Occurrence of *Fusarium* Species in Roots and Stalks of Symptomless Corn Plants During the Growing Season

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ABSTRACT

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The same *Fusarium* spp. were isolated throughout two seasons (1974-1975) from roots and stalks of three corn hybrids differing in resistance to root lodging. Whereas *Fusarium* spp. infected 90% of the plants sampled by July and 100% by mid-August, they were isolated infrequently from stalks in July until after silking. By early September, about 90% of the stalks were infected, even though no symptoms of stalk rot were apparent. As the season progressed, often more than one *Fusarium* spp. was isolated from a single stalk and as many as five species were isolated from some stalks by mid-October. *Fusarium oxysporum* and *F. solani* were isolated from roots more frequently than from stalks, and *F. moniliforme* and *F. tricinctum* were isolated from stalks more frequently than from roots. *F. roseum* appeared more frequently in roots than in stalks until the end of August when it occurred more frequently in stalks. Of *F. roseum* populations, those in the cultivar Equiseti predominated followed by Acuminatum; Graminearum was only occasionally isolated from roots or stalks. When cornstalk stubble was sampled from the same plot in spring 1976, the *Fusarium* spp. were the same as those isolated the previous fall, except that *F. moniliforme* was absent.

Fusarium species are ubiquitous in roots and stalks of corn and most other plants. They exist as saprophytes in moribund tissues of living hosts (2,5,17,23) or as opportunistic pathogens awaiting stress in the host (20). Five of the nine *Fusarium* spp., *sensu* Snyder and Hansen (19) and at least six cultivars of *F. roseum* (18) have been isolated from roots and stalks of corn (6,7,22). The same species and cultivars frequently are found in soils where cereals, including corn, are grown (8,21,24). Yet, when tested singly, many of the species and cultivars are not pathogenic, or are weakly so, and do not cause root or stalk rot of the severity generally seen in cornfields. We commonly isolate several species of *Fusarium* from the same small fragment of host tissue, whether the host is living or dead (25). It is not clear whether *Fusarium* spp. cause disease as part of a *Fusarium* spp. complex or whether they are part of an ecological succession also involving other fungi (5,27).

We attempted to ascertain (i) the colonization of roots and stalks of corn by *Fusarium* spp. through the growing season before stalk rot symptoms appear and (ii) if a relationship exists between incidence of root and of stalk infection through the season.

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MATERIALS AND METHODS

Three hybrids of corn (*Zea mays* L.), differing in resistance to root lodging, were planted in 1974 and 1975. Minhybrid 5302 was rated as resistant, Minhybrid 508 as moderately resistant, and Minhybrid 511 as susceptible to root lodging (Corn Performance Trials, University of Minnesota). Field plots were located at the University of Minnesota, St. Paul. In 1974, corn was planted in a randomized complete block design in a corn-on-corn plot, but because of a potentially high corn rootworm population, in 1975 the experiment was done on an adjacent plot that had been planted to oats the previous season. There were three rows per hybrid in 1974 and four rows per hybrid in 1975 for each of four replicates. Corn was planted mechanically at about 120 kernels per 40-m row on 22 May 1974 and 14 May 1975. The herbicide cyanazine (2-[[4-chloro-6-(ethylamino)-*s*-triazin-2-yl]amino]-2-methylpropionitrile) was applied in both years.

Roots and stalks of corn were sampled every 2 wk from mid-July to early October 1974 and from early July to mid-October 1975; stalks only were sampled an additional time in late October 1975. Stalks were sampled by collecting a core from the first internode above the brace roots using a bark increment hammer (Fig. 1). At each sampling time, 25 cores were collected for each hybrid per replicate. Every tenth plant in the row was sampled and a 10-cm stake was placed by each as a marker to avoid resampling the same plant.

Root samples were collected by inserting an Oakfield soil sample tube at an angle of 45° directly under the corn plant. Root systems of each hybrid per replicate were sampled from 10 plants that also had been sampled for stalk cores. In 1975, five root systems rather than 10 were sampled the first two times. Soil was washed from the roots in a sieve and 10 adventitious root fragments, 1–2 cm long, were selected at random from each root system.

