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Title: Biological Assessment of Soils for Potential Development of Take-all Root Rot

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Take-all root rot (Gaeumannomyces graminis var.tritici) is a major disease of wheat (Triticum aestivum) in western Oregon. Control of take-all is dependent on management practices such as crop rotation and soil fertility-plant nutrition relationships. The objective of this study was to develop a bioassay that could measure the influences of crop sequence, lime and sewage sludge applications on soil suppression of take-all. Soil was collected from six experimental field plots exhibiting different management and disease histories. Seedlings were grown in inoculated soil in a growth chamber and disease severity assessed at 35, 65, and 90 days after sowing.

Inoculum efficiency and relative infection rates were determined using epidemiological techniques. Inoculum efficiency was greatest in lime and sludge amended treatments, moderate in nonlimed sludge amended treatments, and least in samples that received neither lime nor sludge. Relative infection rates of G. graminis followed a similiar trend. Second year wheat after oats was more suppressive to take-all than fifth year wheat, especially on lime-amended soils.

Field observations of disease progress were made in the same plots where soil had been collected for the growth chamber bioassay. Final disease readings and relative infection rates were greatest for the limed sludge amended treatments. Final disease readings and

relative infection rates were moderate for unlimed treatments with no sewage sludge present. The lowest disease levels and infection rates were exhibited by the unlimed plots with a history of sewage sludge.

In contrast to the results of the bioassay, fifth year wheat field plots overall had less severe disease than did the second year plots. The presence of sewage sludge in the unlimed field plots appeared to have an ameliorating effect on suppression of take-all, particularly in second year wheat.

BIOLOGICAL ASSESSMENT OF SOILS FOR POTENTIAL DEVELOPMENT OF TAKE-ALL ROOT ROT

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This thesis is dedicated to my mother, Geraldine B. McGeehan.

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INTRODUCTION

Wheat is one of the highest value crops produced in Oregon. Total cash receipts from grain sales for 1979 were close to 180 million dollars. Since 1965, it has been estimated that hay and grain sales have increased more than 200 percent with grain accounting for approximately 70% of this increase (Miles and Grader, 1979). The quantity of wheat produced in Oregon increased by more than 50% between 1971 and 1979.

As the number of acres planted to wheat continued to rise, a concurrent increase in crop loss due to take-all root rot, Gaeumannomyces graminis var. tritici (Ggt) occurred. This rise in root disease may be partially attributed to the weather endemic to western Oregon. While the modified marine climate is quite good for winter wheat production, the mild winters and cool wet springs are also conducive to the take-all fungus. The number of acres of irrigated wheat east of the Cascades has also increased. This has increased wheat yields relative to nonirrigated production but at the same time increased the potential for take-all. Further, it has become economically attractive for growers to plant consecutive crops of wheat. Monocropping results in a build-up of infected roots and stubble during the second and third years of wheat. Thus, at least two factors are responsible for the increase in take-all in Oregon: (1) increased inoculum density and (2) a conducive environment allowing rapid growth of the pathogen.

Worldwide, take-all exhibits a "cosmopolitan distribution in temperate climates" (Asher and Shipton, 1981). The U.S., Europe, and Australia are among the major wheat producers and historically

have suffered the greatest take-all losses. However, significant losses have been reported in South America, Africa, the Soviet Union, The Netherlands, China, Japan, Korea, and New Zealand (Asher and Shipton, 1981).

Control of the take-all fungus is dependent on agronomic practices that create conditions favorable to the host and resident antagonists while at the same time disfavoring the pathogen. A combination of techniques offers the best means of control by integrating a specific technique to a specific phase of the pathogen's life cycle.

Postharvest management of residual fertility as well as tillage and cultural practices may facilitate decomposition of infected host fragments. This encourages competition between the pathogen and saprophytic microbiota and hastens the displacement of Ggt from organic debris, thus reducing inoculum density.

Establishing populations of beneficial microorganisms may induce host resistance, restrict colonization of Ggt, or increase antagonism toward Ggt during pathogenisis.

Proper plant nutrition maintains host vigor and decreases susceptibility to disease. Judicious selection of fertilizers and organic amendments as well as careful timing of application can create rhizosphere conditions unfavorable to Ggt.

Currently there are no varieties of wheat with specific resistance to take-all. However, obtaining plants with a horizontal resistance may offer some hope for improving tolerance to root damage. Possibilities include varieties of wheat tolerant to acid soils, varieties susceptible to cross protection by other fungi, or those varieties with root exudates that depress the chemotrophic response of Ggt hyphae.

Crop rotation and sequencing are the most widely practiced forms of take-all control. A single year of rotation to a nonsusceptible crop is generally sufficient to reduce the inoculum density to tolerable levels. Alternatively, wheat monocropped 4 to 5 seasons induces take-all decline; a biological suppression

that is thought to persist for the duration of the monoculture sequence.

Growers for many years have recognized differences in the incidence and severity of take-all root rot in different fields, suggesting the disease was encouraged in some cases and naturally controlled in others. It has been only in the last three decades however that the potential for biological control through suppressive soils has been appreciated.

Suppressive soils have been defined as those soils in which disease development is restricted or suppressed even though the pathogen is introduced in the presence of a susceptible host (Baker and Cook, 1974).

It is the responsibility of agronomists and plant pathologists to apply knowledge regarding soil suppression of Ggt toward the development of management practices that reduce the potential for crop losses due to take-all root rot.

The objectives of this investigation were (1) to develop a bioassay that could measure the effects of different soil management practices for potential suppression of take-all root rot, and (2) to evaluate the effect of sewage sludge on soil suppression of Ggt.

LITERATURE REVIEW

The objective of this literature review is to provide a synopsis of the current knowledge regarding edaphic, nutritional, microbial, and cultural effects on take-all root rot. It is not within the scope of this review to discuss all of these factors in great detail. The reader is referred to Butler (1961), Nilsson (1969), Walker (1975), and Asher and Shipton (1981) for more detailed information and complete summary.

As of 1975, more than 1000 papers had been published on aspects of Gaeumannomyces and cereal root rot (Walker, 1975). Considering that nine years have since past, it is likely that number of papers has greatly increased. The vast amount of work regarding take-all and its control indicate the importance of this pathogen to wheat production. The information base that subsequently evolved has not only increased our ability to control take-all but has also done much to increase our understanding of soil ecology, integrated pest management, and biological control principles.

This voluminous work has been conducted in various laboratories and fields around the world so it is not suprising that apparent inconsistencies and discrepancies exist in the literature. This is no doubt due in part to nonstandardized experimental conditions as well as interactions of the pathogen with different environmental and management practices.

It is difficult, if not impossible, to standardize the large number of variables and concurrent interactions that influence the take-all disease. For example, soil pH exerts an influence over the solubility, speciation, and uptake of mineral nutrients as well as the distribution and activity of the soil microflora. Alternatively, fertilizers, organic additions, and microbial metabolism can strongly influence soil pH. Thus take-all researchers must contend with soil exhibiting a continuous chemical and biological flux.

While it is instructive to examine singular effects of a given variable, one must be constantly aware of the interactive nature of all of the components contributing to the take-all pathosystem. The uncertainties surrounding take-all research are a reflection of the complexity of the task.

Gaeumannomyces graminis: The Pathogen

A complete summary of the taxonomy of the take-all fungi has been published by Walker (1975). Gaeumannomyces was originally described as Rhaphidophora graminis by Saccardo in 1875 and then transferred to the genus Ophiobolus in 1881. Arx and Olivier in 1952 established a new genus, Gaeumannomyces, creating the new taxonomic combination Gaeumannomyces graminis (Sacc.) Arx and Olivier. Walker in 1972 concluded there were three distinct varieties of G. graminis based on morphology and host specificity. Gaeumannomyces graminis var.tritici is the wheat take-all fungus while G. graminis var. avenae has longer ascospores and typically attacks oats as well as wheat. A third member of this genus, var. graminis is known to be a weak pathogen of rice and various other grasses (Walker, 1975).

The wheat take-all fungus exhibits two basic phases in its life cycle: an active parasitism of a Graminaceous host or, in the absence of a suitable host, Ggt survives as saprophytic mycelium in crop debris.

The infective inoculum units of Ggt in soil are most likely the colonized host debris and other organic fragments. Macrohyphae, growing from this inoculum to the roots of the wheat plant provide a more effective inoculum potential than single ascospores due to microbial competition within the rhizosphere (Weste, 1972).

Although Ggt is a relatively slow growing fungus, rapid ectotrophic growth of macrohyphae over the host's root surface may be

induced by root exudates and a favorable rhizosphere environment. The availability of soluble sugars, amino acids, and vitamins in the rhizosphere encourages the take-all fungus to colonize the surface of the roots and thus even a relatively low soil population of infective fragments can result in severe disease development (Walker, 1975).

Penetration normally occurs through root hairs and the epidermis of the meristematic zone. Brown and Hornby (1971) suggest that prior to infection, G. graminis may require an ephemeral feeding stage to build up cell mass, particularily if the inoculum was low in food reserves. A thin infection thread is produced by an appressorium-like structure and after penetration the thread swells to a full-sized hypha which travels through the root hair or epidermal cell into the cortex of the root. The cytoplasm of the invaded cell becomes granular, the nucleus disintegrates and ultimately cell plasmolysis and collapse occurs (Weste, 1972). From the initial penetration point, runner hyphae grow up and down the root surface producing fine microhyphae which penetrate at many new points.

As colonization continues, the fine hyaline hyphal strands fuse laterally forming a dense mass of dark brown mycelium. Tissue maceration proceeds the hyphae through the infected tissue, probably due to the action of proteolytic and pectolytic enzymes produced by the fungus (Gothoskar et al., 1959). The necrotic tissue develops into a lesion as both inter- and intracellular mycelium attacks new host cells. Two to four weeks after penetration, typical take-all symptoms begin to develop. Root and stem bases become blackened and leaves turn yellow-green and flaccid (Weste, 1972). Lignitubers may be produced as the invading hyphae induce a thickening of the teritiary layer of the cell wall (Fellows, 1928b). Penetration of the stele by infection and runner hyphae is accompanied by intense vascular discoloration. Hyphae growing within and between the xylem

elements cause disintegration of tissue and leads to dark masses of material clogging the xylem vessels.

The established parasite competes with the host for nutrients and other essential growth factors. This competition coupled with impaired uptake and transport of water and nutrients results in reduced plant performance. Grain heads may form prematurely leading to sterile kernals (whiteheads) and as a result yields are of lower quality and quantity.

Although perithecia are produced by parasitic Ggt if moisture is adequate, ascospores are thought to be of little importance for the spread of take-all over large areas in a wheat field. Spread between distantly located host plants is considered to take place by dissemination of infected plant residues by wind, water, and farm equipment. The primary means of spread between closely situated plants occur via the growth of runner (macro-) hyphae along the roots (Walker, 1975).

Edaphic Factors

During the 1940's, serious take-all in the Pacific Northwest was generally limited to the temperate wheat growing regions of western Oregon and Washinton. However, Cook et al. (1968) reported a drastic rise in crop loss due to take-all in the irrigated wheat soils of eastern Washington and Oregon as well as southern Idaho. Losses in Washington alone during 1967 appear to have been between one and two million bushels. Cook et al.(1968) attributed the dramatic increase in take-all east of the Cascade mountains to be associated with the rise in acres of wheat planted in these alkaline, coarse-textured soils being brought under irrigation and intense cereal monoculture.

The take-all fungus thrives in a soil that offers an abundant supply of available water. On solid media, growth of Ggt was maximal at -1.2 to -1.5 bars, reduced by half at -20 bars, and prevented at

water potential values below -50 bars (Cook et al., 1972). It has been reported that wheat tissues produced under nonirrigated conditions exhibit water potentials of -25 to -35 bars between the tillering and heading stages (Asher and Shipton, 1981). Water at these low potentials in unavailable for the growth of Ggt and this fact probably explains the absence of take-all in the dryland wheat producing areas. These host-pathogen water relations might also explain why the colonization of wheat by Ggt does not proceed into the upper plant tissues where increasingly more negative water potentials are encountered (Noble, 1974).

While Ggt grows optimally in pure culture at a temperature near 24°C (Cook and Christen, 1976), field epidemics of take-all are generally most severe in soils exhibiting a temperature between 10° and 15°C (Asher and Shipton, 1981). This phenomenon was explained by Henry (1932) as a differential effect of soil temperature on microbial antagonism toward Ggt. Henry reported that take-all was controlled at soil temperatures of 27°C but at lower temperatures (less than 20°C), disease severity was increased.

Temperature, moisture availability, and suppressive microorganisms no doubt play a role in the occurrence of severe take-all commonly observed when a mild winter is followed by an unusually cool, wet spring (Cook et al., 1972; Glynne, 1951; Jackson et al., 1982; Walker, 1975). Prevailing rain and cool temperatures during this part of pathogenisis maintain rhizosphere conditions that are highly favorable to Ggt and restrictive to the growth and metabolism of potentially suppressive microorganisms. This may become especially critical if other more controllable factors such as pH, position and size of inoculum, and nutrition are allowed to become conducive to the pathogen. A highly conducive rhizosphere environment during the crown root formation period may result in complete devastation of the effective root system and cause severe yield loss.

