyrin at 0.55 kg a.i./ha to inhibit nitrification.

<sup>b</sup>Percent whiteheads.

<sup>c</sup>Values followed by a common letter are not significantly different ( $P = 0.05$ ).



tubers) (3,49). The plant may provide sufficient manganese through manganese uptake efficiency (redox potential, root morphology, kinetics of uptake, siderophore production) or increased availability of the manganese in soil (root exudates inhibitory to manganese-oxidizing organisms, etc.).

*Tolerance*, the ability to yield or produce in the presence of disease, may be expressed if the functional requirement for the tissue damaged by the disease has passed, i.e., older hard red winter wheats that partition vegetatively stored nutrients to meet the "sink" demand of developing kernels as contrasted to higher yielding wheats that require nutrient uptake throughout the grain-fill period (55). *Disease escape* can occur through phosphate-, nitrogen-, and/or manganese-stimulated root growth, in which the roots develop faster than the fungus can destroy their function, or through environmental (temperature) and microbial interactions that inhibit or reduce virulence of the pathogen (biological control and suppressive soils). Although the pathogen is present in most soils cropped to wheat, disease is avoided if the pathogen is not present, is inactive (dormant or fungistasis), or is nonpathogenic (avirulent, hypovirulent). Disease is suppressed in fertile soils where manganese is available and biological activity is adequate to provide full sufficiency for the plant. The pathogen also may be avirulent because of specific microbial interactions that block manganese oxidation.

Organisms for potential biological control of take-all have been chosen because of their ability to suppress growth of the pathogen through antibiotic products (phenazine-1-carboxamide, phloroglucinol, etc.) (56,57). At one time, iron siderophore production was thought to reduce disease (35). Siderophores may be of microbial or plant origin and affect the availability or uptake of manganese as well as of iron and other mineral ions. The multiple component evaluation indicates several approaches for *biological control* besides the classical antagonism to the pathogen. The inadvertent universal selection of manganese-reducing organisms as plant-growth-promoting and biological control organisms (Huber,

*unpublished*) suggests that a generalized mechanism with other soilborne diseases may involve manganese. The ability of several of these potential biological control organisms to block manganese oxidation by the pathogen and prevent infection without altering growth rate indicates that biological control may be through inhibition of virulence (blockers) rather than antagonism (eradicating the pathogen). This is consistent with observations in suppressive soils and the general conditions observed with take-all in the field. Organisms that create a more acidic environment in the rhizosphere could also increase the availability of manganese and other essential elements, thereby indirectly influencing disease severity. Genetic manipulation of rhizosphere-compatible, manganese-reducing organisms to increase their activity in inhibiting virulence also could be of value.

### Integrating the Components for Disease Control

Our focus on manganese initially indicated a direct approach to disease control similar to that used in ameliorating other nutrient deficiencies, i.e., if a pathogen-induced soil deficiency of manganese was the critical factor for take-all, then manganese amendment should provide disease control. Evaluation of the multiple components that influence take-all, however, indicates that control can best be achieved by an integrated approach, since each component exerts a variable effect on manganese availability.

All of the approaches we have used to apply manganese directly have been only partially successful. Broadcast applications of manganese sulfate to the soil require a high rate and are inefficient and readily oxidized by soil organisms. Manganese applied to foliage relieves aboveground symptoms of deficiency but is not basipetally translocated and does little to reduce take-all severity (17, 22,39,58). Coinjection of 0.5 kg/ha of manganese with stabilized anhydrous ammonia to prevent nitrification was as effective as 18 kg/ha of manganese sulfate broadcast to a moderately manganese-deficient soil (loamy sand). Although application of manganese with the ammonia provided a reducing environment, benefit to roots outside the ammonia band was limited because of restricted basipetal distribution in the plant. Likewise, seed treatment with manganese stimulated root growth and reduced seedling infection, but roots outside the treated areas were not affected and yield responses were erratic. Manganese seed treatment frequently stimulated the population of manganese-oxidizing organisms in the rhizosphere so that availability was limited to a relatively short period (43,54). Seed treatments with peat, which immobilizes

manganese, increased take-all and nullified the beneficial effects of seed bacterization with plant-growth-promoting rhizobacteria or potential biological control organisms (25,45). Seed treatments combining manganese with manganese-reducing bacteria reduced disease severity in seedlings and increased manganese uptake (14), whereas application of manganese with several manganese-oxidizing organisms had little effect on disease. This is consistent with results of biological control of take-all, since all of the more than 150 reported or potential biological control organisms we have evaluated are manganese-reducers (although some can also oxidize manganese under field conditions, as previously discussed for *P. aureofaciens* and *B. subtilis*). In our studies, the early growth response and reduced disease after seed bacterization with manganese-reducing organisms generally have failed to persist throughout the long infectious period common with take-all in the Midwest.

### Manipulating the Components for Disease Control

Various approaches and their combination have improved the reliability of disease control (Fig. 12). The plant can be manipulated genetically to increase its manganese uptake efficiency, accumulation of manganese in seed, root exudate suppression of manganese oxidizers in the rhizosphere, or root morphology (13, 14,44). Microorganisms that can inhibit the pathogen's manganese-oxidizing ability (virulence) or its growth, and/or reduce manganese in the rhizosphere and increase manganese uptake by the plant, could all contribute to biological control of take-all.

