

## Effect of Mineral Nutrition on Take-all of Wheat

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### ABSTRACT

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Take-all of wheat caused by *Gaeumannomyces graminis* var. *tritici* developed on significantly fewer roots, and plants had a lower disease severity index when phosphorus (P), potassium (K), and magnesium (Mg) were made available to the wheat roots in a silica sand rooting medium at twice, compared with one-half, the concentration in normal Hoagland's solution. Calcium (Ca) and sulfur (S) had no significant effect on take-all either at half or twice the concentration in normal Hoagland's solution. The increased P, K, and Mg also resulted in the greatest increase in root development compared with Ca and S, which had the least effect on numbers of roots. Increasing nitrogen (N, as nitrate) from half to twice Hoagland's resulted in significantly more roots per plant, but disease severity on a given plant did not change significantly. Zinc (Zn) and copper (Cu) treatments each resulted in more roots and less take-all per plant when

supplied either to roots or leaves compared with treatments where those nutrients were withheld completely. Manganese (Mn), and possibly iron (Fe), also had suppressive effects on take-all as the supply was increased when applied in the rooting medium but not when applied by foliage sprays. In the field, the addition of Zn and Zn plus P each resulted in less take-all in wheat plots under irrigation at Lind, WA; and Zn, Cu, and a mixture of Zn, Cu, Mn, and Fe each reduced take-all of nonirrigated (rainfed) wheat in plots at Puyallup, WA. The reduction of disease in the field was significant ( $P=0.05$ ) only at low and moderate levels of disease intensity. The results indicate that certain macronutrients and micronutrients have the potential for limiting take-all, either by lessening susceptibility of the host tissues to the pathogen, promoting the formation of new roots, or by both mechanisms.

*Additional key words:* *Triticum aestivum*, soilborne pathogens.

Take-all of wheat (*Triticum aestivum* L.), caused by *Gaeumannomyces graminis* (Sacc.) von Arx and Olivier var. *tritici* Walker, is important in many wheat-growing areas throughout the world, especially where soils are moist and of neutral or alkaline pH. In the Pacific Northwest, the disease can be severe on irrigated

wheat grown in the Columbia Basin and on wheat grown under high rainfall west of the Cascade Mountains. In Brazil, take-all has become a major constraint to wheat production in the southern part of the country where rainfall is abundant and where once-acid soils have been limed to prevent aluminum toxicity.

Take-all has been recognized for more than 50 yr as a disease favored by deficiencies in host-plant nutrition (2,7,8,14-17,20). In spite of this, little is known about the influence of specific plant nutrients (other than nitrogen [N] and phosphorus [P]), on the disease. Many reports are available on the relationship of N to take-all (3,6,7,11-16,18). Ideally, available N should be low between cultivation of susceptible crops, to shorten saprophytic

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existence of the pathogen in infested stubble (6), and high during cultivation of a susceptible crop, to promote root development so that diseased roots become replaced with new roots (3,7). The form of N also is important; take-all may be suppressed by ammonium-N and favored by nitrate-N (12), apparently because of reduced and increased rhizosphere pH, respectively (19).

Increased amounts of P (7,17,18,20), and possibly potassium (K) (7) and magnesium (Mg) (11), also reduced take-all. At least part of the benefit of P is enhanced new root development by the host. Garrett (5) suggested further that superphosphate reduces take-all because of its acidifying properties. Goss and Gould (9) reported that K as KCl had a suppressive effect on the amount of *Ophiobolus*-patch (*G. graminis* var. *avenae*) of turf, but offered no explanation for the effect.

This study was undertaken to evaluate the influence of each of several important macronutrients and micronutrients on development of take-all, and to determine whether the disease is favored by any nutrient deficiency of the host plant or only by specific nutrient deficiencies. A major objective of the present study was to provide information that might help in the design of a fertility program for take-all control in the northwestern USA, southern Brazil, or both areas.

## MATERIALS AND METHODS

**Preparation of inoculum.** All isolates of *G. graminis* var. *tritici* were started from single ascospores from perithecia formed on diseased wheat plants originally collected in the state of Washington. The isolates were maintained on fifth-strength potato dextrose agar (PDA). To prepare inoculum, an isolate was grown for 5–7 days on PDA in petri plates (9 cm diameter), and then transferred as mycelium and accompanying medium to glass jars (0.978 L) containing autoclaved oat kernels. Two hundred fifty cubic centimeters of oat seeds per jar plus 120 ml of water were autoclaved at 121 C for 30 min on each of 2 consecutive days. The jars were then incubated at 25 C until the fungus had colonized the oat kernels (generally 3–4 wk). The jars were shaken once during the incubation period. After colonization, the kernels were removed from the jars, allowed to dry on a laboratory table, and then stored in new paper bags until used. For use, the kernels first were ground in a Waring Blender to increase the number of particles per unit mass of inoculum and thus to improve distribution of inoculum in the rooting medium.