Cook and Christen (1976) found the response of Ggt to water potential to be affected by temperature and reported that as the temperatures of incubation are increased, Ggt requires progressively lower water potentials. At 20°C, maximal hyphal growth was found to occur at -1 to -2 bars whereas at a 30°C incubation, maximimum growth of Ggt occurred at a water potential of -10 bars. Thus it appears this fungus is able to maintain pathogeninsis, perhaps at a less vigorous rate, as the soil conditions change from cool and wet to warm and dry.

The influence of soil aeration on Ggt, like temperature and moisture is intricately linked to the total microbial activity of the soil. Since the take-all fungus appears dependent on wet soil conditions for maximum parasitic activivty, it must operate under conditions that limit gaseous exchange. Ggt has been reported to be unusually intolerant to increased concentrations of carbon dioxide (Garrett, 1936). However, Cook (in Asher and Shipton, 1981) states that Ggt may be no more sensitive than other pathogens to low O_2, high CO_2, ethylene or other volatiles but the effects of restricted gas exchange may simply be more evident with this fungus because of its dependence on wet soil.

Fellows (1928a) found that variations in O_2 and CO_2 concentrations are not great enough to restrict the growth of Ggt in arable soils, with the exception perhaps of waterlogged conditions. Later work by Garrett (1937) however suggests the growth of Ggt along roots grown in acidic poorly aerated soil was checked by the accumulation of respiratory carbon dioxide and that accelerated growth of the pathogen in alkaline soils is due to the lower ratio of carbon dioxide to bicarbonate ion. A further study of this was suggested by Garrett and conducted by Ferraz in 1973. Ferraz's work indicates that the effect of soil pH on the growth of Ggt is unrelated to its effect on the equilibrium between undissociated carbon dioxide and the bicarbonate ion. Rather, the relationship

between adequate aeration and increased growth of Ggt is most simply explained by an improvement in oxygen availability at the root surface (Ferraz, 1973).

Conditions that favor accumulation of respiratory CO_2 and consequently HCO_3^- also favor production and accumulation of ethylene. This gas has been shown to be inhibitory in some cases to Ggt in poorly aerated soils (Cook and Rovira, 1976; Smith, 1975).

Several reports of severe take-all epidemics in loose, light textured soils may be found in the literature (Garrett, 1936; Griffiths, 1933; Nilsson, 1969). Nilsson offers two explanations for the increased parasitic activity observed: facilitated hyphal spread and/or retarded host development. The ectotrophic infection habit of Ggt leaves this fungus vunerable to the inhibitory effects of gases present in the rhizosphere. These effects are minimal in well aerated, light textured soils thereby favoring the rapid spread of the colonizing hyphae of Ggt. Secondly, sandy soils are typically less fertile and have a lower water holding capacity than a heavier textured soil. Low fertility can increase the susceptibility of a seedling to root attack and make it more difficult for the plant to compensate for a reduced water supply. Additionally, Garrett (1936) notes the poorer growth of Ggt along roots in heavier textured soils may be attributed to higher organic matter contents and an increase in the general supppression of Ggt.

In general, a proportional increase in take-all severity is observed as the soil pH is increased (Garrett, 1934; 1936, 1937; Huber and Watson, 1974; Trolldenier, 1981). For this reason, liming a moderately acid soil where Ggt is present may result in a decrease in grain yield, assuming all other factors to be equal.

Garrett (1934, 1936, 1937) has found that Ggt is markedly susceptible to soil pH and its hyphal extension rate increases in a regular manner with the transition from acid to alkaline soil reaction. A reduction in take-all was observed by Smiley and Cook

(1973) when the predominant form of nitrogen is NH_4-N. The control of take-all was correlated with a fall in rhizosphere pH but not with a change in the pH of the bulk soil. These authors report the ameliorating affects of NH_4-N on take-all can be cancelled by the addition of lime.

Although take-all is associated with alkaline soils, some severe infections have occurred in acid soils and Gerlagh (1968) reports Ggt to be capable of satisfactory growth over a wide pH range (3.2 to 9.6) in pure culture. The reduction of take-all after acidification of the soil is probably an indirect effect and may reflect a reduced rate of nitrification (Huber and Watson, 1974) or possibly increased numbers of microbial antagonists such as the fluorescent pseudomonads.

The only reports of liming reducing take-all have been when wheat was planted into very acid soils where nutrients were either severely deficient or unavailable, thus predisposing the host to disease. Taylor et al. (1983) found liming improved grain yield and reduced the percentage of tillers with whiteheads where soil pH and phosphorus were previously limiting. Conversely, a negative yield response to lime occurred when soil pH and P were previously adequate. Liming severely acid soils (pH < 5.2) presumably has a positive influence on host vigor through decreased manganese and aluminum toxicity and phosphorus availabilty. In a moderatey acid soil (pH 5.6 to 5.8), these elements are less limiting to the host and the addition of lime benefits the pathogen more than the host, resulting in a negative yield response due to increased take-all.

Garrett (1936) and Griffiths (1933) have described the take-all of wheat grown in the mallee soils of South Australia. The mallee soils are sandy textured and overlay limestone. Climate conditions during the growing season for wheat, while somewhat drier, are similiar to that of the Willamette Valley. Thus a cool, well-aerated, alkaline environment exists and of course severe

take-all epidemics are common. Cook (in Asher and Shipton, 1981) suggests the name "take-all" originated among the early wheat farmers in this area because the disease literally "took-all". This example is illustrative of the multiplicity of just four of the factors affecting take-all.

In the Willamette Valley, two of the four are usually present, cool moist soils, and yield losses due to take-all are generally no greater than 10%. However, in one experiment, wheat yields were reduced from 120 bu/ac in one year to 5 bu/ac for a specific treatment (unpublished data). Accounts of these devastating losses serve as a dramatic reminder of just how severe attacks by Ggt can be if a highly conducive combination of soil conditions exist.

Nutrition

A balanced plant nutrition is a main objective in the fertilization and management of wheat. It is apparent that any nutritional stress, especially during seedling and tillering stages of growth, predispose the wheat plant to take-all root rot. Nitrogen receives much attention due to its essential requirement for plant growth and its limited availability in soil. To maximize yields on intensively cropped soils, it has become standard practice to apply nitrogen fertilizers on an annual basis. With regard to plant disease management, it is important to realize that the effects of this macronutrient go beyond the direct nutritional requirements of the host. The influences of nitrogen are also manifested in the pathogen's food base as well as more subtle effects on soil organic matter and rhizosphere chemistry.

In the study of the take-all disease, several facets of the nitrogen cycle merit special consideration. These include the abundance and form of N available in the root zone as well as the affects of this available N on the activities of the soil microflora,

host resistance to Ggt attack, and influences on the life cycle of the parasite.

Some of the factors influencing the nitrogen cycle include soil moisture, temperature, pH, timing of fertilization, and carbohydrate availability. These factors are important because of their affects on leaching, plant uptake, and the microbial processes of immobilization, mineralization, nitrification, denitrification, and nitrogen fixation. These processes in turn may have a pronounced effect on take-all incidence and severity largely through the determination of the forms and abundance of nitrogen available to the host and pathogen.

When the availability of nitrogen is not limiting plant growth, the chemical species of nitrogen predominating in the soil rather than the total amount of nitrogen is of primary importance in controlling take-all (Hornby and Brown, 1977; Huber and Watson, 1974; Hornby and Goring, 1972; MacNish and Speijers, 1982; Smiley, 1978; Smiley and Cook, 1973). Conclusions arising from both laboratory and field observations indicate ammoniacal forms of nitrogen tend to reduce the severity of take-all while nitrate nitrogen increases infection by Ggt. This "form of N" hypothesis was originally advanced by Huber et al. (1968). An excellent review of nitrogen form and plant disease was published by Huber and Watson (1974).

Although many mechanisms have been proposed, none have completely explained the relationship between nitrogen form and take-all severity. None-the-less, a consistant pattern of reduced take-all following NH_4-N application has emerged. Less root damage, lower numbers of whiteheads, higher yields, and higher test weights have been attributed to use of ammonium fertilizers (Hornby and Brown, 1977; Huber et al., 1968; MacNish and Speijers, 1982; Taylor et al., 1983).

When attempting to ascertain the differential effects of ammonium and nitrate nitrogen on take-all, it is important to

consider the effects of the nitrogen on both the host and pathogen. Huber et al. (1968) observed an increase in activity of Ggt but reduced disease severity when wheat plants were exposed to increasing levels of NH_4-N. They hypothesized that reductions in take-all associated with ammonium fertilization may be due to increased host resistance rather than decreased pathogenicity of Ggt.

Further evidence that N-form modifies host resistance arises from the observation that reduced infection and smaller lesions occur with NH_4-N treatments (Hornby and Goring, 1972; Smiley and Cook, 1973). Nitrate nitrogen, while increasing host growth and vigor is also thought to stimulate the pathogenicity of Ggt (Huber et al. 1968). Garrett (1948) concluded the individual effect of nitrogen was twofold: N may increase the intrinsic susceptibility in individual roots while concurrently promoting disease escape by stimulating production of new crown roots.

It should be noted that depending on the pH of the medium, NH_4-N can be toxic to plants when equilibrium conditions favor ammonia (NH_3) formation. NH_3 particularily affects root growth where nitrification is restricted (Mengle and Kirkby, 1982). In a comparison of forms of N, Hornby and Goring (1972) found that take-all was most severe when plants were supplied with NH_4-N only, intermediate with NO_3 alone, and least with a mixture of both forms of N. They further report that the maximum resistance to take-all occurred with an optimum ratio (2:1) of NO_3-N and NH_4-N.

Much of the ameliorating affects of NH_4-N on control of take-all may be attributed to acidifying effects and the resultant drop in rhizosphere pH (pH_r) (Smiley, 1974; Smiley and Cook, 1973).

The so-called physiological acidity of alkalinity or a salt depends on which ion of the salt, the cation or the anion is most rapidly absorbed by the plant (Moore, 1974). For instance, $(NH_4)_2SO_4$ is considered physiologically acid and results in H^+ efflux from the roots. Depending on the rate of release of

protons and assuming the solution immediately adjacent to the root is relatively static, substantial changes in pH_r may result from the electrochemical balance maintained during the absorption of fertilizer salts by roots, many times with little change in bulk pH (pH_b). NH_4-N salts further contribute to soil acidity as they are oxidized via the nitrification process.

In greenhouse experiments, Smiley and Cook (1973) obtained a difference in pH_r of 1.5 units when a Puyallup fine sandy loam (initial pH 5.5) was fertilized with either an ammoniacal or nitrate fertilizer. The severity of take-all was lowest with an ammonium sulfate treatment, but this control was negated when the soil was limed to pH 7.7. Disease ratings were highly correlated with pH_r values and only moderately correlated with bulk pH pH_b.

In an effort to explain the effect of pH_r changes on take-all severity, Smiley and Cook (1973) have proposed a binary mechanism. The effect of pH_r induced by form of N is direct at pH_r values less than 5.0. At these pH_r values, decreased pathogenisis and inoculum potential was observed. At a pH_r greater than 5.0, Smiley and Cook conclude the effect is indirect, possibly through stimulation of soil microorganisms antagonistic to the ectotrophic growth of Ggt.

Smiley (1974) reports the magnitude of change in pH_r was often more highly correlated with disease severity than either the initial or final pH. Further, the controlling influence of NH_4-N was eliminated by methyl bromide fumigation and reintroduced by additions of 1% nonsterile soil (Smiley, 1978). This indicates suppression of disease by manipulation of N-forms may be linked to changes in the composition of the rhizosphere microflora.

The timing of fertilization may also be critical for take-all management through effects on form, availability, and abundance of nitrogen in the root zone. Split nitrogen applications are common in western Oregon due to the mild wet winters. A portion of the

nitrogen is banded at planting to overcome early nitrogen deficiencies created by low residual levels or immobilization caused by straw decomposition. The majority of annual N is applied during the spring, thus avoiding winter losses and problems due to nitrification and subsequent denitrification.

Inhibition or reduction of nitrification maintains a high NH_4/NO_3 ratio and can facilitate a reduction in take-all root rot. This may be particularly true of fall applied nitrogen. Huber and Watson (1974) report nitrogen that was rapidly nitrified increased take-all of irrigated spring wheat. Spratt and Gasser (1970) report wheat seedlings may exhibit more vigorous root growth when supplied with NH_4-N (67). Increased host resistance and reduced pathogenicity and survival of Ggt have been associated with reduced nitrification (Huber and Watson, 1974). The benifit of a high NH_4/NO_3 ratio on pH_r and microbial antagonism has been discussed by Smiley (1974, 1978).

Smiley and Cook (1973) and Huber et al. (1980) found fall application of N-Serve (2-chloro-6-(trichloromethyl)-pyridine) markedly reduced the severity of take-all by maintaining N in the cationic form throughout the winter. It was reported the decrease in severity of take-all resulted from the increased availability of N in the root zone as well as maintenance of a high NH_4/NO_3 ratio, thus promoting host vigor and conditions suppressive to the pathogen.

Several researchers have reported a positive response to phosphorus (Garrett, 1941; Huber and Watson, 1974; Riley and Barber, 1971; Slope and Gutteridge, 1978; Taylor et al., 1983). The beneficial effects of P probably result from stimulated seminal root growth and development. Several interactions between nitrogen and phosphorus have been reported. The effectiveness of phosphorus application on reducing take-all was reduced when nitrogen was limiting plant growth (Asher and Shipton, 1981). Form of nitrogen may play a role in phosphorus uptake. Riley and Barber (1971) found

increased phosphorus solubility and plant uptake occurred following a decrease in pH_r. In this respect, an increase in P concentration in leaf tissue followed NH_4-N fertilization. Banding phosphate with ammoniacal fertilizers at planting would also be beneficial for take-all control. The acidifying effects of banded ammonium fertilizers are well known (Miller, 1974; Mengle and Kirkby, 1982) and the increased availability of soil and fertilizer P undoubtedly have a positive result on host vigor.