Chemical control may be achieved by the application of seed treatment chemicals or soil fungicides that are toxic to the fungus or that modify the soil microflora to increase manganese availability. Cultural controls selected to increase manganese availability, such as a firm seedbed, crop rotation, manganese amendment, and inhibiting nitrification of manure, should be integrated into the overall disease control plan.

### Conclusions

Take-all is the expression of specific interacting favorable components of the plant, fungal pathogen, biotic environment, and abiotic environment (Fig. 13). These components are all interrelated to influence the availability, plant uptake, and physiological function of manganese in the plant's defense against fungal invasion and pathogenesis. Manganese, as well as other nutrients that influence take-all, appears to exert its greatest influence on the plant's resistance by delaying disease development and restricting lesion size. Manganese also

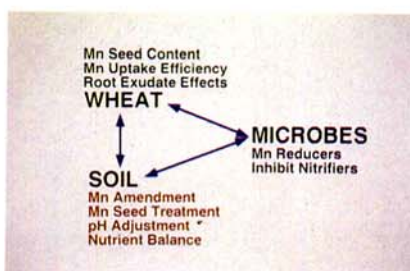


Fig. 12. Approaches to improving the control of take-all by increasing the uptake or availability of manganese.



increases root growth and influences ammonium metabolism to effect a means of disease escape complementary to resistance. Thus, biological control of take-all may be accomplished through increasing manganese availability and uptake by the plant or by inhibiting manganese oxidation to block virulence of the pathogen. Cultural conditions that increase manganese availability may enhance or induce disease control through their effect on the biological component of the soil environment that conditions manganese availability or the manganese oxidation activity of the pathogen. The pathogen may modify the availability of manganese in a localized area of the root or in the more general infection court to induce susceptibility by overcoming the plant's normal defense reactions. Normally resistant species of cereals, i.e., oats, become susceptible to take-all in soils that are very low in manganese probably because of the requirement of this essential element in their defense mechanisms. Through its effect on manganese availability, the biotic environment interacts with the plant, pathogen, and physical environment to exert a dynamic influence on take-all. Take-all can be effectively controlled by compounding the unfavorable components for the disease, although several components individually can have a profound effect.

Similar interactions of the favorable and unfavorable components of such diseases as *Phymatotrichum* root rot, *Verticillium* wilt, and *Streptomyces* scab indicate a central involvement of manganese for which take-all of cereals may be a model (14,29,32). Specific mineral elements may interact similarly with other diseases, e.g., zinc with diseases on beans and wheat caused by *Rhizoctonia* and *Fusarium* spp. (12,14,23), silicon with *Pyricularia* blast and *Rhizoctonia* brown spot of rice (10), and numerous

other diseases influenced by nutrient interactions and conditions (14,24). The central role of many minerals in disease response can be anticipated, since the nutrition of a plant determines in large measure its histological or morphological structure and properties, the function of tissues to hasten or slow pathogenesis, and pathogen virulence and ability to survive. Mineral elements are directly involved in all mechanisms of defense as integral components of cells, substrates, enzymes, and electron carriers or as activators, inhibitors, and regulators of metabolism. It is doubtful that a completely satisfactory understanding of most host-parasite interactions will be reached until associated nutrient relationships are elucidated. The effective manipulation of nutrient interactions relative to the plant, pathogen, and environment could provide a powerful approach to management of many plant diseases.

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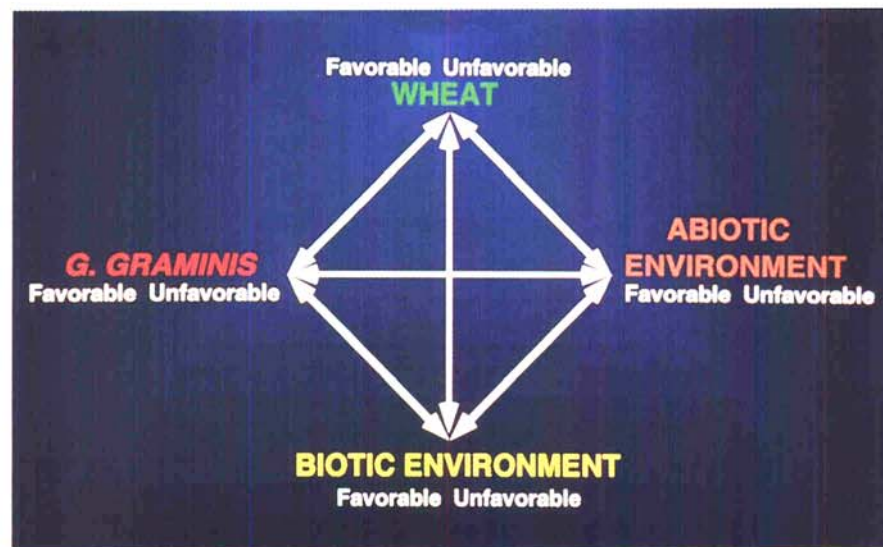


Fig. 13. Interactions of favorable and unfavorable components determining take-all severity, plant resistance, or disease escape.



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