**Methods of plant culture under controlled conditions.** Quartz sand (0.70 mm [30-mesh]) was used as an inert rooting medium for all growth chamber studies. The sand was 99.7% SiO<sub>2</sub>, 0.21% Al<sub>2</sub>O<sub>3</sub>, 0.028% Fe<sub>2</sub>O<sub>3</sub>, 0.02% Na<sub>2</sub>O, and 0.04% K<sub>2</sub>O. Sand (500 g) containing 5 g of ground oat inoculum (uniformly mixed) was used per 9- × 11-cm paper (disposable) pot. A layer of inoculum-free sand 1.5 cm thick was added to the top of the infested sand and then each pot was sown with eight seeds of the spring wheat cultivar Fielder. This procedure permitted the roots to grow for a short distance before coming into contact with the fungus (4,8). Seeds were surface-disinfected before planting, by soaking in a 2.7% solution of sodium hypochlorite for 5 min, rinsing three times in distilled water, and then allowing them to dry. A 1.5-cm layer of uninfested sand was used to cover the seeds. After emergence, the stand in each pot was thinned to five seedlings. Temperature of the growth chamber was set at 15 C, with a day-length photoperiod (18,000 lux) of 12 hr.

**Nutrition studies under controlled conditions.** Hoagland's solution (10) was used as the basic treatment, with full-strength Hoagland's (1 H) as the standard for comparative purposes. The concentration of a given element was adjusted to fractions or multiples of the amount in 1 H. Nitrogen, P, K, calcium (Ca), magnesium (Mg), and sulfur (S) each were adjusted to one-half H or 2 H, while keeping all other nutrients at 1 H. Copper (Cu), iron (Fe), manganese (Mn), and zinc (Zn) each were tested at 0 and 2 H, again by manipulating the concentration of only one nutrient per treatment, keeping all other nutrients at 1 H.

Two experiments were conducted to further clarify the influence of trace nutrients on take-all. In one study, Cu was applied directly

to the sand at nutrient-solution concentrations of 0, 0.02 (1 H), 0.04, 0.06, and 0.08 μg/ml; or as a solution (0.1% CuSO<sub>4</sub>·5H<sub>2</sub>O) applied through the leaves. For foliar application, plants were sprayed once in one treatment (plants 10 days old) and twice in another treatment (plants 10 and 15 days old, respectively). The sand surface was covered with cotton balls during each spray application to avoid contamination of the rooting medium with the test nutrient. In the other experiment, Cu, Fe, Mn, and Zn were tested individually and as a mixture at 0 or 4 H (ie, Cu, 0.08 μg/ml; Fe, 20.0 μg/ml; Mn, 2.0 μg/ml; and Zn, 0.2 μg/ml) applied to the rooting medium. A foliar treatment also was included in this experiment, in which leaves were sprayed four times (when the plants were 10, 13, 25, and 28 days old) with solutions containing 0.1% CuSO<sub>4</sub>·5H<sub>2</sub>O, 0.5% FeSO<sub>4</sub>·7H<sub>2</sub>O, 0.1% MnSO<sub>4</sub>·7H<sub>2</sub>O, or 0.5% ZnSO<sub>4</sub>·7H<sub>2</sub>O. For all treatments with nutrients applied to the leaves, the plants were watered with solutions devoid of the respective test element(s). Pots were watered every other day by using the appropriate treatment solutions.

**Field studies.** A field experiment was established with irrigated wheat at Lind, WA. The Lind site, on the Dryland Research Unit of Washington State University, is in the semiarid (250 mm annual precipitation) wheat-fallow area of eastern Washington on the edge of the irrigated Columbia Basin. The soil is Ritzville silt loam with a saturated paste pH (in 0.01 M CaCl<sub>2</sub>) of 7.5. This field experiment was designed specifically to test the influence of P and Zn on take-all of irrigated wheat. Standard soil tests revealed ~2 ppm available Zn and 8–10 ppm P in the unfertilized soil. Main plots were split into fumigated and unfumigated blocks. Methyl bromide was introduced under plastic tarps in treated plots at a rate of about 450 kg/ha. The tarp was removed after 3 days and the plots were seeded after 6 days. Each fumigated and unfumigated block, in turn, was divided into inoculated (whole oat-kernel inoculum added at planting time) and uninoculated (sterile oat-kernels added at planting time) subblocks. This provided a test for each nutrient treatment in the presence of (i) "no" inoculum (fumigated) soil, (ii) native inoculum only, (iii) native inoculum augmented with introduced inoculum, and (iv) introduced inoculum but with native inoculum of *G. graminis* var. *tritici* and other possible wheat root pathogens eliminated by the fumigation. Each subblock was divided further into four plots (each about 4.5 × 5.0 m) that received, at random, no P or Zn, P only (as a solution of H<sub>3</sub>PO<sub>4</sub>) at 58 kg P/ha, Zn only (as a solution of ZnCl<sub>2</sub>) at 10 kg Zn/ha, and P plus Zn. The nutrients were sprayed onto the soil surface and then mixed to about 10 cm deep by rototilling. The area was sown 21 March 1978 to Fielder spring wheat at 90 kg seed per hectare. All plots received equal amounts of N as ANS (25% (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> + 75% NH<sub>4</sub>NO<sub>3</sub>) at about 130 kg N/ha applied to the entire experimental area in the spring before planting.