Chloride fertilizers have been shown to have an influence on take-all severity of winter wheat. Taylor et al. (1983) found that while chloride significantly enhanced the yield of wheat grown on take-all infested soil, this capacity of Cl^- to suppress Ggt was influenced by planting date, phosphorus, and nitrogen form.

Reduced plant water potential and take-all severity have been reported by Christensen et al. (1981) who found the susceptibility of wheat roots to Ggt colonization was decreased by lowering the water potential of the plant with chloride applications.

Halsey (1981) isolated greater numbers of fluorescent pseudomonads antagonistic to Ggt from the rhizosphere of wheat grown in soil infested with take-all and amended with NH_4Cl.

The benificial effects of chloride on take-all suppression may also be linked to this ion's affect on nitrification (Golden et al., 1981; Hahn et al., 1942). Inhibition of nitrification has been achieved in the field through proper use of nitrogenous fertilizers and commercial potassium chloride (Hahn et al., 1942).

The effects of Cl^- on increased host resistance, decreased nitrification and enhanced microbial antagonism indicate the necessity for further study of the role of chloride in take-all control techniques

Response to several other essential nutritients has been reported. However, few references identify a direct role of these nutrients relative to take-all. It appears that any nutrient

deficiency or toxicity, if sufficiently severe is likely to predispose the host to take-all and intensify the loss in yield through increased disease.

Microbial Effects

Control of take-all with disease suppressive soils usually involves at least one of three microbial mechanisms: cross protection or induced resistance, direct antagonism, and competition during the saprophytic stage of the pathogen.

The role of avirulent or weakly pathogenic fungi is well documented in the literature (Deacon, 1976; Mangan, 1967; Slope et al., 1979; Walker, 1975; Wong and Southwell, 1979). Philophora radicola var. graminis (PRG) and Gaeumannomyces graminis var. graminis (GGG) may be described as aggressive parasites but mild pathogens of wheat. Both assume an ectotrophic infection habit similiar to Gaeumannomyces graminis var.tritici. These fungi colonize the root cortex but unlike Ggt, this colonization causes no vascular discoloration, no check to plant growth and no reduction in yield (Balis, 1970; Wong and Southwell, 1979).

The effects of PRG and GGG appear to be indirect as no adverse effects of these fungi on the hyphae of Ggt have been reported. Deacon (1976) hypothesizes that control of Ggt by PRG and GGG is probably the result of interactions between fungi at the root surface which might involve a competition for infection sites as well as a modification of the rhizosphere microflora. Since these fungi utilize similiar infection processes, it is probable that initial infection by PRG or GGG also induces some form of host resistance to attack by Ggt, perhaps as the production of lignitubers. This mechanism of course relies on the avirulent fungi colonizing the wheat root prior to Ggt. Introduction of PRG and GGG must occur through use of selective crop sequencing or through direct inoculation.

Prospects for the biological control of take-all using PRG and related fungi seem best when wheat follows a grass crop, provided sufficient weed control is practiced (Balis, 1970; Deacon, 1976; Slope et al., 1979; Wong and Southwell, 1979). An examination of the grass-ley cropping system common to British agriculture supports this hypothesis. Deacon (1976) found that populations of Ggt were low in grassland and at high levels in second year wheat and subsequent crops with no grass ley. But when cereals followed grasses and were therefore exposed to high residual populations of PRG, the level of take-all attack was correspondingly reduced. In these same experiments, PRG was found to be virtually absent from soils with a pH less than 4.5 whereas Ggt managed to maintain a low resident population. When these very acid soils were limed, Ggt grew unimpeded by PRG while the vigor of the latter fungus was slowly restored. Deacon (1976) attributes some of the serious epidemics of take-all associated with liming to be a result of this phenomenon.

Similiar results are reported by Slope et al. (1979). These researchers found that serious take-all developed sooner in wheat grown after a lucerne ley than after a grass-clover ley. Microscopic examination of the wheat roots showed PRG to be more common in the grass-clover ley than in the lucerne ley.

While high levels of PRG present on grasslands can be maintained an several successive crops of wheat, low levels of PRG cannot be increased under wheat (Deacon, 1976).

Balis (1970) and Wong and Southwell (1979) concluded that effective use of PRG for the control of take-all will be achieved only if the pathogen population is low and that of the control agent is high. Thus, this form of take-all suppression may be best employed at the beginning of a wheat monoculture, after a grass break crop. It is possible that inoculation of wheat with PRG and hypovirulent strains of GGG and Ggt could be used to reduce the severity of take-all in the second and third years of monoculture,

allowing growers to maintain reasonable yields until the onset of take-all decline.

Similiar to the effective control of Ggt with avirulent fungi is the role of mycorrhizal fungi. Schenck and Kellem (1978) list four methods by which ectomycorrhizae might afford protection to plant roots: utilizing surplus carbohydrates, producing antibiotics, favoring beneficial rhizosphere microorganisms, and providing a physical barrier in the form of a hyphal mantle. In addition, improved water uptake and phosphorus nutrition are common benefits of mycorrhizal infections. Take-all is exacerbated by deficiency of phosphorus and inoculation of wheat roots with vesicular- arbuscular mycorrhizae (VAM) has been reported to be suppressive to Ggt in P-deficient soils (Cook and Baker, 1983; Graham and Menge, 1981). As with PRG, protection of wheat through use of ectomycorrhizae and VAM fungi appears to operate best at low levels of Ggt inoculum.

In 1943, Ludwig and Henry (1943) identified Trichoderma viride as a specific antagonist to Ggt in steilized recontaminated soil. In 1968, Gerlagh reported Gliocladium spp. as an organism resopnsible for the decline of G. graminis in the newly reclaimed polders in the Netherlands. Cook and Baker (1983) suggest that much of the early literature attributing take-all control to Trichoderma viride is misleading due to the fact that this fungus was probably incorrectly identified. Thus the control of take-all through production of gliotoxins observed by Ludwig and Henry was probably a result of the same organism reported and correctly identified by Gerlagh as Gliocladium. To add to the confusion in the literature, there are reports of Trichoderma spp. controlling soilborne pathoginic fungi through hyperparasitism. Pythium oligandrum has also been reported by Cook and Baker (1983) to be moderately parasitic to Ggt hyphae.

Many reports of bacteria causing suppression of take-all may be found in the literature. Streptomyces lavendulae has been shown

to cause lysis of Ggt haphae (Cook and Baker, 1983) and Campbell and Faull (1979) found an isolate of Bacillus mycoides caused similiar haphal destruction in a take-all decline soil.

Most researchers support the hypothesis that fluorescent pseudomonads are involved in the specific suppression of Ggt (Cook and Rovira (1976: Sands and Rovira, 1971b; Smiley, 1979; Stanek, 1979). Pseudomonads are common inhabitants of the rhizosphere and rhizoplane of wheat, they are 100 to 1000-fold more numerous on lesioned than on healthy roots, and a large proportion of fluorescent pseudomonads tested were antagonistic on agar to Ggt (Cook and Rovira, 1976). Sands and Rovira (1971a) report that while these bacteria are distributed unevenly through field soils, the highest number of fluorescent pseudomonads occured on partially decomposed wheat straw in contact with wet soil. Further work by Sands and Rovira (1971b) showed Pseudomonas fluorescens Biotype G to be the dominant pseudomonad in the rhizosphere of eleven out of fifteen soils surveyed.

Smiley (1979) reports that not all strains of Pseudomonas fluorescens are antagonistic toward Ggt; the highest proportion of antagonistic pseudomonads occurred on the rhizoplanes of infected roots growing in soils which have supported long-term wheat monoculture. Apparent numbers of pseudomonads on wheat rhizoplanes and numbers that were antagonistic to Ggt did not differ when wheat was supplied with NH_4-N or NO_3-N. However, Smiley (1979) reports more intense antagonism was expressed by colonies selected from soils treated with NH_4-N than with NO_3-N and from isolation media prepared at pH 5.5 rather than at 7.0. These results suggest that different environmental conditions caused by nitrogen form and pH may cause a reditribution to occur among the dominant strains of fluorescent pseudomonads colonizing wheat rhizoplanes. Findings such as these along with the observation of high numbers of antagonistic pseudomonads in long-term wheat soils indicate careful crop

sequencing and soil amending practices may encourage populations of soil bacteria that suppress the activity of the take-all fungus.

Two other forms of antagonism are commonly referred to in the literature. Villyrampid amoeba have been found to cause perforation and destruction of the pigmented hyphae formed by Ggt in its parasitic and saprophytic growth stages (Homma et al., 1979; Chakraborty, 1983). However, Cook and Homma (1979) found that amoeba activity was too slow and their water potential requirements too restrictive to be of significant value for take-all suppression. Virus-like particles have also been reported to infect Ggt hyphae and reduce pathogenicity but their role in the control of take-all is generally assumed to be quite limited (Cook and Baker, 1983).

The competitive saprophytic ability and thus the survival of Ggt in soil is largely a function of the chemical and microbial environment existing in the soil after the wheat grain is harvested. The take-all fungus has been shown to exhibit excellent saprophytic longevity in some cases. MacNish and Dodman (1973) report 82% of the field sites sampled had viable Ggt on buried stubble after 50 weeks. Likewise, Shipton (1972) found Ggt survived in soil under nonsusceptible break crops for up to 66 months and that the fungus seemed to have survived in stubble rather than on the roots of weeds or self-sown cereals. Gerlagh (1968) found the competitve saprophytic ability of Ggt to increase at temperatures less than 10°C and Walker (1975) reports strongly pathogenic isolates survive better than weaker ones.

Although the effects of C:N ratios and available N on the survival of Ggt are complex and the literature often confusing, the majority of research indicates the saprophytic survival of Ggt in buried wheat straw is favored by high soil nitrogen levels (Garret, 1972; Garrett and Buddin, 1947; Walker, 1975). Garrett (1972) suggests this response is due to the low cellulolysis rate of the take-all fungus. His research indicates Ggt exhibits a low ability

to produce new cellulolysing hyphae in a high C:N environment. This inability to colonize low nitrogen substrates such as wheat straw can be compensated by external sources of nitrogen thus allowing Ggt to survive saprophytically by a continuous slow rejuvination of mycelium.

When Ggt is forced to survive outside of the specialized niche to which it is adapted, that is a live wheat root, the fungus becomes more vunerable to attack by the nonspecialized soil saprophytes. Manipulation of soil nitrogen levels can create conditions that tip the balance in favor of the soil saprophyted and lead to decreased survival of Ggt inoculum form one season to the next. To be of practical value to crop production though, it is essential that sufficient nitrogen be present during the growing season to maintain high yields.

A decrease in the availability of nitrogen during the saprophytic phase of the life cycle of Ggt is one of the benifits of a system developed by F.P. Chamberlain to control take-all under intensive barley production (Cook and Baker, 1983). The Chamberlain system involves sowing barley together with trefoil (Medicago lupulina) and Italian ryegrass (Lolium multifolium). Harvesting the barley crop releases the trefoil and ryegrass causing rapid growth and depletion of much of the available nitrogen in the topsoil containing the barley residue infested with Ggt. Garrett and Buddin (1947) concluded the benifits of this system are two-fold: first, the nitrogen levels are high during growth of the barley crop allowing for disease escape through increased root production. Second, available nitrogen is low between barley crops when the pathogen needs the external nitrogen to survive in the crop residue.

It should be stressed that not all authors are in agreement regarding the effects of soil nitrogen levels on the longevity of saprophytic Ggt mycelium. Cook and Baker (1983) suggest crop residues with a low C:N ratio theoretically will result in more

intense microbial activity and hence probably more antagonisms among the associated microflora. They suggest pathogens successful as inhabitants of crop residue are mainly those that colonize high C:N substrates such as wood or cereal straws.

The size of the crop debris should also be considered as it serves as the primary inoculum source for take-all infections. Ggt has been shown to be more infectious if it has maintained itself in fragments of wheat crown and basal stem rather than in root fragments (Cook and Baker, 1983). In field experiments involving wheat grown after red colver, Scott (1969) found that early rotovation of wheat stubble greatly reduced the incidence of whiteheads and infected tillers in the second and third crops of wheat. He suggests that the exposure of the infected straw to the activities of the soil microflors for three months between wheat crops shortened the survival of Ggt, and that this effect was more prounounced under the conditions of good aeration and competition for nitrogen in the rotovated treatments.

Displacement of soilborne pathogens from crop residue appears to be influenced by manipulation of the C:N ratio, debris size and edaphic factors such as temperature, moisture, and aeration. Studies identifying methods that encourage the microbial and chemical decomposition of wheat stubble will likely add to the list of management factors offering hope for take-all control.

The potential for anaerobes to induce biological control of soilborne plant diseases also requires further exploration. Survival for most soilborne propagules of plant pathogens is poorest in flooded or warm wet soil, especially if organic materials are also added (Cook and Baker, 1983). Anaerobic microsites are known to exist in virtually all agricultural soils, occuring at the centers of clay peds as well as in the rhizospheres of various crop plants (Smith, 1975).