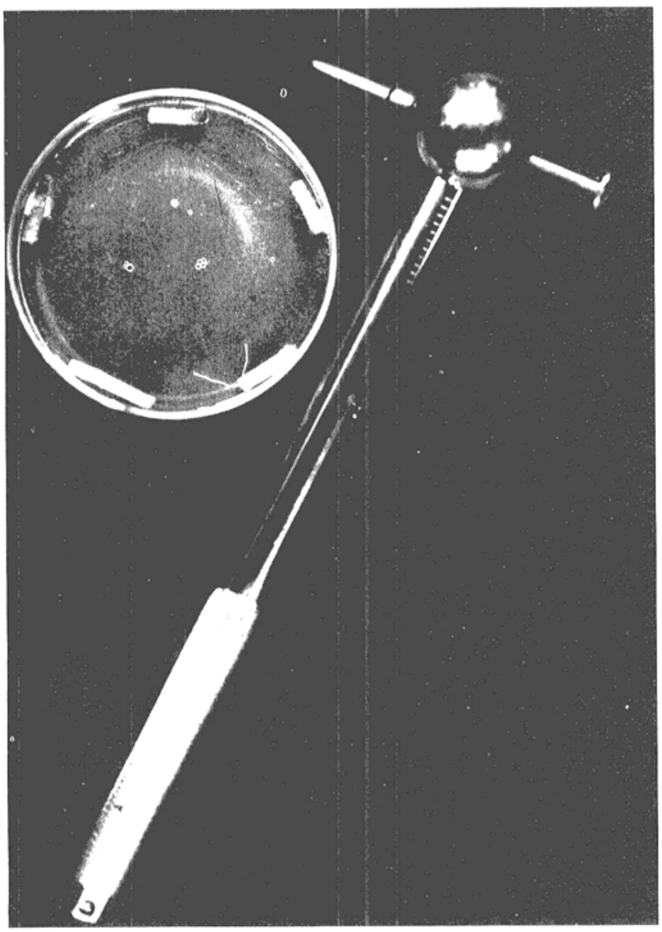

Fig. 1. Bark increment hammer used to obtain sample cores from corn stalks. Cores are on the surface of the assay medium at the periphery of the petri dish.

The stalk cores and root sections were surface-treated in 0.5% sodium hypochlorite for 30 sec, drained, and placed on Aureomycin-supplemented pentachloronitrobenzene (PCNB) agar, a selective medium for isolation of *Fusarium* spp. (11).

One-hundred seeds of each hybrid were surface-treated in 1% NaOCl for 2 min to determine if the sown kernels carried *Fusarium* spp. Kernels were cut in half longitudinally with a sterile bone cutter, and both halves were placed on PCNB agar.

After 7–10 days, *Fusarium* colonies were transferred from PCNB agar to acidified homemade potato dextrose agar (PDA) and incubated under fluorescent light at 5,300 lux, 16 hr/day, for at least 7 days to stimulate sporulation. Cultures were identified to species using the system of Snyder and Hansen (19).

Analyses of variance were calculated from data collected for each sampling date for each species isolated from the three corn hybrids. Correlation coefficients between root and stalk infections were computed for each sampling date for *F. moniliforme*, *F. oxysporum*, and *F. roseum* to determine if a relationship existed between their incidence in roots and stalks.

RESULTS

Seedborne *Fusarium* spp. The incidence of *Fusarium* spp. in the kernels planted in 1974 and 1975 was low (averaging only 4%); only *F. moniliforme* (Sheld.) emend. Snyd. & Hans. and *F. oxysporum* Schl. emend. Snyd. & Hans. were isolated. Thus, kernels were a possible but unlikely source of inoculum for infection of roots and stalks.