A second field experiment was carried out at Puyallup, WA, on Pilchuck loamy fine sand with trace-nutrient treatments only. All plots were on Farm 5 of the Western Washington Research and Extension Center at Puyallup. The site was limed in years past and had a saturated paste pH (in 0.01 M CaCl<sub>2</sub>) of 5.3. A soil test revealed about 1.8 ppm Zn, 2.4 ppm Cu, 10.0 ppm Fe, and 4.8 ppm Mn in unfertilized soil from the site. The pathogen was introduced in colonized oat kernels at the time of seeding into half of each of the four replications, leaving the other half of each replication with natural inoculum only. Each block (with or without introduced inoculum) was divided into four 5.0- × 5.0-m plots that received, at random, no added trace nutrient, Zn as ZnSO<sub>4</sub>·7H<sub>2</sub>O at 10 kg/ha, Cu as CuSO<sub>4</sub>·5H<sub>2</sub>O at 5 kg/ha, or a combination of Zn, Cu, Fe, and Mn. The Fe (as FeSO<sub>4</sub>·7H<sub>2</sub>O) and Mn (as MnSO<sub>4</sub>·7H<sub>2</sub>O) in the combination treatment were each at 10 kg/ha. Each chemical was dissolved in water, sprayed onto the soil surface and then incorporated by rototilling. Nitrogen (as 25% (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> and 75% NH<sub>4</sub>NO<sub>3</sub>) was applied to the entire experimental area at 160 kg N/ha before seeding 'Yamhill' winter wheat on 20 September 1978.

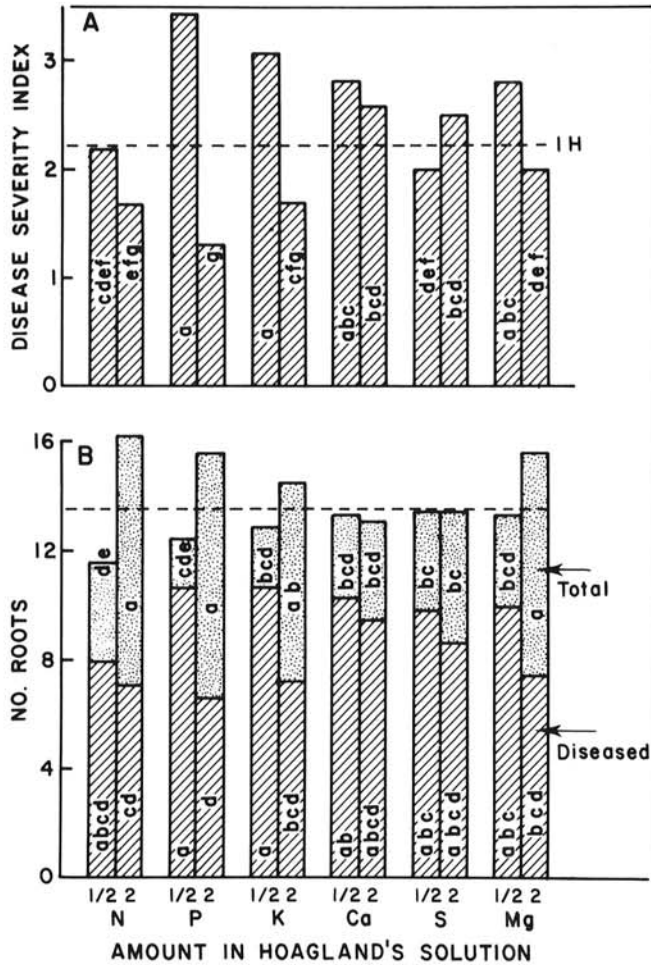
**Methods of disease assessment.** For the growth-chamber experiments, both total number of roots and number of diseased roots were counted. In addition, plants were indexed visually for disease on a scale of 0 to 4 in which: 0 = no symptoms; 1 = a few small lesions on half or fewer of the roots; 2 = multiple small lesions

on about half of the roots; 3 = multiple small to large lesions on most roots; and 4 = multiple large lesions on all roots and with disease extending into the crown. No distinction was made between seminal or crown roots. There was no significant difference in any of the experiments between total number of roots in uninoculated (control) and inoculated plants and therefore all results reported here for total number of roots are for inoculated plants only. The sampling was done at tillering, 40–50 days after seeding. Wheat roots were washed free of sand before rating and were assessed while floating in water against a white background. For plants from the field trials, 25 plants were collected per replicate at tillering. Both the total number of roots and number of roots with lesions were recorded. Again, no distinction was made between seminal or crown roots.

Data were analyzed by using SAS (Statistical Analysis System) (1) computer programs for analysis of variance and Duncan's multiple range test. The Student's *t*-test was also used to compare the difference between two means. Programs were executed on the Amdahl 470 V/6 computer at the Washington State University Computer Center.