Decomposition of carbohydrate-rich root exudates by anaerobic microorganisms occupying these microsites results in the production of a sequence of gaseous products including ethylene. Cook and Rovira (1976) and Smith (1975) suggest that ethylene produced by anaerobic soil bacteria may be suppressive to certain aerobic organisms, particularily fungi. Cook and Rovira (1976) found ethylene at concentrations below 5 ug/g in the soil atmosphere were suppressive to Ggt in its parasitic stage. These authers further suggest that ethylene may play a role in the "general suppression" of take-all. Gerlagh (1968) has described general suppression as a property of all soils, present in varying degrees, that is nontransferable, resistant to 80^{o}C moist heat for thirty minutes, and resistant to methyl bromide fumigation.

The fact the additions of certain organic amendments, minimum tillage, inhibition of nitrification, or warm soil temperatures are known to increase ethylene production (Cook and Rovira, 1976; Smith, 1975) indicate the need for further research regarding the role of anaerobic bacteria and ethylene in the biological control of take-all root rot.

Cultural Practices and Take-all Decline

The rate of growth of the fungus along the root system is one of the primary factors determining the extent of colonization and subsequent severity of take-all. If Ggt manages to establish itself around the crown, new roots may be infected and destroyed almost at their inception.

Position of inoculum in the root zone and point of attack on the root system is instrumental in determining the amount of root surface area affected by Ggt (Garrett, 1948). Fellows and Ficke (1934) found attack was only fatal when the inoculum penetrated at a position

three inches or less below the seed. Age of the wheat roots at the penetration point may also be a factor. Deacon and Henry (1980) found wheat roots were more extensively diseased when the growing tips were inoculated on regions 5 days old rather than 15 days. This appears to be related to the necrotrophic colonization habit of Ggt; that is as the root ages and its cortex cells begin to die, the inoculum potential of the parasite is enhanced through reduced cortical resistance (Deacon and Henry, 1980).

Related to these findings, Taylor et al. (1983) and Prew et al. (1983) report grain yields were significantly influenced by seeding date, early seeded tratments displaying a higher incidence and severity of take-all than late-seeded wheat. Late seeding might also reduce severity by simply reducing the period of contact between the active parasite and wheat roots as well as extending the period during which the fungus must survive saprophytically in the soil. In addition, lower temperatures associated with late seeding (8-16^{o}C) favor development of a more vigorous host plant which can better tolerate infection (Glynne, 1951; Glynne and Slope, 1959). There is evidence that certain types of tillage practices may facilitate spread of Ggt in soil. Prew (1980a) found that the autonomous spread of Ggt from a discreet line source of inoculum consisting of naturally infected stubble and roots averaged a distance of 10 cm. However, with the aid of cultivations (plowed, harrowed, or disc drilled) spread in a first year wheat crop frequently occurred to a distance ranging from 9 cm to 25 cm. However, the following crop (second year wheat) was uniformly infected, probably as a result of a rapid build-up of background inoculum in the first crop so that any affect of cultivation appeared to be masked (Prew, 1980b).

Comparisons of no-till or minimum tillage versus conventional plowing have been made (Brooks and Dawson, 1968; Prew, 1981). Prew (1981) found greater proportions of roots were infected in a zone 12 to 22 cm below the soil surface with plowing than with direct

drilling. Brooks and Dawson (1968) also reported winter wheat drilled into stubble without seedbed preparation was found to be less severely attacked be Ggt and this reduction was assumed to be associated with a limited rate of spread in the undisturbed soil. It should be noted that at the first field sampling (February), the plots without seedbed preparation had a higher percentage of infected plants than did the plowed plots, probably due to more immediate contact with inoculum in the undisturbed stubble. However, a sampling in May showed a drastic increase in disease severity in the plowed treatments with only a slight increase in the direct drilled plots. This is in agreement with the findings of Slope and Cox (1965) that up until April, take-all develops slowly but from then on in a soil conducive to disease development, spread is very rapid. Apparently the factors reducing the spread of the fungus, poor aeration being one possibility, were missing or inoperative in the plowed treatments. No till and minimum tillage practices could have different effects under different moisture and temperature conditions. In the Willamette Valley for instance, where moisture and temperature are rarely a problem, no till may increase take-all losses due to seeding into infested stubble. Also, nondisturbance of the soil favors the development of perennial grasses than may act as carriers of Ggt (Yarham, 1981) Conversely, no-till planting of winter wheat has reduced take-all in some cases by minimizing late season moisture stress and decreasing hyphal spread in the root zone due to aeration effects. Additionally, no-till practices may result in increased microbial antagonism to Ggt (Yarham, 1981)

Control of take-all with crop rotation depends largely on whether the preceeding crop is a host or nonhost to Ggt. This will influence the survival of the take-all fungus as well as the density of Ggt inoculum available for infection of the next wheat crop. Other factors that play a role in the effects of crop rotation on Ggt

include residual fertility, the soil microflora, weeds, residue management, and duration of wheat monoculture.

In short-term rotations lucerne, subclover, alfalfa, and soybeans have been reported to increase take-all in a suceeding wheat crop (Butler, 1959; Cook, 1981; Huber and Watson, 1974; Louw, 1957a, 1957b). It is presumed that these crops tend to create soil conditions conducive to Ggt by maintaining high nitrogen levels and enhancing nitrification as well as increasing the saprophytic survival of Ggt. Also, soils are generally limed when these crops are produced and the higher soil pH values favor both nitrification and the take-all fungus.

Barley has also been implicated as a crop that may create more conducive conditions for severe take-all. Though not seriously damaged by Ggt, barley serves as an host for maintenence of the pathogen. This can result in more disease when a susceptible host such as wheat is sown into soil containing barley residue (Gerlagh, 1968). Weeds too have been implicated as reservior hosts and severe take-all has been associated with fields exhibiting poor weed control. Species from the following genera have been identified as carriers of the take-all fungus: Agropyron, Agrostis, Bromus, Dactylus, Elymus, Festuca, Holcus, and Hordeum. The subject of wild and cultivated grasses acting as carriers of Ggt is covered quite well by Brooks (1965) and an extensive review of Graminaceous hosts is supplied by Nilsson (1969).

Wheat following oats or field beans usually supports lower levels of take-all than wheat following first year wheat (Cook, 1981; Slope and Etheridge, 1971). These crops are not susceptible to Ggt and therefore can be used to decrease the inoculum density of the fungus. Slope and Etheridge (1971) however cite possible limitations of using short-term break crops to control take-all. While first year wheat following oats was generally disease-free, take-all was more prevalent in the second and third successive wheat crops than in

the second or third years of continuous wheat. These researchers concluded that the use of short break crops to control take-all may be of limited value to farmers wishing to grow mostly wheat due to the interuption of take-all decline.

Take-all decline (TAD) was first described by Slope and Cox in a Rothamstead Experiment Station report in 1963 as a "unique example of naturally imposed biocontrol" (Hornby, 1979). Hornby has defined take-all decline as "the depression of disease that often occurs after a peak of take-all in wheat or barley monoculture" (Hornby, 1979). Henry (1932) observed that unsterilized soil protected wheat against added Ggt inoculum and that the effect was lost by sterilization. However, the first conclusive evidence that the suppressiveness in TAD was microbial in nature came from the work of Gerlagh (1968). Gerlagh was able to increase Ggt suppression in soil by growing four successive crops of wheat per year under greenhouse conditions. He also showed the antagonists in the suppressive soil were destroyed by steam sterilzation. Since 1968, take-all decline has been well documented as a biological phenomenon associated with continuous cereal cropping (Brown et al., 1973; Hornby, 1979; Shipton, 1972; Shipton et al., 1973; Walker, 1975; Zogg and Jaggi, 1974).

Hornby (1979) has summarized the findings of the research cited above as evidence for microbial antagonism being the primary mechanism of TAD. Antagonism in the field is reduced by discontinuing cereal cropping and antagonism in greenhouse trials is reduced by discontinuing the addition of the living pathogen in the presence of the living host. Chemical sterilization eliminates the antagonism, as does 60^{o}C steam for 30 minutes indicating asporogenous bacteria as likely candidates. This antagonism can be transferred to nonsuppressive soil and can also be diluted logarithmically with a corresponding decrease in suppressive charecter.

When considering the vast amount of information and reproducible experiments concerning TAD, it should be noted that there is still much debate as to the mechanisms inducing this phenomenon as well as the specific organisms and soil conditions involved.

Many researchers feel that the suppression of Ggt associated with TAD is at least partially mediated by a balanced community of microbial antagonists. Brown (1981) writes that due to the wide range of environments in which TAD has been observed, it is unlikely that a single group of organisms is soley responsible. Bacteria, especially fluorescent pseudomonads as well as actinomycetes antagonistic to Ggt have been found in greater abundance in TAD soils than in non-decline soils (Brown, 1981; Cook and Baker, 1983; Cook and Rovira, 1976; Zogg and Jaggi, 1974). Species of Phialophora fungi are generally discounted from being involved in TAD since they are normally present in low numbers during cereal monoculture (Deacon, 1976; Slope and Gutteridge, 1978).

Pope and Jackson (1973) and Brown et al. (1973) do not believe that specific microbial antagonism can fully expain take-all decline. Pope and Jackson (1973) report a less sensitive chemotropic response of hyphae to wheat seedling roots in decline soils. Since Ggt hyphae respond to substances exuded by wheat roots as well as microbial metabolites, any changes in the quality or quantity of these chemicals will alter hyphal responses.

Brown et al. (1973) report TAD results from an intricate relationship between soil microorganisms and rhizosphere nutrition. These researchers feel that the balance of soil microflora changes in response to disease progress during cereal monoculture. An increase in pathogen density in the root zone induces a qualitative change in the rhizosphere microflora and nutrient status. In response to altered nutrient availability, the microflora adjust qualitatively and quantitatively and by competition and antagonism restrict

subsequent disease development. In the words of Brown et al., cereal monocropping is a means of "presenting the take-all fungus to an increasingly inimical environment."

MATERIALS AND METHODS

Growth Chamber Bioassay

The objective of this investigation was to develop a bioassay that could measure the influence of soil management practices on development of Ggt on inoculated wheat seedlings. Additionally, the effects of sewage sludge applications on Ggt pathogenisis were evaluated.

Experimental plots of winter wheat (Triticum aestivum L. cv. Stephens) located at the North Willamette Experiment Station (Canby, Oregon) were sampled for the presence of take-all during April 1983. Inspection of the root systems of the seedlings indicated that dramatic differences in take-all severity were exhibited by plots with different soil treatments. Based on these observations six plots representing different management and disease histories were selected for further investigation.

Soil samples for the growth chamber bioassay were collected in November 1983. Soil was collected from plots in a fifth year wheat crop sequence or from plots in second year wheat following oats. Within each crop sequence, three combinations of lime and sewage sludge treatments were tested. Thus plots that had received both lime and sewage sludge applications, sewage sludge but no lime, or niether lime nor sewage sludge were sampled for the fifth year sequence. Similiar lime and sewage sludge treatments were sampled from the second year wheat plots. Plots with a sewage sludge treatment received applications of sewage sludge in 1976, 1977, 1978, 1981, and 1982. Sludge was applied at a rate of approximately 100 kg N/ha. Limed plots received approximately 13.5 metric tons/ha in 1976. Additional lime applications were made in 1977 and 1978. Table 1 lists the physical and chemical properties of the six soil management systems tested.

Twelve 10 cm deep cores were taken at random from each plot. The subsamples were bulked and allowed to dry on a greenhouse bench to a moisture content of approximately 3 bars. Prior to planting, the soils were screened (8 mm) to remove unwanted debris and establish a particle size that would mix uniformly with Ggt inoculum.

Ggt inoculum known to be strongly pathogenic to wheat was obtained from R.L. Powelson, Department of Botany and Plant Pathlolgy, Oregon State University. Ggt was isolated by placing pieces of severly infected wheat tissue onto potato dextrose agar (Difco, PDA) with 100 ml streptomycin added. Ggt mycelium was transferred to moistened autoclaved oat kernels and incubated 4 to 5 weeks at 17 C. The colonized oats were dried, milled (Wylie Mill, A.H. Thomas Co., Philadelphia) and passed through a 1 mm screen.

A mechanical mixer was used to uniformly blend the ground oat inoculum at a rate of 2.5 g inoculum per 1000 cm^3 soil. An aliquot of this inoculated soil was removed and replaced with the same volume of noninoculated soil establishing an inoculum density of 1.2 g per 1000 cm^3 soil. This dilution procedure was repeated once more and four inoculum levels were established: 2.5, 1.2, 0.6, and 0.0 g inoculum per 1000 cm^3 soil.

Plastic pots (Ray Leach Cone-tainer, Canby, Oregon) were surface disinfested using a bleach solution (1:10 Clorox) and rinsed twice with tap water. The bottom of each pot was plugged with a cotton ball. 100 cm^3 soil was added to each pot beginning with the lowest inoculum level of each soil and proceeding sequentially to the highest. Before switching to a new soil, all utensils were surface disinfested with bleach solution to prevent transfer of microbial contaminants and Ggt propagules.

Fertilizer was applied as a band to all pots at rates intended to represent typical field rates for fall planted wheat:

22.4 kg N/ha, 22.4 kg P/ha, and 56.0 kg Cl/ha (Jackson et al., 1982). Actual material incorporated into each pot was 87 mg monoammonium phosphate, 42 mg ammonium chloride, and 50 mg potassium chloride. No direct attempt was make to modify the soil reaction. All fertilizer materials were dissolved in water and applied at a rate of 2 ml fertilizer solution per pot. All pots were then wet to field capacity and incubated for 24 hr before planting.