***Fusarium*-infected roots and stalks.** More roots than stalks were infected by *Fusarium* spp., regardless of the hybrid or sampling date. There were no statistical differences among cultivars in colonization of roots for each sampling date. Therefore, each point in the figures gives the average infection based on 120 root systems. The degrees of freedom used in the figures differ for total colonization and for each species because, when the incidence of colonization was low (<1%) or high (>98%), variances were small and therefore not used when homogeneous errors were pooled.

Fusarium spp. occurred in roots of 80% of the plants in July and in about 100% in August (Fig. 2A). The order of prevalence of *Fusarium* spp. in roots throughout most of the season for both years was: *F. oxysporum*, *F. solani* (Mart.) Appl. & Wr. emend. Snyd. & Hans., *F. roseum* (Lk.) emend. Snyd. & Hans., *F. moniliforme*, and *F. tricinctum* (Cda.) emend. Snyd. & Hans. More than one species was sometimes found per root fragment, and generally *F. oxysporum* and *F. solani* were included; several *Fusarium* spp. could be found in the root system of one plant.

For each sampling date, there were no statistical differences among hybrids in colonization of stalks. Therefore, each point in

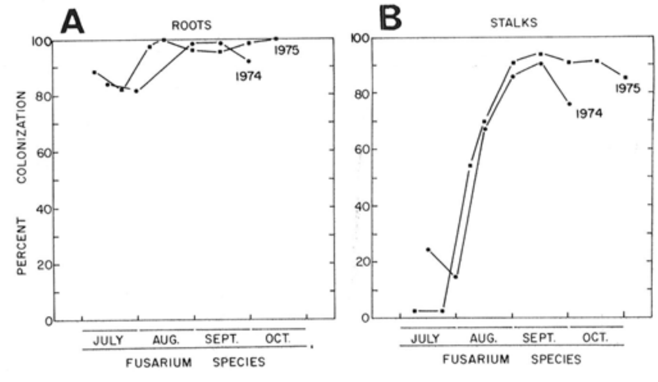

Fig. 2. Incidence of *Fusarium* spp. in 1974–1975: **A,** corn roots (SD = 1.49, df = 48) and **B,** corn stalks (SD = 0.99, df = 90). Each point represents the average number of isolations from 120 root systems and the average isolations from 300 cornstalks.

the figures represents the percentage of 300 cornstalks from which the fungus was isolated.

Fusarium spp. occurred infrequently in stalks in early July but increased steadily during both seasons until early September, when *Fusarium* spp. were isolated from 90% of the stalks (Fig. 2B). The order of prevalence throughout most of the season for 1974 was: *F. moniliforme, F. roseum, F. oxysporum, F. tricinctum,* and *F. solani.* In 1975, the order of occurrence was: *F. roseum, F. oxysporum, F. moniliforme, F. tricinctum,* and *F. solani.*

F. moniliforme. This species was not found in cornstalks until the end of July, which coincided with silking. From then on, the species was isolated more frequently from stalks than from roots (Fig. 3). By mid-September, *F. moniliforme* was isolated from twice as many stalks in 1974 as in 1975 (55 vs. 28%) (Fig. 3B and D). *F. moniliforme* colonized a greater number of stalks of Minhybrid 508 (rated as moderately resistant to root lodging in the corn performance trials at Minnesota) in mid-August of both seasons ($P = 0.05$ in 1974 and 1975) and was consistently the most frequently colonized hybrid throughout both seasons, although no statistical significance was found. This species also was more frequently isolated from roots of Minhybrid 508, although the trend was not as pronounced for roots as for stalks (Fig. 3A and C). The incidence of *F. moniliforme* in stalks was lowest in Minhybrid 5302 (rated as resistant to root lodging).

F. roseum. This species was isolated more frequently from roots than from stalks until the beginning of September, when it was isolated more frequently from stalks than from roots (Fig. 4). There were no statistical differences among the hybrids in either roots or stalks colonized by *F. roseum* for any of the sampling dates. *F. roseum* occurred more frequently in roots and stalks in 1975 than in 1974. It was more than twice as prevalent on roots in 1975 than in 1974, but the incidence decreased to about 20% by the end of both seasons (Fig. 4A).