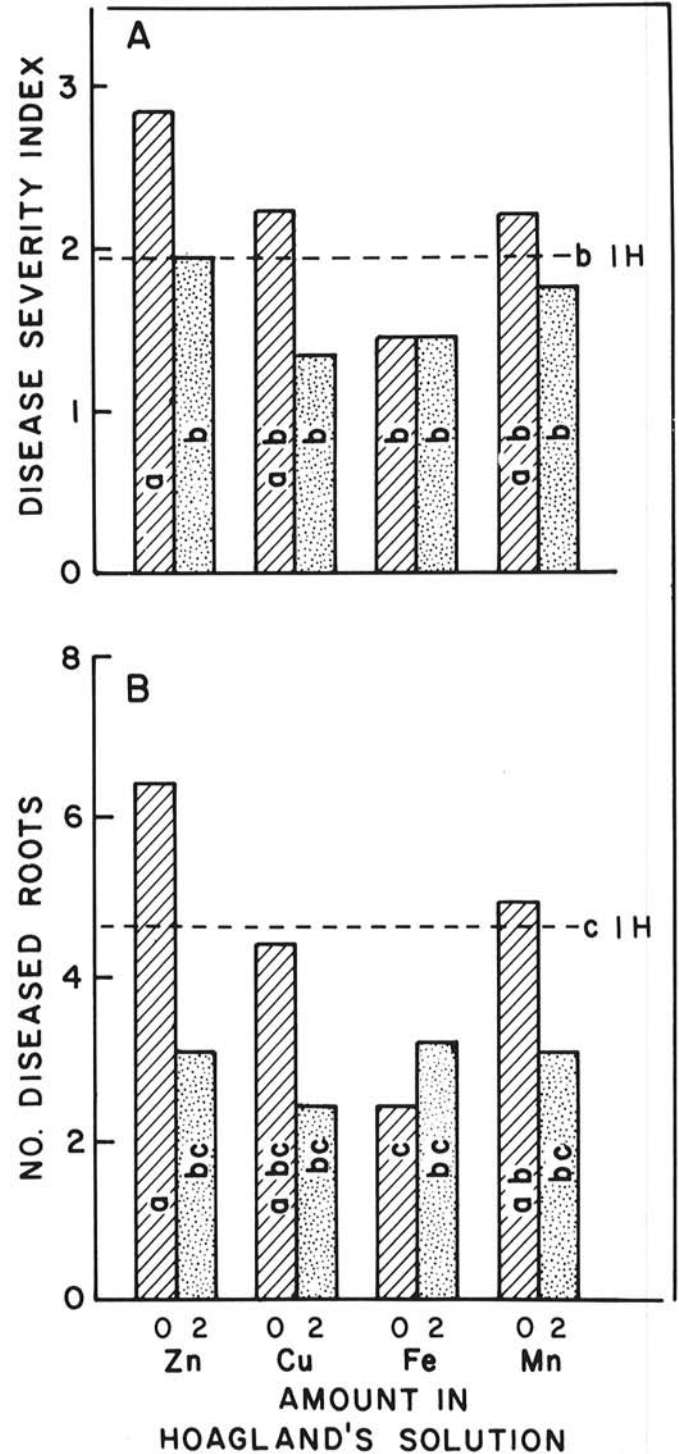
## RESULTS

**Influence of macronutrients on take-all of wheat.** Nitrogen, P, K, and Mg each resulted in a greater number of roots when provided at 2 H compared with 1/2 H (Fig. 1). The increase was significant at  $P=$



**Fig. 1.** Influence of macronutrients on take-all caused by *Gaeumannomyces graminis* var. *tritici* on Fielder spring wheat grown in silica sand, with the nutrient concentrations adjusted individually to one-half or two times the concentration in normal Hoagland's solution. **A**, Disease severity index on a scale of 0–4. **B**, Total number of roots and number of diseased roots per plant. Broken horizontal line is the disease severity index (A) and total number of roots (B) obtained with standard Hoagland's (1 H) solution. Bars not sharing a common letter are significantly different at  $P=0.05$  according to Duncan's multiple range test.

0.05 for N, P, and Mg, but not for K. Of these four macronutrients, increases in available P, K, and Mg each resulted in a significantly ( $P=0.05$ ) lower absolute number of infected roots and a lower disease severity index at 2 H compared with 1/2 H. Similar trends occurred for N, but differences were not significant. Changing the amount of Ca or S from 1/2 H to 2 H had no significant or consistent effect on either total roots per plant, number of infected roots per



**Fig. 2.** Influence of micronutrients on take-all caused by *Gaeumannomyces graminis* var. *tritici* on Fielder spring wheat grown in silica sand, with the nutrient concentrations adjusted individually from zero to two times the concentration in normal Hoagland's solution. **A**, Disease severity index on a scale of 0–4. **B**, Number of diseased roots per plant. Broken horizontal line is the disease severity index (A) and total number of roots (B) obtained with standard Hoagland's (1 H) solution. Bars not sharing a common letter are significantly different according to Duncan's multiple range test,  $P=0.05$ .

plant, or disease severity index.