A thin layer of the appropriate soil was spread over the fertilizer band and one seed of soft white winter wheat (Triticum aestivum L. cv. Stephens) was placed in each cone. The seeds had been soaked in distilled water for 24 hr prior to planting. Care was taken to select uniform seeds showing no signs of cracking or shriveling. The seed was then covered with 20 cm^3 noninoculated soil. Approximately 2 cm of vermiculite covered this uppermost soil layer to reduce evaporative loss. A complete description of the growth container design may be found in Appendix Table 1. Treatments were arranged in a completely randomized design.

The plants were grown in a growth chamber (Sherer) at a temperature of 10 C and a photoperiod of 12 hr days. Lighting was a combination of fluorescent and incandescent fixtures. The distance between the lights and the tops of the pots remained at approximately 120 cm throughout the growing period. Trays of seedlings were periodically moved to new positions in the growth chamber in an effort to minimize the effects of environmental variability within the growth chamber. Plants were watered as needed at a rate of 5 ml tap water per pot.

Plants were assessed for root discoloration at 35, 65, and 90 days after sowing. The maturity of the seedlings at these dates corresponded to cereal growth stages 14-19 (Zadoks et al., 1974). Pots containing the plants and soil were soaked for 2 hr to loosen the soil and minimize root breakage during washing. Soil was carefully washed from the roots with a hose and each root system

Table 1. Selected chemical properties of plots[1] sampled at the North Willamette Experiment Station, November 1983.

YEARS IN WHEAT	TREATMENT	SOIL ANALYSIS VALUES pH[2]	P	K	Ca	Mg
			ug/g		cmol/kg	
5	+L, +SS	5.7	135	254	6.7	1.0
2	+L, +SS	5.8	132	230	6.2	1.0
5	-L, +SS	5.2	135	238	4.8	0.9
2	-L, +SS	5.4	145	238	5.0	1.0
5	-L, -SS	5.3	137	281	4.7	1.0
2	-L, -SS	5.5	130	316	5.0	1.0

1. Taxonomic classification: Willamette series; fine silty, mixed mesic Pachic Ultic Argixeroll

2. Soil pH measured using a 2:1 water paste.

further washed by hand to remove clay particles still clinging to the roots. Ggt attack was assessed by measuring lesion length on each seminal root. Crown roots were not present on any seedlings assessed in this experiment. A disease severity index (DSI) was calculated by multiplying the lesion length by its position index and dividing by the total root length (Appendix Table 2).

The disease severity index was plotted as a function of inoculum density and the data subjected to the standard least squares-simple regression analysis (Rowe and Brenne, 1982) to determine correlation coefficients and the slope values of the curves. Regression lines were compared and significance of the regression coefficients determined by analysis of covariance (Snedecor and Cochran, 1980). ED-10 values were determined for each observation where the ED-10 was defined as the density of Ggt required to obtain a DSI value of 10%.

Relative infection rates were determined by calculating the slope of the disease progress curve between two intervals: 0 to 65 days and 65 to 90 days after planting. Final DSI ratings were defined as the mean DSI value at the highest inoculum level (2.5 g/1000 cm^3) occurring at the last date of disease assessment. Mean disese ratings were analyzed by analysis of variance and differences among means compared using a "protected" least significant difference test (Steel and Torrie, 1980).

Field Study

Field samples from the 1984 wheat crop were collected from the same plots that were sampled for the growth chamber study. Seedlings were sampled at 5 to 7 m intervals along the border rows of each plot. These plants represented the next crop in the cereal sequences that were in effect in November 1983. The plots were sampled on March 21, May 7, and June 25. The maturity of the plants at these

dates corresponded approximately to the decimal growth stages 22, 41, and 90 respectively (Zadoks et al., 1974).

The plants and root systems were dug with a spade to a depth of 25-30 cm. The soil mass covering the roots was left intact and the samples were transported in plastic bags to the lab where the roots were first soaked overnight and then washed under running water.

Root disease was assessed as the percentage of the total root area attacked (PA) by Ggt and exhibiting dark necrotic lesions. The logarithmic PA values were then converted into degree of attack (DA) values according to the methods of Zadoks (1961). A take-all score (average DA value) was calculated by multiplying the number of observations in each DA class by the class number (1-10), summing these values and dividing by the number of observations.

During the first set of samples (March 21), both seminal and crown roots were assessed. During the final two samplings (May 7 and June 25), crown roots only were assessed. Relative infection rates were determined by calculating the slope of the disease progress curve between two intervals: March 21 to May 7 and May 7 to June 25 planting. Final disease readings (mean DA on June 25) were analyzed by analysis of variance and differences among means compared using a "protected" least significant difference test (Steel and Torrie, 1980).

RESULTS

Growth Chamber Bioassay

Slopes of the inoculum density - disease severity index (ID-DSI) curves and final disease ratings for the six soil management systems tested are listed in Tables 2, 3, and 4.

As the density of Ggt inoculum was increased there was a corresponding rise in the proportion of root area attacked by the pathogen (Figure 1). The slopes of the regression lines are 0.092 and 0.096 respectively for the limed (pH 5.8) and unlimed (pH 5.4) second year wheat treatments (both sludge amended). In contrast, the limed (pH 5.7) sludge amended fifth year treatment had an ID-DSI slope of 0.155 whereas the unlimed (pH 5.2) sludge amended treatment was 0.084 for the same crop sequence. Thus the combination of lime plus sewage sludge significantly ($P < 0.05$) increased the slope of the ID-DSI curve for the fifth year crop sequence. The effect of lime on the ID-DSI slope for the second year crop sequence was not significant at the 5% probability level (Table 2).

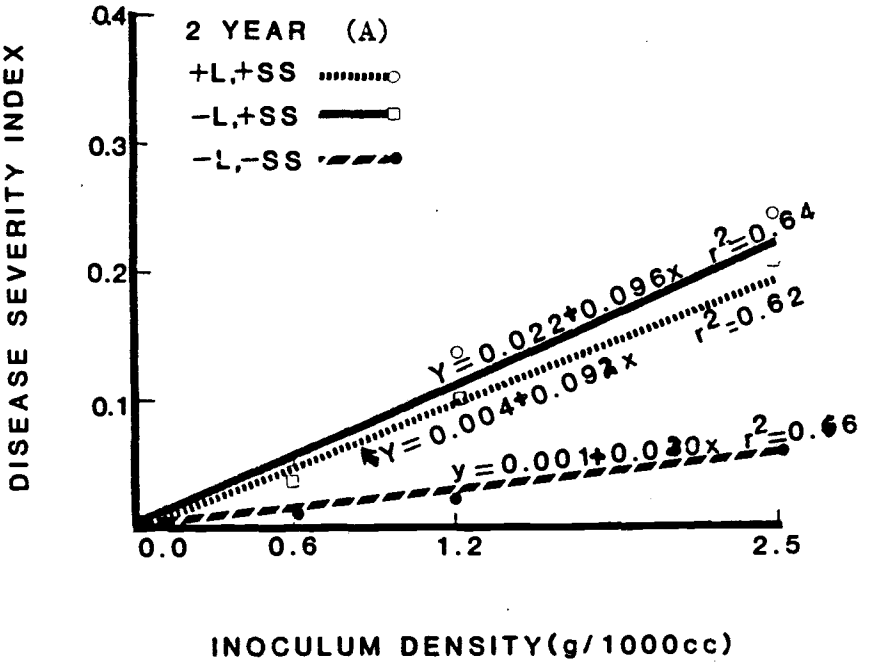
Sewage sludge also had a significant influence on the slopes of the ID-DSI curves. The fifth year sequence with neither sludge nor lime had a slope of 0.040 while the unlimed sludge amended treatment exhibited a slope of 0.084. The presence of sewage sludge resulted in similiar increases in disease in the second year wheat seqeuence. Slope values were 0.030 and 0.096 for the minus lime minus sludge and minus lime plus sludge second year treatments respectively. The increase in ID-DSI slopes caused by the presence of sewage sludge in these unlimed treatments was highly significant ($P < 0.01$) for both the second and fifth year crop sequences (Table 2).

Another method that may be used to compare these soil treatments is to determine the density of Ggt inoculum required to cause a standard amount of root damage. The slopes of the ID-DSI curves and

Table 2. Pairwise comparison of slopes of inoculum density-disease relationships (90 days after planting) for fifth year and second year crop sequences. Growth chamber data, 1984.

YEARS IN WHEAT	TREATMENT[1]	SLOPE	r^2	SIGNIFICANCE LEVELS (5%)	(1%)
5	+L, +SS	0.155	0.77	*	NS
5	-L, +SS	0.084	0.59		
2	+L, +SS	0.092	0.62	NS	NS
2	-L, +SS	0.096	0.64		
5	-L, +SS	0.084	0.60	*	*
5	-L, -SS	0.040	0.59		
2	-L, +SS	0.096	0.64	*	*
2	-L, +SS	0.030	0.66		
5	+L, +SS	0.155	0.77	*	*
2	+L, +SS	0.092	0.62		
5	-L, +SS	0.084	0.60	NS	NS
2	-L, +SS	0.096	0.64		
5	-L, -SS	0.040	0.56	NS	NS
2	-L, -SS	0.030	0.66		

1. L = lime application; SS = sewage sludge application.



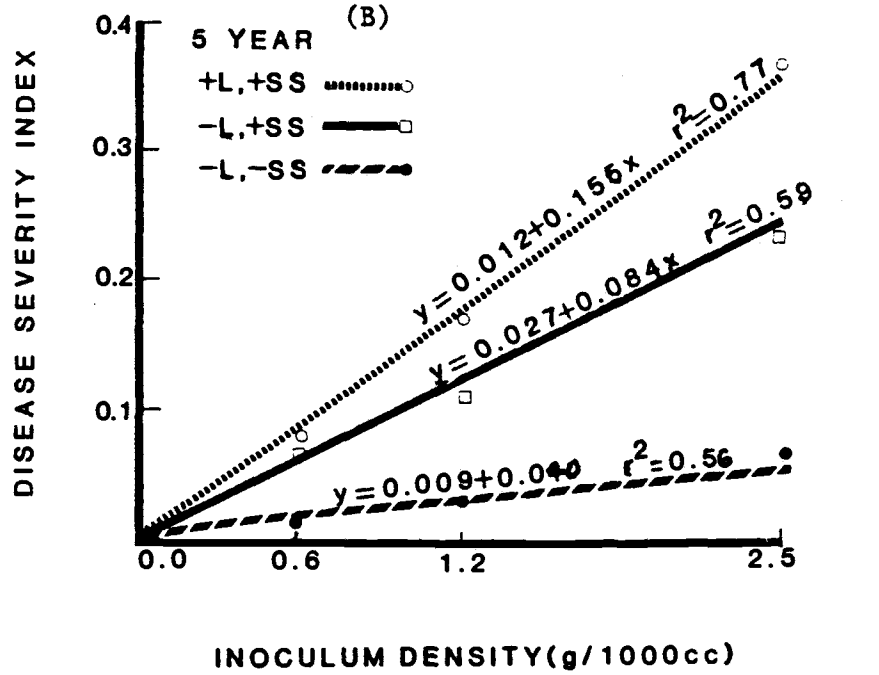


Figure 1. Effect of inoculum density on disease severity index, 90 days after planting on second (A) and fifth (B) year wheat sequence. Growth chamber data, 1984.