F. roseum was isolated from stalks early in July and with increasing frequency through the season (Fig. 4B). *F. roseum* was isolated from 10% of the stalks in July 1974, reached a high of 46% in September, and decreased to 40% by October. However, *F. roseum* infected fewer than 5% of the stalks in July 1975, but it was recovered from 78% by mid-September; then it decreased to 63% by the end of October. The order of prevalence in both seasons of *F. roseum* cultivars isolated from both roots and stalks was: Equiseti, Acuminatum, and Graminearum (Fig. 5). Equiseti and Acuminatum were isolated more frequently from stalks than from roots; Graminearum was rarely isolated.

In both seasons *F. roseum* 'Equiseti' was more common in roots than in stalks until the end of August when it became more common in stalks than in roots (Fig. 5A and B). Differences among hybrids

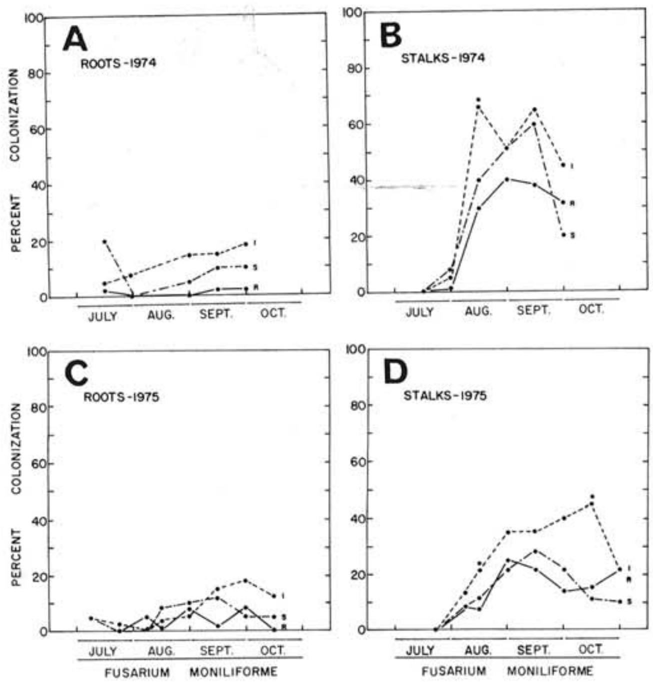

Fig. 3. Incidence of *Fusarium moniliforme* in corn roots **A**, in 1974, and **C**, in 1975 (SD = 1.37, df = 66), and in stalks in **B**, 1974 and **D**, 1975 (SD = 2.39, df = 66). R = resistant (Minhybrid 5302); I = intermediate (Minhybrid 508), and S = susceptible (Minhybrid 511). Each point represents the average number of isolations from 120 root systems and the average isolations from 300 cornstalks.

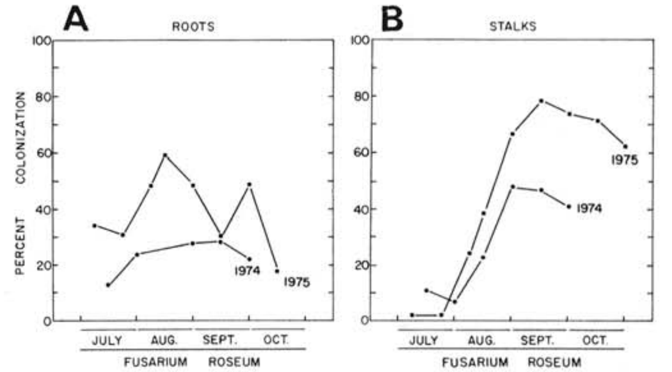

Fig 4. Incidence of *Fusarium roseum* in 1974–1975: **A**, corn roots (SD = 1.74, df = 78) and **B**, cornstalks (SD = 1.23, df = 90). Each point represents the average number of isolations from 120 root systems and the average isolations from 300 cornstalks.