The percentages of diseased roots at 1/2 H and 2 H, respectively, were 87 and 43 for P, 84 and 51 for K, 75 and 48 for Mg, 69 and 43 for N, 77 and 65 for Ca, and 73 and 64 for S. Except for N, treatments that promoted the greatest number of roots per plant also resulted in the fewest diseased roots per plant ( $r = -0.68$ ).

**Evidence that deficiencies of micronutrients favor take-all.** In the first growth-chamber experiment, the number of diseased roots and the disease severity index both were significantly higher when Zn was omitted from the nutrient solution compared with Zn supplied at 2 H (Fig. 2). Omission of Cu and Mn also increased disease compared with the 2-H treatment, but the increase was not significant,  $P = 0.05$ . There was no detectable effect of Fe in this experiment.

The second growth-chamber experiment involved only Cu, applied to the rooting medium as solutions with 0, 0.02, 0.04, 0.06, and 0.08  $\mu\text{g/ml}$  Cu, respectively, and to the leaves once or twice as a 0.1% solution of  $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$ . The presence of Cu, whether applied through the roots or leaves, resulted in more total roots and less root disease compared with no Cu (Fig. 3). There was considerable variability, however, with the result that the increase in total roots was significant at  $P = 0.05$  in only two treatments, 0.04  $\mu\text{g Cu/ml}$  (2 H) added to the rooting medium and the foliar treatment with leaves sprayed twice. Similarly for number of diseased roots, there was considerable variability and the benefit of Cu was significant at  $P = 0.05$  for only three treatments, 0.06 and 0.08  $\mu\text{g Cu/ml}$  (3 and 4 H, respectively), and the foliar treatment with leaves sprayed once. Nevertheless, the plants receiving Cu through the roots or leaves had visually less take-all, and this was reflected in the disease severity index ratings (Fig. 3) which, compared with 0 Cu, were significantly lower for four treatments, ie, 0.04 and 0.06  $\mu\text{g Cu/ml}$  applied to the rooting medium and both foliar treatments.

In the third growth-chamber experiment Cu, Zn, and Mn each resulted in significantly more roots per plant when applied through the leaves, but not when applied to the rooting medium (Table 1). Iron and the combination treatment also increased the total number of roots, but the increase was not significant,  $P = 0.05$ . The number of diseased roots and the disease severity index were less for Cu and Zn whether supplied through either the leaves or roots. In contrast, application of Mn, Fe, or the combination treatment (a mixture of Cu, Zn, Mn, and Fe) reduced disease when supplied through the roots, but not when supplied through the foliage.

In all experiments with trace nutrients, uninoculated plants (controls) from treatments lacking a particular nutrient were about the same size as plants supplied with the nutrient, at least during the 40–50 days the plants were allowed to grow in the pots. Deficiency symptoms were apparent mainly in the leaves and disappeared when the missing nutrient was supplied.

**Influence of P and trace nutrients on take-all under field conditions.** Four levels of disease intensity occurred in the respective split-split blocks in the experiment at Lind. These four levels were distinguished by the mean percentage of diseased roots in respective check plots where N, but no P or Zn, was applied (Table 2). The four levels of intensity were: (i) 13.7% diseased roots in the blocks where the soil was fumigated but no inoculum was introduced (disease from inoculum that survived the fumigation); (ii) 34.0% diseased roots in unfumigated, uninoculated blocks (ie, those having natural inoculum only); (iii) 73.0% diseased roots in blocks where the pathogen was introduced into unfumigated soil; and (iv) 83.0% diseased roots in blocks where the pathogen was introduced into fumigated soil.

Total number of roots per plant in unfumigated soil at Lind without added inoculum (treatment ii, natural inoculum only) was highest when P alone was added (average of 26.3 roots per plant with P compared with 22.0 roots per plant for no added P), but the increase was not significant. Moreover, the number of diseased roots per plant and the percentage of diseased roots were generally less when P alone was added, but again the differences from the control were not significant at  $P = 0.05$  (Table 2). The number and percentage of diseased roots was reduced significantly ( $P = 0.05$ ) over that in the control only by Zn or by P plus Zn, and then only at

the lower levels of disease intensity (Table 2).

At Puyallup, in plots with natural inoculum only, addition of either Cu or Zn resulted in significantly ( $P = 0.05$ ) fewer diseased roots, sufficiently so that the benefit was also measurable as a significantly lower percentage of diseased plants (Table 3). The same pattern of less disease measured by either a lower proportion of diseased roots and diseased plants probably occurred in response to the combination (mixture of Cu, Zn, Mn, and Fe) treatment, but the difference fell slightly short of significance at  $P = 0.05$  for percentage of diseased roots. Disease intensity was greater in blocks in which the pathogen was introduced and under this condition all three trace nutrient treatments gave significantly fewer diseased roots, with the benefit from Zn being sufficiently great to also be measurable as a significantly lower percentage of diseased plants (Table 3).