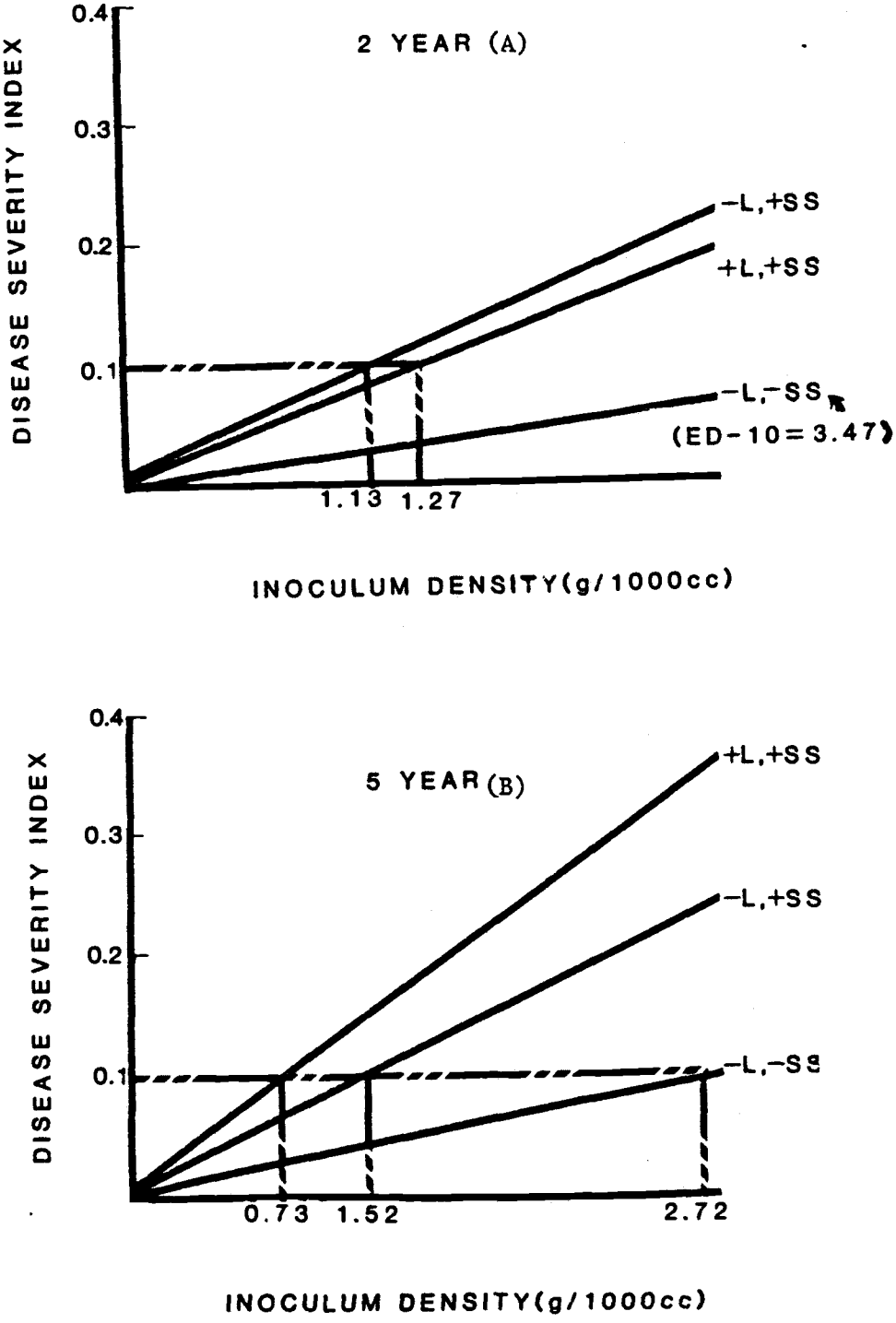


Figure 2. Effect of lime and sewage sludge on effective dose values of *Gaeumannomyces graminis* var. *tritici*, 90 days after planting on second (A) and fifth (B) year wheat sequence. Growth chamber data, 1984.

subsequent effective dose (ED) values give an indication of the efficiency with which Ggt inoculum caused root damage under different soil conditions. Figure 2 shows the effective dose of Ggt inoculum that was necessary to obtain a 10% disease reading (ED-10).

The ED-10 values for the fifth year wheat sequence are 0.73, 1.52, and 2.72 for the plus lime plus sludge, minus lime plus sludge, and minus lime minus sludge treatments respectively. The second year sequence showed a similiar trend with ED-10 values of 1.13, 1.27, and 3.47 for the plus lime plus sludge, minus lime plus sludge, and minus lime minus sludge treatments respectively. Thus it appears that Ggt inoculum was most efficient in the limed sludge amended fifth year wheat sequence and moderately efficient in the unlimed sludge amended treatments for both sequences. The greatest ED-10 value was exhibited by the second year wheat sequence with neither lime nor sewage sludge treatments.

Disease progress curves are another tool that may be used to analyze take-all epidemics in differently managed soils. Inferences concerning the different soil treatments were made by comparing final disease levels and relative infection rates (RIR).

There was a positive relationship between the age of the seedlings, measured as days after planting, and the disease severity index (Table 3, Figure 3). Additionally, the take-all epidemics appeared to proceed in two distinct phases. RIR values (change in DSI per unit change in time) were minimal during the first 65 days of the assay, regardless of the treatment. The disease progress data indicates a rapid increase in DSI occurred between 65 and 90 days after planting (Table 4). The limed sludge amended treatments exhibited the greatest RIR values for both the fifth year sequence (RIR = 0.008) and second year sequence (RIR = 0.012). Intermediate infection rates were exhibited by the nonlimed sludge amended treatments and the lowest RIR values were associated with the fifth

Table 3. Effect of crop sequence, lime and sewage sludge applications on the severity of take-all caused by Gaeumannomyces graminis var.tritici. Growth chamber data, 1984.

YEARS IN WHEAT	TREATMENT[1]	DISEASE RATINGS[2] 35 DAYS	65 DAYS	90 DAYS
5	+L, +SS	0.063	0.072	0.374
2	+L, +SS	0.001	0.018	0.243
5	-L, +SS	0.025	0.034	0.246
2	-L, +SS	0.018	0.074	0.244
5	-L, -SS	0.009	0.041	0.102
2	-L, -SS	0.004	0.035	0.073
	S_d[3]	0.09	0.02	0.01
	LSD[4]	NS	0.041	0.021

1. L = lime application; SS = sewage sludge application.

2. Disease ratings represent mean DSI values at 35, 65, or 90 days after planting.

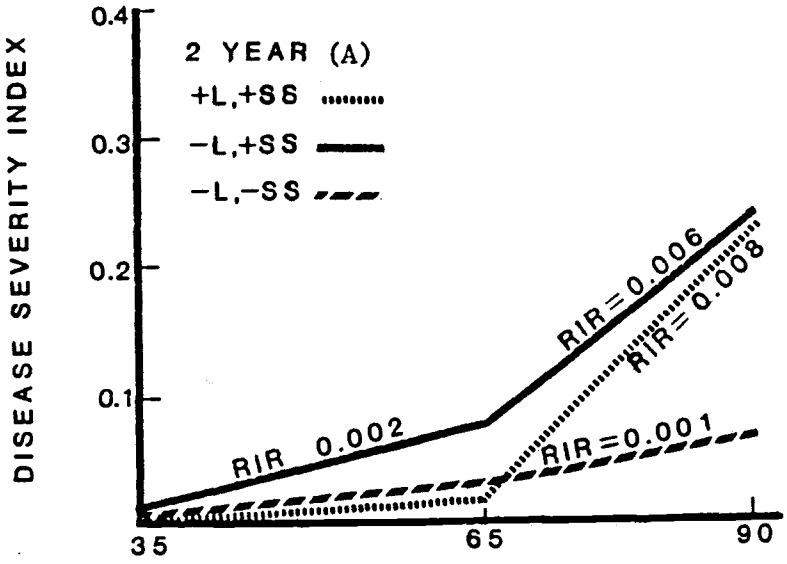
3. Standard error of a mean difference.

4. Least significant difference at the 5% probability level; NS = not significant.

Table 4. Effect of crop sequence, lime and sewage sludge applications on disease progress of Gaeumannomyces graminis var. tritici during the final twenty five days of the bioassay. Growth chamber data, 1984.

YEARS IN WHEAT	TREATMENT[1]	DISEASE RATINGS[2] 90 DAYS	65 DAYS	S_d[3]	LSD[4]
5	+L, +SS	0.374	0.072	0.136	NS
2	+L, +SS	0.243	0.018	0.093	0.22
5	-L, +SS	0.246	0.034	0.103	NS
2	-L, +SS	0.244	0.074	0.280	NS
5	-L, -SS	0.102	0.041	0.045	NS
2	-L, -SS	0.073	0.035	0.032	NS

1. L = lime application; SS = sewage sludge application.
2. Disease ratings represent mean DSI values.
3. Standard error of a mean difference.
4. Least significant difference at the 5% probability level; NS = not significant.



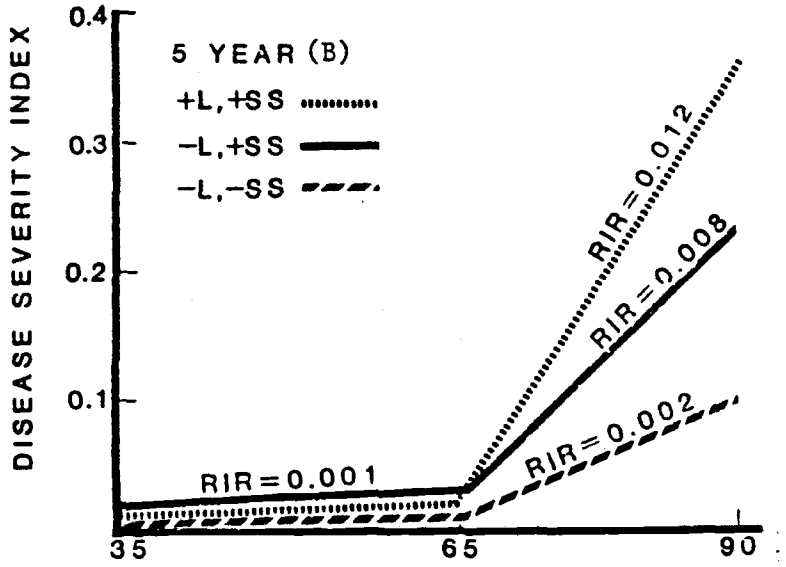


Figure 3 Effect of time on disease severity index at an inoculum density of 2.5 g/1000cc on second (A) and fifth (B) year wheat sequence. Growth chamber data, 1984.

and second year sequences (RIR = 0.002 and RIR = 0.001 respectively) that received neither lime nor sludge amendements.

Final disease levels (mean DSI of the highest inoculum level at 90 days) were used to compare and contrast the six soil treatments (Table 3). A reading of 0.10 indicates that approximately 10% of the root area was covered with black lesions at the time of assessment. The final disease levels for the fifth year wheat sequence were 0.374, 0.246, and 0.102 for the plus lime plus sludge , minus lime plus sludge, and minus lime minus sludge treatments respectively. Final disease levels for the second year wheat sequence were 0.243, 0.244, and 0.073 for the plus lime plus sludge, minus lime plus sludge, and minus lime minus sludge treatments respectively.

Analysis of variance F-values for the final disease levels indicate significant differences ($P < 0.05$) exist among the means of the lime and sewage sludge treatments (Appendix Table 3). Thus a "protected" least significant difference (Steel and Torrie, 1980) may be used to make pairwise comparisons of the treatment means. Employment of this test criterion indicated that the final disease means of the lime and sewage sludge treatments in the fifth year sequence were significantly different at the 5% probablility level. Within the second year sequence, the difference between disease levels of the limed and unlimed sludge amended treatments was not significant. However, the difference between the unlimed sludge amended means and the unlimed non-sludge amended means were significant at the 5% probability level.

Field Study

Final disease readings for the six soil treatments investigated are presented in Tables 5 and 6. Additionally, final disease

readings and grain yield data for the 1983 and 1984 wheat crops are listed in Table 7.

In 1983, the effect of crop sequence on take-all severity was the most striking of the three management factors being assessed. Take-all was almost absent from plots containing first year wheat following oats (Table 7). Comparing treatments within this sequence, it can be seen that the individual or combined effects of lime and sewage sludge were minimal. The first year wheat sequence with neither sludge nor lime had a mean DA reading of 0.13. When sewage sludge alone was present, the mean DA reading was 0.14 and plots containing both lime and sludge were found to have the lowest DA readings, averaging 0.05.

1983 grain yields were consistenly higher in first year wheat as compared to fourth year wheat, regardless of lime or sludge treatment. First year wheat that received both lime and sewage sludge amendments had a mean grain yield of 84 bu/ac. The unlimed sludge amended treatment had a grain yield of 75 bu/ac while the plots receiving neither sludge nor lime exhibited a mean grain yield of 82 bu/ac. Conversely, yields of fourth year wheat were 57, 43 and 60 bu/ac for the lime plus sludge, sludge only, and neither lime nor sludge treatments.

Take-all, as measured by percent root area covered with blackened lesions, was much more severe in fourth year wheat. Within this sequence, the effects of liming and sewage sludge were more apparent. Plots that had been limed and sludge amended had a mean DA value of 1.53. Plots that received sludge amendments but no lime had similiar take-all readings (mean DA = 1.60). The DA value decreased to 1.37 in those plots that had been neither limed nor sludge amended.

Analysis of the 1984 field data indicates the effects of crop sequence were still apparent but in a manner somewhat different from the 1983 field observations.

In general take-all severity decreased between May 1983 and May 1984 as the cropping sequence advanced from fourth year to fifth year wheat. Comparing root assessments from May 10, 1983 (Table 7) to those conducted on May 7, 1984 (Table 5), it can be seen that the severity of take-all in fifth year wheat plots was less than that observed in the same plots in 1983. Fifth year wheat plus lime and sewage sludge treatments had a mean DA of 1.05 in 1984. This same plot in 1983 (fourth year wheat) had a mean DA of 1.53. The unlimed, sludge amended fifth year wheat plot had a mean DA of 0.89 in May 1984, and this value was 1.60 a year earlier. Likewise, fifth year wheat with neither lime nor sludge had a mean DA of 1.00 in 1984 and a reading of 1.37 during May 1983.

Accompanying the decrease in severity of take-all in these plots was an increase in grain yields. In 1984, fifth year wheat receiving both lime and sewage sludge had a yield of 113 bu/ac. Fifth year plots that received neither lime nor sludge, or sludge only, exhibited yields of 113 and 87 bu/ac respectively.

The trend was just the opposite when the first and second year wheat plots are considered. There were striking increases in take-all symptoms when the data from first year wheat plots (1983) are compared with that of second year wheat (1984). The mean DA in May 1983 in first year wheat plots that received lime and sewage sludge treatments was 0.05. In May 1984, the then second year wheat plots (plus lime and sludge) had a mean DA of 1.33. Similiarly, plots receiving only sewage sludge had a mean DA of 0.14 in 1983 and this value increased to 1.06 in 1984. First year wheat with neither lime nor sludge had a DA value of 0.13 in 1983 and a mean disease reading of 1.11 during the same month in 1984.