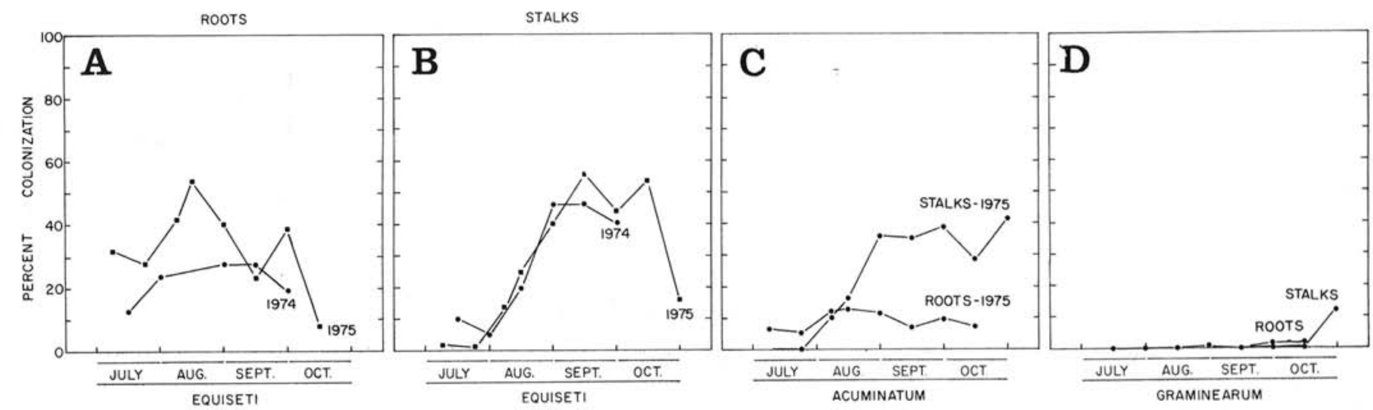

Fig. 5. Incidence of *Fusarium roseum* on corn roots and stalks in 1974–1975: **A**, Equiseti in roots (SD = 1.69, df = 78); **B**, Equiseti in stalks (SD = 1.51, df = 78), **C**, Acuminatum in roots and stalks in 1975 only (SD = 1.39, df = 48), and **D**, Graminearum in roots and stalks. Each point represents the average number of isolations from 120 root systems and the average number of isolations from 300 cornstalks, except for Graminearum, where each point represents the average isolations of 240 root systems and 600 cornstalks.

colonized by Equiseti were not significant ($P = 0.05$) in either roots or stalks. *F. roseum* 'Equiseti' was isolated from nearly twice as many roots in 1975 as in 1974, but in both years, Equiseti reached its highest incidence in roots by mid-August. Occurrence in stalks was similar for both years, and the greatest frequency was reached in September.

Our earlier use of the name Gibbosum is not consistent with the use by Nash and Snyder (12), who included both Acuminatum and Equiseti. In the earlier work of Snyder et al (18), only six cultivars of *F. roseum* were listed and Gibbosum was not one of them. In our work we recognized three distinct morphological types within Gibbosum, which we identified as Acuminatum, Equiseti, and a third type that we previously called Gibbosum (6–9, 24–26) because it differed from Acuminatum typically found. We now think it is a variant of Acuminatum and we have isolated it more frequently than the typical "red" Acuminatum populations. "Wild type" isolates of this Acuminatum were light pink to peach, floccose, rather fast growing, and usually with orange sporodochia in the center of the colony. In reverse, cultures ranged from peach to buff and occasionally were interspersed with carmine. Macroconidia varied in shape and size, but most spores appeared to be intermediate between Equiseti and Acuminatum. These characteristics remained stable in most single-spored isolates, but with subsequent transfers, some cultures became pionnotal and others became more carmine. Macroconidia were extremely variable in shape and smaller in size than those of the wild type; some resembled microconidia.