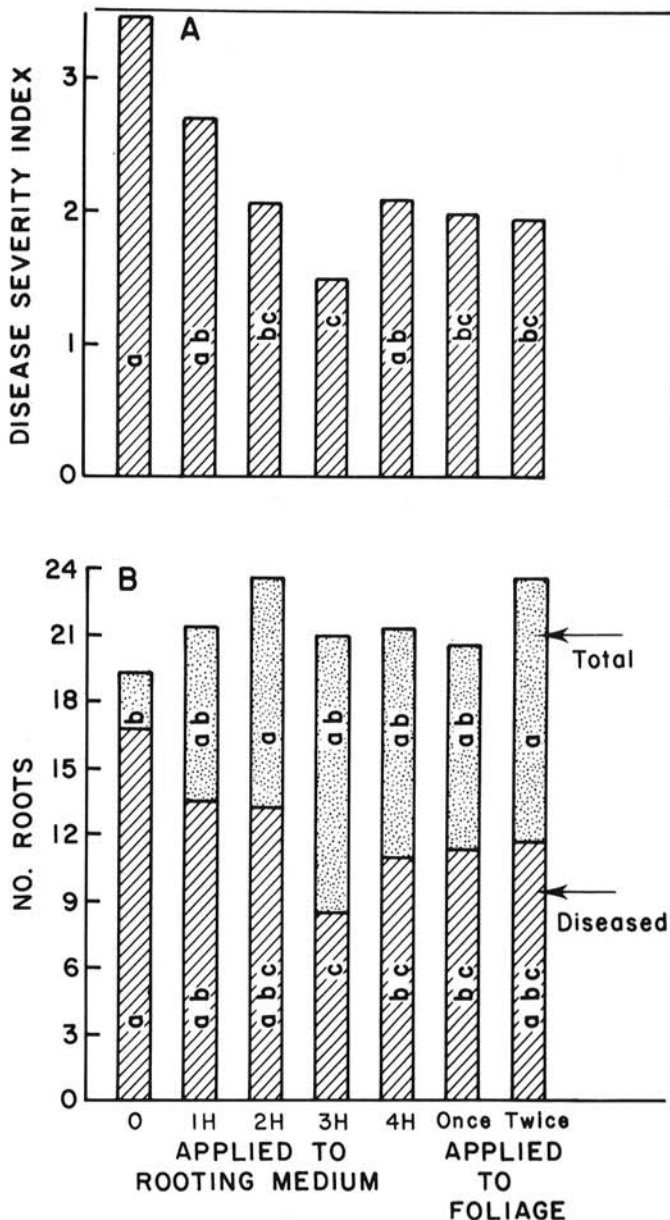


Fig. 3. Influence of copper on take-all caused by *Gaeumannomyces graminis* var. *tritici* on Fielder spring wheat grown in silica sand, with the copper applied at zero, 1 H (normal Hoagland strength), 2 H, 3 H, or 4 H to the rooting medium, or as a water solution sprayed once or twice on the foliage. A, Total number of roots and number of diseased roots per plant. B, Disease severity index on a scale of 0–4. Bars not sharing a common letter are significantly different according to Duncan's multiple range test,  $P = 0.05$ .

TABLE 1. Effect of micronutrients, applied in solutions to the rooting medium or sprayed on the leaves, on take-all of wheat caused by *Gaeumannomyces graminis* var. *tritici*

| Micronutrient tested | Total roots         |                                |                            | Diseased roots  |                                |                            | Disease rating 0—4 |                                |                            |
|----------------------|---------------------|--------------------------------|----------------------------|-----------------|--------------------------------|----------------------------|--------------------|--------------------------------|----------------------------|
|                      | Nutrient absent     | Solution to roots <sup>x</sup> | Foliage spray <sup>y</sup> | Nutrient absent | Solution to roots <sup>x</sup> | Foliage spray <sup>y</sup> | Nutrient absent    | Solution to roots <sup>x</sup> | Foliage spray <sup>y</sup> |
| Cu                   | 12.1 b <sup>z</sup> | 11.4 ab                        | 13.7 a                     | 56.8 a          | 47.3 bc                        | 49.7 ab                    | 1.9 c              | 1.1 a                          | 1.7 ab                     |
| Zn                   | 12.5 b              | 12.1 c                         | 13.3 a                     | 63.0 a          | 53.5 b                         | 53.6 b                     | 2.5 a              | 1.4 bc                         | 1.9 b                      |
| Mn                   | 11.6 c              | 12.7 ab                        | 13.3 a                     | 70.1 a          | 47.6 c                         | 60.7 b                     | 3.2 a              | 1.4 b                          | 3.3 a                      |
| Fe                   | 12.1 ab             | 11.4 c                         | 12.5 a                     | 66.3 a          | 47.7 c                         | 60.1 ab                    | 3.0 a              | 1.2 c                          | 2.5 ab                     |
| Cu, Zn, Fe, Mn       | 11.0 b              | 11.8 a                         | 12.5 a                     | 74.3 ab         | 47.7 c                         | 84.7 a                     | 3.4 ab             | 1.3 c                          | 3.7 a                      |

<sup>x</sup>Concentrations were four times the amounts of Hoagland's solution: Cu, 0.08 ppm; Zn, 0.2 ppm; Mn, Fe, 20 ppm.