Final disease readings were generally higher in second year wheat plots than in the fifth year plots (Table 5). Disease readings on June 25, 1984 were 3.72, 1.44, and 2.44 for plus lime plus sludge, minus lime plus sludge, and minus lime minus sludge second year

Table 5. Effect of crop sequence, lime and sewage sludge applications on the severity of take-all caused by Gaeumannomyces graminis var.tritici. North Willamette Experiment Station, 1984.

YEARS IN WHEAT	TREATMENT[1]	DISEASE READINGS[2] MARCH 21	MAY 7	JUNE 25
5	+L, +SS	0.72	1.05	2.11
2	+L, +SS	0.94	1.33	3.72
5	-L, +SS	0.67	0.89	1.72
2	-L, +SS	0.44	1.06	1.44
5	-L, -SS	0.72	1.00	2.00
2	-L, -SS	0.50	1.11	2.44
	S_d[3]	0.27	0.33	0.45
	LSD[4]	NS	NS	0.88

1. L = lime application; SS = sewage sludge application.
2. Disease readings represent mean DA values.
3. Standard error of a mean difference.
4. Least significant difference at the 5% probability level; NS = not significant.

Table 6. Effect of crop sequence, lime and sewage sludge on disease progress of Gaeumannomyces graminis var. tritici during the final forty eight days of field observations. North Willammette Experiment Station, 1984.

YEARS IN WHEAT	TREATMENT[1]	DISEASE READINGS[2]		S_d[3]	LSD[4]
		JUNE 25	MAY 7		
5	+L, +SS	2.11	1.05	0.408	0.82
2	+L, +SS	3.72	1.33	0.535	1.08
5	-L, +SS	1.72	0.89	0.333	0.67
2	-L, +SS	1.44	1.06	0.361	NS
5	-L, -SS	2.00	1.00	0.289	0.58
2	-L, -SS	2.44	1.11	0.386	0.78

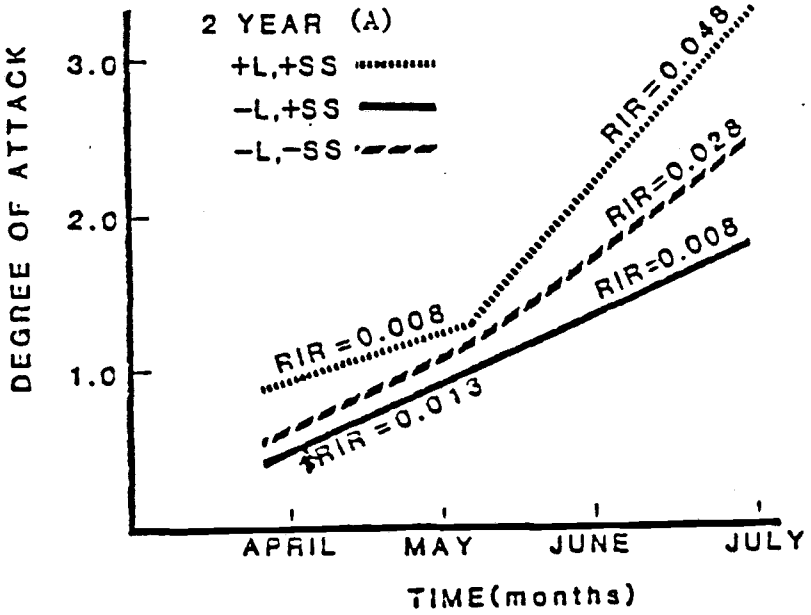
1. L = lime application; SS = sewage sludge application.
2. Disease ratings represent mean DA values.
3. Standard error of a mean difference.
4. Least significant difference at the 5% probability level; NS = not significant.

Table 7. Effect of crop sequence, lime and sewage sludge applications on final disease levels and grain yields. Data represents 1983 and 1984 field plot observations from the North Willamette Experiment Station.

YEARS IN WHEAT	TREATMENT[1]	FINAL DISEASE READING[2]	GRAIN YIELD (bu/ac)	FINAL DISEASE READING	GRAIN YIELD (bu/ac)
		------1983------		------1984------	
5	+L, +SS	1.53	56.9	2.11	113
2	+L, +SS	0.05	84.7	3.72	101
5	-L, +SS	1.60	42.5	1.72	87
2	-L, +SS	0.14	74.7	1.44	88
5	-L, -SS	1.37	60.3	2.00	113
2	-L, -SS	0.13	82.5	2.44	97

1. L = lime application; SS = sewage sludge application.

2. Final disease readings represent mean DA values recorded in April 1983 and June 1984.



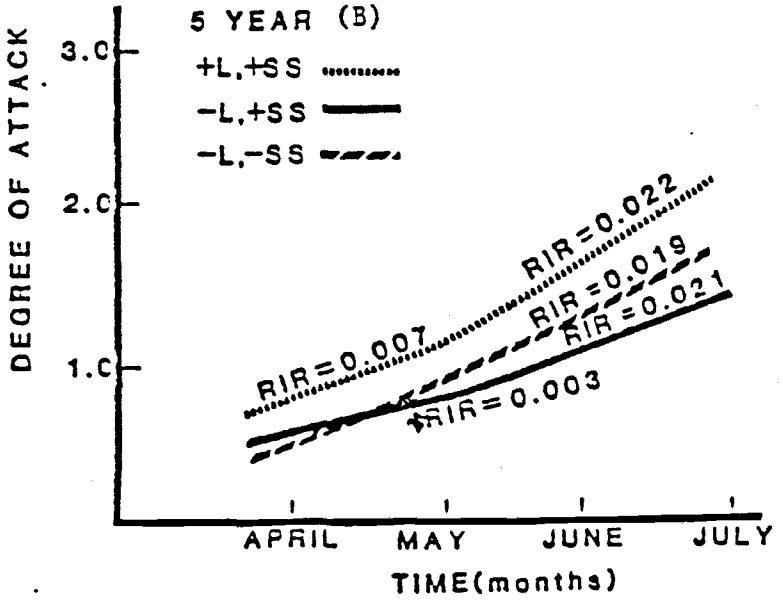


Figure 4. Effect of time on degree of attack on second (A) and fifth (B) year wheat sequence. North Willamette Experiment Station, 1984.

treatments respectively. Within the fifth year sequence, final disease readings were 2.11, 1.72, and 2.00 respectively for the same treatments as discussed above.

As was the case with the growth chamber bioassay, the field take-all epidemics appeared to proceed in two distinct phases (Figure 4). RIR values were generally much less for the first 48 days of the field study than were observed during the final 49 days. The fifth year wheat sequence exhibited RIR values of 0.022. 0.019, and 0.021 for the plus lime plus sludge, minus lime plus sludge, and minus lime minus sludge treatments respectively. In comparison, the second year wheat sequence exhibited RIR values of 0.048, 0.019, and 0.021 for the plus lime plus sludge, minus lime plus sludge, and minus lime minus sludge treatments respectively.

Analysis of variance F-values for the final disease readings indicate highly significant differences (p 0.01) exist among the means of the lime and sewage sludge treatments (Appendix Table 4). The "protected" LSD test indicates the final DA (June 25) of the limed fifth year wheat treatment is not significantly different from the final DA of the unlimed treatment (both sludge amended) at the 5% probability level. The mean DA of the fifth year wheat treatment receiving neither lime nor sludge was not significantly different from the above treatments at the same probability level.

In contrast, the final DA of the limed sludge amended second year wheat treatment was significantly different at the 5% level from both the minus lime plus sudge and minus lime minus sludge treatments. There was a trend of higher disease levels in the non-sludge amended as compared with the sludge amended treatments, particularily in the second year sequence. However, the mean DA readings were not found to be significantly different at the 5% probability level.

DISCUSSION

According to Baker and Drury (1980), the relationship between inoculum density and disease holds only when other influencing factors are held constant. The effeciency of Ggt inoculum and magnitude of the observed disease symptoms may be profoundly influenced by environmental and/or crop management factors. Thus a growth chamber bioassay was developed to study the ID:DSI relationships of six soil samples representing different management practices. Uniform levels of inoculum were mixed with the samples and wheat was grown under consistent environmental conditions. Experimental procedures were designed to ensure disease incidence and severity resulted only from the Ggt inoculum applied. Thus differences observed in the resultant epidemics can be attributed to the differences in the unique chemical and microbial charecter of each soil treatment.

There was an overall trend towards increased take-all in limed soils. Fifth year wheat soils amended with lime and sewage sludge (pH 5.7) had the greatest DSI values, greatest ID:DSI slope and RIR values, and the least ED-10 value. The low ED-10 value indicates the least amount of Ggt inoculum was required to achieve 10% disease severity.

Within the fifth and second year crop sequence, the lowest disease levels occurred in the unlimed, no sludge treatment (pH 5.3). Soil samples that received sludge but no lime (pH 5.2) exhibited intermediate values. A comparison of regression coefficients of sludge amended fifth year wheat samples indicated the effect of lime was significant at the 5% confidence level. The effect of lime on sludge amended second year wheat samples was not significant.

The effects of lime on take-all severity do not appear to be associated with compromised host vigor as the pH values at the time of sampling were within the pH range suggested for winter wheat

production (Jackson et al., 1982). The increase in take-all associated with the higher pH values in the limed treatments may be due to a direct effect on the pathogen. Garrett (1934, 1936, 1937) has reported that Ggt is markedly susceptible to soil pH and its hyphal extension rate increases in a regular manner with the transition from acid to alkaline soils. Thus limed treatments could have increased take-all by enhancing the rate of colonization of the host by Ggt hyphae. In addition, the increase in take-all in the limed soils may be due in part to a number of indirect effects. Severe take-all in the limed soils may reflect an increased rate of nitrification (Huber and Watson, 1970) or decreased number of microbial antagonists such as the fluorescent pseudomonads (Smiley, 1979).

The pattern exhibited by the ID:DSI slopes and final disease ratings of the various soils was also evident in the ED-10 values. The more conducive a soil treatment is to take-all, the lower its ED-10 value will be. Thus ED-10 values give an indication of the efficiency with which Ggt inoculum operates in a given soil sample.

The ED-10 values for limed and unlimed fifth year wheat treatments (sludge amended) were 0.73 and 1.52 respectively. The fact that half as much inoculum was required in the limed soil to cause 10% disease is indicative of enhanced inoculum efficiency of Ggt caused by liming a moderatey acid soil. Increased quantities of Ggt inoculum were necessary to achieve a 10% disease level as the soil treatment changed from limed-sludge amended to sludge only to neither lime nor sludge.

Brown and Hornby (1971) have suggested that prior to infection, Ggt may require an ephemeral feeding stage to build up cell mass, particularity if the inoculum was low in food reserves. It is possible that the C/N status of the non-sludge amended treatments soils may cause an extension of this feeding period, resulting in a delay of infection. While this hypothesis is highly speculative, it

provides one approach to interpreting the effects of sewage sludge applications. For example, the non-sludge amended treatments exhibited the lowest final disease levels in the bioassay. However, final disease readings and relative infection rates of these treatments were fairly high. In particular, the unlimed second year wheat treatment without sludge exhibited the lowest final disease levels in the growth chamber. Additionally, this soil had a fairly low disease level in the May 1984 field sampling. However, the relative infection rate and final disease reading exhibited by this treatment after May was second only to the limed second year wheat treatment. Perhaps the low N status of this soil, due to large amounts of decomposing straw and no sewage sludge amendment resulted in a delayed infection. Based on the infection rates, this treeatment has the potential to attain high disease levels given sufficient time.

Comparison of the RIR values shows that rates of infection, like the other epidemiological parameters assessed, seemed to separate the soils treatments into three distinct groups. Disease increased most rapidly in the limed sludge amended second year wheat treatment (RIR=0.048). The fifth year wheat samples all exhibited somewhat similiar RIR values: 0.022, 0.019, and 0.021 for plus lime plus sludge, minus lime plus sludge, and minus lime minus sludge treatments respectively. The second year wheat sequence receiving neither lime nor sludge comprised a third group with an RIR value of 0.028.

The relative suppressiveness of a soil to Ggt inoculum aver time may be inferred from the relative rate of infection. On the basis of reduced RIR values calculated for the final 65 days of the experiment, second year wheat treatments were more suppressive than fifth year wheat treatments in the growth chamber bioassay. However, RIR values calculated from the 1984 field daya indicate just the

opposite. That is, fifth year wheat exhibted lower RIR values than did second year wheat plots.

This points out the extreme importance of carefully choosing sampling dates. It is possible that the bioassay RIR values would be higher for second year wheat soil samples on 4 or 5 month old wheat, rather than 3 month old wheat as was assessed in the bioassay.

When comparing field disease observations from different crop years, it is imperative to keep in mind the effect an additional growing season will have on the take-all pathosystem. In 1984, first year wheat plots had advanced to second year wheat while fourth year wheat plots were converted fifth year wheat. In addition to the effects of the crop residues, Ggt inoculum levels and distribution patterns would be expected to change. Prolonged presence of the pathogen may mean shifts in populations of antagonistic microorganisms as well as differences in soil pH, nitrogen form, and nitrogen availability. It is also important to consider the ramifications of take-all decline and its effects on disease levels. Finally, yearly variation in weather, the impact of other pests and diseases, and management practices such as planting date, timing of ferilizer application, and seeding rates combine to make interpretation of field disease data a formidable task.

In 1983, field data was collected on a survey (one-time) basis. Analysis of this data and review of the literature pointed out the need for a more in-depth approach to the field study. Thus in 1984, take-all severity was assessed periodically throughout the growing season on a smaller number of crop sequence and management systems.