F. roseum 'Acuminatum' was isolated from fewer than 2% of the roots in 1974 and 15% in 1975 (Fig. 5C). Acuminatum was isolated from fewer than 3% of the stalks throughout the season in 1974, but in 1975 it was isolated from stalks in early August and increased steadily to more than 40% by the end of October, the last sampling date (Fig. 5C). Minhybrid 508 was significantly more frequently colonized by Acuminatum in early and mid-October than were the other two hybrids.

Both *F. roseum* 'Graminearum' and the typical "red" 'Acuminatum' were isolated infrequently from stalks. At the end of October 1975, however, Graminearum was isolated from 12% of the stalks (Fig. 5D) and the typical "red" Acuminatum from only 5%.

F. oxysporum. This species was isolated more frequently from roots than from stalks throughout both seasons (Figs. 6A and B). There were no statistical differences among the three hybrids in either roots or stalks colonized by *F. oxysporum* for any of the sampling dates. Infection of roots was more than 70% in July and increased to more than 90% by mid-August, whereas *F. oxysporum* was isolated from fewer than 10% of the stalks in July and reached its peak occurrence of about 40% by mid-September in 1974 and late September in 1975.

F. solani. This species was isolated from roots more frequently than from stalks in both years (Figs. 6C and D). There were no statistical differences among the three hybrids colonized by *F. solani* for any of the sampling dates in either roots or stalks. In 1974, *F. solani* infected 40% of the root systems by mid-July, and increased to 80% by mid-September; but in 1975, it was isolated from 20% of the roots in mid-July and reached 60% by mid-October. The average incidence of cornstalks infected by *F. solani* was less than 5% in both seasons.

F. tricinctum. This species occurred infrequently but was more common in stalks than in roots (Fig. 6E). There were no overall differences in occurrence of *F. tricinctum* in the two seasons, so root and stalk data for 2 yr, respectively, were combined. There were no differences among hybrids in 1974, except during mid-September when *F. tricinctum* was isolated from 32% of the stalks of Minhybrid 5302 ($P = 0.05$) and from fewer than 5% of the stalks of Minhybrid 511 and 508. By the end of October, it was isolated from 5% of the stalks of Minhybrid 5302. In 1975, there were no differences among hybrids throughout the season, but *F. tricinctum* became more prevalent in stalks at the end of the season. It was isolated from 30% of the stalks by the end of October.

***Fusarium* spp. in stalk debris after harvest.** Of the cornstalks collected at the end of October 1975, 85% were colonized by *Fusarium* spp., whereas of the stalk debris collected from the same field in May 1976, 78% were colonized. Percentage of stalks colonized in fall 1975 and spring 1976, respectively, were similar for *F. roseum* (63 vs. 68%), *F. tricinctum* (31 vs. 30%), and *F. solani* (<1 vs. 2.5%). *F. oxysporum* was isolated more frequently in the fall than in the spring (30 vs. 15%), and *F. moniliforme* was not isolated in the spring (20 vs. 0%). Occurrences of *F. roseum* populations in the fall and spring, respectively, were: Acuminatum (46 vs. 58%), Equiseti (15 vs. 5%), Graminearum (12 vs. 10%), and Avenaceum (<1 vs. 5%).

Multiple stalk infections by *Fusarium* spp. As the season progressed, the incidence of more than one *Fusarium* spp. per tissue fragment increased (Fig. 7A). Single *Fusarium* spp. were found in most colonized stalks in early July; but by the end of July, two species could be isolated per core sample; in mid-August, three species; in late August, four species, and in October, five species. In July, *F. roseum* 'Equiseti,' *F. moniliforme,* and *F. oxysporum* were isolated singly; but by the beginning of August these species were found with another *Fusarium* spp. in the same core sample 50% of the time (Figs. 7B, C, and D). Although, frequency with which *F. roseum* 'Equiseti' was isolated singly increased throughout the season (Fig. 7B), *F. oxysporum* remained the same (Fig. 7D), and *F. moniliforme* decreased (Fig. 7C).