<sup>y</sup>Solutions sprayed at four intervals on the foliage: Cu as 0.1% CuSO<sub>4</sub>·5H<sub>2</sub>O; Zn as 0.5% ZnSO<sub>4</sub>·7H<sub>2</sub>O; Mn as 0.1% MnSO<sub>4</sub>·7H<sub>2</sub>O; and Fe as 0.5% FeSO<sub>4</sub>·7H<sub>2</sub>O. Plants watered with solutions lacking the element to be applied as a foliar spray.

<sup>z</sup>Each value is the mean of four replicates with five seedlings per pot. Analyses for a given micronutrient treatment are based on differences among absence, supplied to roots and sprayed on leaves of any given method of assessment. Reading across, values with a common letter are not significantly different according to Duncan's multiple range test, *P* = 0.05.

TABLE 2. Effect of phosphorus and zinc on take-all caused by *Gaeumannomyces graminis* var. *tritici* in field plots of spring wheat at Lind, WA, 1978

| Treatment               | Plots not fumigated |         |                     |        | Plots fumigated  |        |                     |        |
|-------------------------|---------------------|---------|---------------------|--------|------------------|--------|---------------------|--------|
|                         | Natural inoculum    |         | Introduced inoculum |        | Natural inoculum |        | Introduced inoculum |        |
|                         | Diseased roots      |         | Diseased roots      |        | Diseased roots   |        | Diseased roots      |        |
|                         | (No.)               | (%)     | (No.)               | (%)    | (No.)            | (%)    | (No.)               | (%)    |
| Control                 | 6.9 a <sup>x</sup>  | 34.0 a  | 15.6 a              | 73.0 a | 2.9 a            | 13.7 a | 12.7 a              | 83.0 a |
| Phosphorus <sup>y</sup> | 6.4 a               | 24.4 ab | 14.6 a              | 68.6 a | 1.8 a            | 7.4 ab | 13.5 a              | 83.3 a |
| Zinc <sup>z</sup>       | 3.6 b               | 19.5 b  | 10.5 b              | 69.1 a | 1.7 a            | 6.2 b  | 11.9 a              | 82.6 a |
| P + Zn                  | 5.4 ab              | 23.6 ab | 14.2 a              | 73.6 a | 1.0 a            | 4.8 b  | 12.7 a              | 86.4 a |
| Mean                    | 5.6                 | 25.4    | 13.7                | 71.1   | 1.9              | 7.8    | 12.7                | 83.8   |

<sup>x</sup>Each value is the mean of four replicates, with 25 plants assessed per replicate. For each variable, values with a common letter are not significantly different according to Duncan's multiple range test, *P* = 0.05.

<sup>y</sup>H<sub>3</sub>PO<sub>4</sub>, 58 kg P/ha.

<sup>z</sup>ZnCl<sub>2</sub>, 10.0 kg Zn/ha.

TABLE 3. Influence of micronutrients on take-all caused by *Gaeumannomyces graminis* var. *tritici* on winter wheat at Puyallup, WA, 1979

| Treatments                  | Natural inoculum     |                     | Introduced inoculum  |                     |
|-----------------------------|----------------------|---------------------|----------------------|---------------------|
|                             | Diseased roots (No.) | Diseased plants (%) | Diseased roots (No.) | Diseased plants (%) |
| Control                     | 1.6 a <sup>w</sup>   | 78.6 a              | 5.2 a                | 92.7 a              |
| Zinc <sup>x</sup>           | 1.2 b                | 55.7 b              | 1.4 c                | 63.6 b              |
| Copper <sup>y</sup>         | 1.1 b                | 57.8 b              | 3.2 b                | 89.2 a              |
| Zn, Cu, Mn, Fe <sup>z</sup> | 1.3 ab               | 66.9 b              | 3.3 b                | 90.6 a              |

<sup>w</sup>Each value is the mean of four replicates with 25 plants sampled per plots. For each variable, values with a common letter are not significantly different according to Duncan's multiple range test, *P* = 0.05.

<sup>x</sup>ZnSO<sub>4</sub>·7H<sub>2</sub>O, 10 kg Zn/ha.

<sup>y</sup>CuSO<sub>4</sub>·5H<sub>2</sub>O, 5 kg Cu/ha.

<sup>z</sup>MnSO<sub>4</sub>·7H<sub>2</sub>O, 10 kg Mn/ha + FeSO<sub>4</sub>·7H<sub>2</sub>O, 10 kg Fe/ha + Zn + Cu.