The most dramatic differences between the 1983 and 1984 field data were associated with changes in the number of years the plots had been in continuous wheat. First year wheat following oats consistently had lower levels of take-all than did fourth year wheat. The effects of lime and sewage sludge treatment were not apparent in the first year wheat plots. This is probably due to very low levels

of Ggt inoculum charecteristic of wheat following a nonhost breakcrop.

During 1983, high levels of take-all and lower grain yields were associated with fourth year wheat. These observations are similiar the those of Brooks and Dawson (1968). In experiments comparing various crop sequences, higher levels of take-all were found in the third and fourth consecutive crops of wheat rather than in first year wheat.

In 1984, a drastic increase in take-all was observed in second year wheat. Accompanying these high disease levels were unexpectedly high grain yields. The increase in lesioned root area was greatest in the limed and sludge amended second year wheat plots and moderate in the nonlimed sludge amended plots. This increase in the DA value may be attributed to an increase in inoculum density associated with the second planting of wheat.

Concomitant with the increased number of infective Ggt propagules is the possibility of nitrogen stress to the seedlings during the winter of 1984. Associated with the high grain yields in first year wheat during 1983 would be a large amount of straw produced. When this high C/N material is plowed under, a significant amount of plant available nitrogen could be immobilized. Any nutrient stress imposed on the young seedling could feasibly contribute to increased host susceptibility and enhanced pathogenisis. Also any delay of spring fertilization would augment this phenomenon, particularily in the crown roots. The ameliorating effect of sewage sludge applications observed on the second year wheat plots is most likely tied to enhanced nitrogen availability. Applying sewage sludge to the straw proir to incorporation should minimize nitrogen stress and maintain host vigor during the fall and winter.

The lack of this crop residue effect may have been a factor contributing to the lack of agreement between the field data and

growth chamber observations. Large pieces of straw and other organic debris were removed as the soils were prepared for inoculation. In addition, supplemental nitrogen fertilizer was added to all soil samples. If one assumes that the presence of large amounts of straw played a role in the high disease levels in second year wheat, it is worth speculating as to the consequences of removing this material from the growth chamber soil samples.

We did not expect to find growth chamber results indicating that the second year wheat sequence was more suppressive to take-all than the fifth year wheat sequence. The literature contains many reports of second year wheat having higher disease levels than similiarly managed fifth year wheat. The take-all decline phenomenon (TAD) has been used to explain these observations.

Careful analysis of the disease levels from 1983 and 1984 indicates patterns similiar to that of the TAD relationship are present. Desease levels in 1984 were much greater in second year wheat than were present in the first year wheat plots a year earlier. In contrast, fifth year wheat plots sampled during May 1984 exhibited lower disease levels than did the same plots in May 1983. Based on these trends, it is likely that the disease progress relationships will conform to the TAD hypothesis of Slope and Cox (1965). Thus it is expected that disease will increase as the second year wheat plots advance to third year wheat and disease should decrease as fifth year wheat plots advance to sixth year wheat.

It is interesting to note that grain yields were generally higher in all plots in 1984 than in 1983, regardless of crop sequence. There exists a great deal of uncertainty surrounding the question of how much impact take-all root rot has upon yield. Cases have been reported where high disease levels have been observed during the growing season yet grain yields remain unexpectedly high. It is possible that many soils in continous wheat may have the potential for severe outbreaks of take-all. The deciding factor may

not always be the presence of the pathogen or even the existence of moderate infections. The key to maintaining high yields in susceptible soils may be the additional effects of proper management and the influence of the environment. The final yield determinant, rather than lesion severity, may be the reaction of an infected host to water stress, nutrient stress, or some other factor. The impact of subtle management and environmental influences on disease severity and grain yield perpetuates the elusuve nature of take-all root rot.

CONCLUSION

A growth chamber bioassay was developed that can measure the effects of different soil management systems on the response of wheat seedlings to take-all root rot. Using epidemiological parameters, it was possible to place soil management systems into three distinct groups based on their relative suppressiveness to Ggt inoculum.

A fifth year wheat sequence plus lime and sewage sludge exhibited the lowest amount of suppression to take-all. This treatment had the highest final disease rating, greatest ID-DSI slope, highest relative infection rate, and required the least amount of Ggt inoculum to obtain a 10% disease severity rating.

Three soil treatments exhibited moderate suppression of take-all. Fifth and second year treatments (unlimed, sludge amended) as well as limed sludge amended second year wheat treatments all had intermediate levels of disease severity. The moderate suppressive charecter of these soil treatments was consistent with regard to all four of the epidemiological parameters examined.

Take-all suppression was greatest in fifth year wheat and second year wheat sequences receiving neither lime nor sewage sludge amendments. These two treatments had the lowest final disease ratings, least ID-DSI slopes, lowest infection rates, and highest ED-10 values. Statistically significant differences were evident when final disease levels were used to compare the six soil treatments. It was not biologically valid to apply statistical analysis to the relative infection rates due to the destructive sampling method used for disease assessment. However, the consistent trends and groupings of the six soil management systems among the four epidemiological parameters examined strongly suggests qualatative differences do exist in terms of suppressive charecter.

Analysis and interpretation of the 1983 field data revealed that dramatic differences in take-all severity were present when first year sequences were compared to fourth year sequences. An additional growing season converted first year wheat plots into second year wheat plots and fourth year plots became fifth year wheat plots. The

added year of continuous wheat resulted in the 1984 disease levels becoming similiar for both second and fifth year wheat. Comparison of the 1983 and 1984 field showed a dramatic increase in take-all as first year wheat were converted to second year treatments. Concurrently, the fifth year wheat sequence showed lower disease levels than were present a year earlier. Observations of increasing take-all in second year wheat and decreasing root disease in fifth year wheat are consistent with disease progress relationships that are predicted by the take-all decline phenomenon.

The impact of sewage sludge on suppressing take-all root rot appears to be linked to improved nitrogen availability during a time critical to the wheat host. Research has indicated that enhanced attack by Ggt occurs when a nutrient stress is imposed on wheat seedlings. This investigation has contributed to that hypothesis.

It was disappointing but not suprising to find that results of the growth chamber bioassay did not agree well with the results of the field study. Attempts to compare lab observations to field observations have confounded researchers since the inception of biological scientific investigation.

The failure to obtain a good correlation between the growth chamber and field data is due in part to a large variation in stand, vigor, and disease levels in the plots sampled. Factors contributing to this large sampling error include uneven and unpredictable distribution of Ggt inoculum and a low seeding rate acompanied by unexpectedly low tillering. The influence of these factors and others undoubtedly had profound effects on take-all severity and grain yields.

This investigation has contributed to our understanding of the take-all disease by shedding some light on the question, "can a growth chamber bioassay be used to assess the potential for development of take-all root rot"? The results indicate that significant differences in take-all epidemics in various soils may be measured using this assessment technique. Perhaps more important is the illumination of the fact that while we may measure and predict a given soil's potential to suppress or enhance take-all, the impact of

crop management and the environment during the growing season may be of the utmost importance in determining yield. The dynamic, complex, and interactive nature of these take-all influencing factors will undoubtedly deep disease forecasters busy for years to come.

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APPENDICES

Table 1. Single plant container design for growth chamber bioassay.

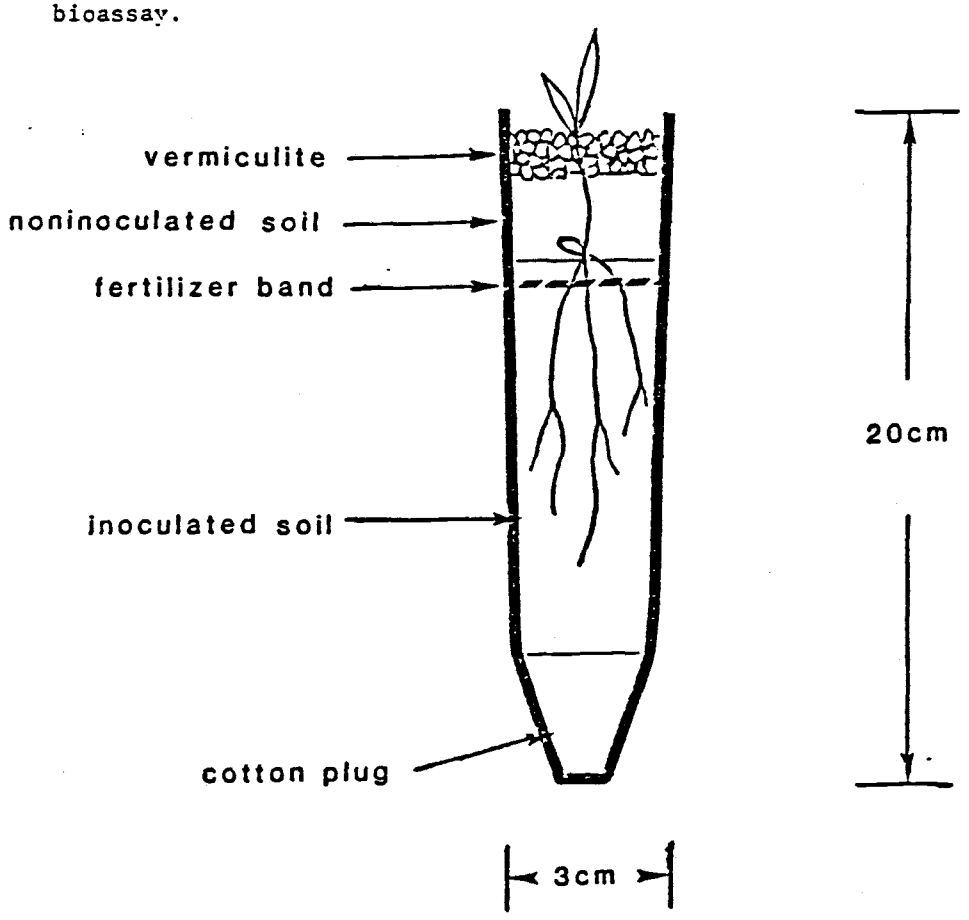
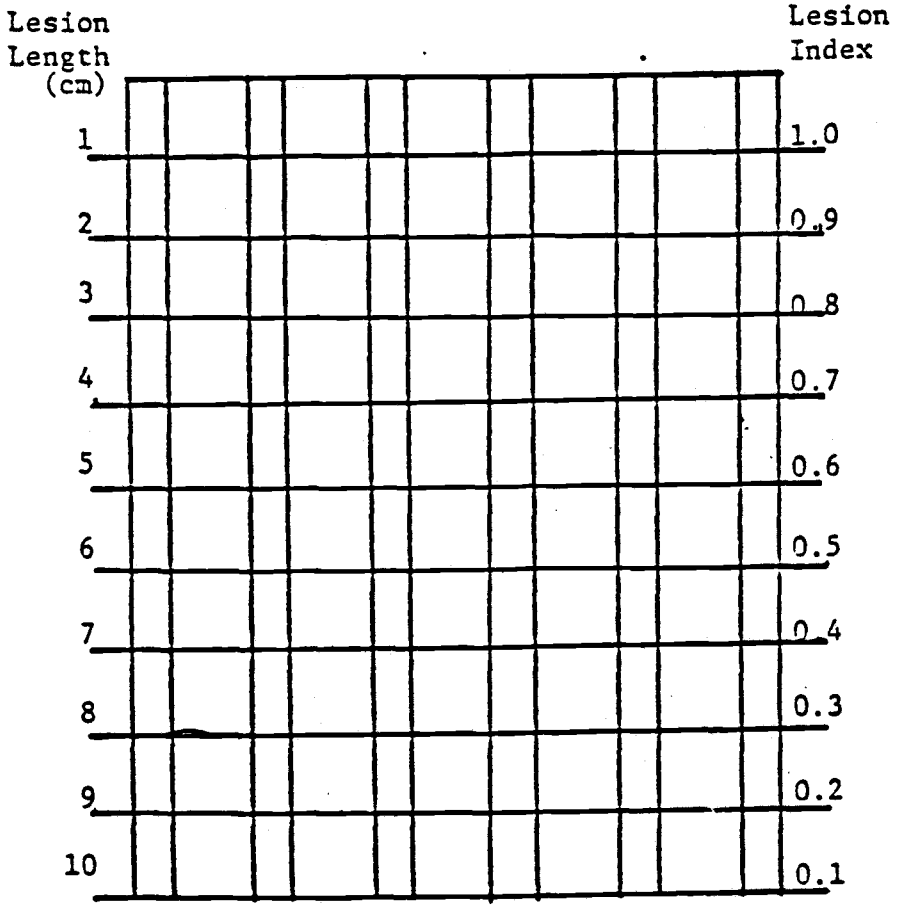


Table 2. Assessment scale for calculation of disease severity index (DSI).



$$DSI = \frac{\Sigma[(\text{Lesion Length})(\text{Lesion Index})]}{\text{Total Root Length}}$$

Table 3. Analysis of variance for final disease ratings of the growth chamber bioassay.

Source	df	MSE	F[1]
Among treatments	5	0.0476	4.14 *
Within treatments	18	0.0115	
Total	23		

1. * Significance at 5% probability level.

Table 4. Analysis of variance for final disease readings of field study.

Source	df	MSE	F[1]
Among treatments	5	11.260	8.09 **
Within treatments	102	1.391	
Total	107		

1. ** Significance at 1% probability level.