## DISCUSSION

Take-all severity on wheat depends on the supply of both macronutrients and micronutrients to the host, but apparently some nutrients are more important than others. Changing the amount of individual macronutrients from half to twice the concentration in Hoagland's solution resulted in significantly less take-all where P, K, and Mg were the variables, but not where N, Ca, or S were the variables. With trace nutrients, changing from none to twice the amount in Hoagland's solution gave significantly less take-all with Cu, Zn, and possibly Mn. The presence of some solid-phase Fe as a natural constituent of the silica rooting medium (0.028%) may have resulted in sufficient available Fe in the wheat root zone to override Fe as a treatment variable. To our knowledge, the data presented herein provide the first demonstration that not only macronutrients such as P, K, and apparently Mg, but also

micronutrients such as Zn, Cu, and Mn may suppress take-all.

A problem encountered throughout this study was how to document, in numerical terms, differences between treatments that commonly were obvious to the eye. Often the data obtained fell short of statistical significance at *P* = 0.05, in spite of apparent differences. The use of two methods of disease assessment, incidence of diseased roots and the disease severity index, partially overcame this problem. A significant difference obtained by one method of assessment within a given treatment is probably a good indication of the effects of that treatment even if data obtained by the other method of assessment fell short of statistical significance. Using this criterion, Cu suppressed take-all in the growth-chamber experiments when provided in the nutrient solution to the roots at 0.04 µg/ml (2 H) in the first experiment (Fig. 2); 0.04, 0.06, and 0.08 µg/ml in the second experiment (Fig. 3); and 0.08 µg/ml in the third experiment (Table 3). Copper also suppressed disease in both experiments when applied to the leaves (Fig. 3 and Table 1), including when applied only once (Fig. 3). The addition of Zn suppressed take-all when provided to the roots in a solution containing 0.1 µg/ml (2 H) in one experiment (Fig. 2), at 0.1 µg/ml in a second experiment (Table 3), and also when provided through the leaves. The disease-suppressing benefits of Zn were confirmed in two field trials, and for Cu in the one (only) field trial where Cu was tested. Neither Mn nor Fe resulted in less disease when provided at 2 H through the roots in one growth-chamber experiment (Fig. 2) but both did so in a second experiment in which the concentration was doubled to 4 H. The results with Mn and Fe are less clear-cut compared with Cu and Zn, but probably these elements are no less important to take-all control, given conditions where they are deficient.

The suppression of take-all by plant nutrients is apparently an effect on the host and not a direct effect against the pathogen. Nutrient treatments resulting in less take-all were generally the same treatments resulting in the greatest root development by the host. Earlier workers made this observation for P (8,20) and N (8);

it appears that the principle can be extended to Mg, K, and certain trace nutrients as well. In addition, the benefits of Cu and Zn when applied only to the foliage provides further evidence of an effect on the host rather than a direct effect against the pathogen.

An increase in number of roots per plant is presumably an indication of enhanced plant vigor resulting from the nutrient treatment. A decrease in absolute number of diseased roots on fertilized plants suggests that host-plant resistance to take-all has been enhanced along with the greater plant vigor. The benefits of plant nutrients are thus twofold: increased resistance to take-all within a given plant and greater capacity of the plant to tolerate infections by producing more roots. Garrett (8) concluded that the plant produced more roots when N was added to soil but that the intrinsic resistance to take-all within a given root was not improved by N fertilization or was even possibly less. His conclusion is supported by our data; N-fertilized plants produced significantly more roots but neither the number of diseased roots nor the disease severity changed significantly.

In one greenhouse experiment with trace nutrients, disease was less when a solution containing either Fe or Mn (at 4 H) was applied to the rooting medium, but not when Fe or Mn were sprayed on the leaves of deficient plants (Table 1). Likewise, when a combination of all four trace nutrients (Cu, Fe, Mn, and Zn) was sprayed on the foliage, disease intensity was not reduced, suggesting that one or more nutrients were still deficient, as measured by the take-all reaction. Manganese deficiency symptoms in the leaves (chlorotic and necrotic flecks) were alleviated by the foliar applications, suggesting foliar uptake of this element. Possibly these elements were not translocated from the leaves to the roots where they were needed for take-all control.

The amount of inoculum of *G. graminis* var. *tritici* may be an important consideration in the ability of micronutrients or macronutrients to reduce take-all in the field. For example, under irrigation at Lind, Zn reduced take-all significantly ( $P=0.05$ ) at the lowest level of disease intensity, but none of the nutrient treatments were significantly effective at higher disease intensities. In the Puyallup experiment, the suppression of disease following applications of Zn, Cu, and a mixture of Zn, Cu, Mn, and Fe was reflected as significantly lower percentage of infected plants in blocks with natural inoculum only. Only Zn resulted in a significantly lower percentage of diseased plants where inoculum of *G. graminis* var. *tritici* was introduced. The field results are encouraging, however, since in both trials the lower disease intensities occurred with natural inoculum and the higher intensities with introduced inoculum. The findings agree with those of Slope et al (18), who showed that P reduced take-all when the inoculum potential of *G. graminis* var. *tritici* was low, but not when the fungus was common in the soil. Some disease control benefit of fertilization should, therefore, be possible by growers if practiced as part of a regular take-all prevention program.

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