Relationship between root and stalk infections. Correlation coefficients between incidence of root and stalk infection for *F. moniliforme, F. roseum,* and *F. oxysporum* were determined. There were no significant correlations between incidence of root and stalk infections for these species. However, in both seasons *F. moniliforme* was most often found only in the stalks and was infrequently found only in roots or in stalks and roots of the same plant (Fig. 8A). Until mid-August *F. roseum* was found more frequently in roots than in stalks of the same plant but thereafter was isolated more frequently from stalks only (Fig. 8B). *F. oxysporum* was more often found only in roots in both seasons, but

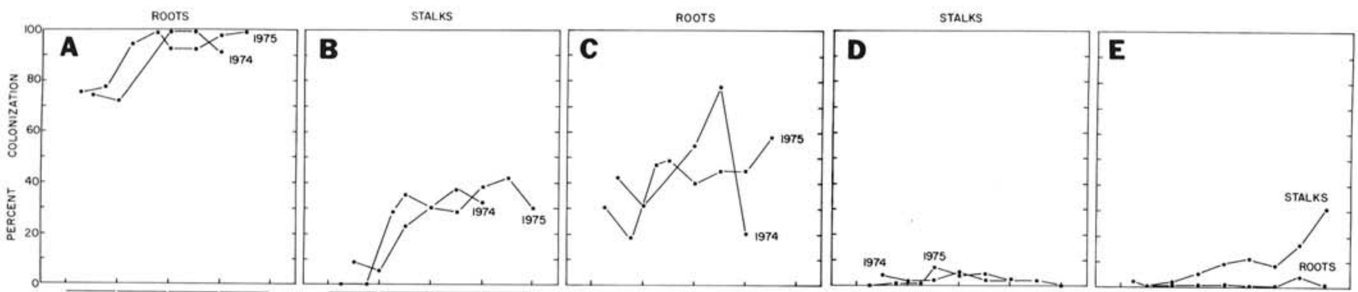

Fig. 6. Incidence of *Fusarium* species in corn roots and stalks for 1974–1975: **A,** *F. oxysporum* in roots (SD = 1.77, df = 54), **B,** *F. oxysporum* in stalks (SD = 1.49, df = 78); **C,** *F. solani* in roots (SD = 1.81, df = 78); **D,** *F. solani* in stalks (SD = 0.59, df = 60) and **E,** *F. tricinctum* in roots (SD = 0.71, df = 54) and stalks (SD = 0.94, df = 66). Each point represents the average number of isolations from 120 root systems and the average isolations from 300 cornstalks, except for *F. tricinctum,* where each point represents the average isolations from 240 root systems and 600 cornstalks.

it also was frequently found in both roots and stalks of the same plants in both seasons and only infrequently in stalks only (Fig. 8C).

DISCUSSION

In these and other studies representing 5 yr (1973-1977) of tissue sampling from cornstalks in commercial fields in Minnesota, one to five species of *Fusarium* were isolated from a given tissue sample from plants in which no symptoms of root and stalk rot were apparent. Thus, in inoculation experiments reported in the literature, the test fungus could have been invading tissue already occupied by fungi and the stalk infection reported was not solely the effect of *Fusarium* spp. but rather of a complex of species. In fact, it may be impossible to select healthy, ie, fungus-free stalks, in the field for inoculation by a single species.

The high degree of colonization of roots prior to colonization of stalks suggests that root infection leads to stalk infection. If so, we would expect a greater incidence of isolation from roots before invasion by these same species in stalks. We found only limited evidence of such a pattern of infection. Moreover, as the season progressed, more stalks than roots were infected with *F. moniliforme, F. roseum,* and *F. tricinctum,* indicating that the inoculum probably does not originate from infected roots.

Because *F. moniliforme* was rarely found in both roots and stalks of a given plant, the evidence seems convincing that infection of roots and stalks occurred independently. Moreover, the inoculum appeared to be disseminated primarily from aboveground sources. Inoculum of *F. moniliforme* disseminated either by wind or rain (16) and spore dispersal by the corn borer (1) or picnic beetle (26) are factors to consider in infection of stalks other than from roots.

F. roseum was more common in roots than in stalks of the same plant until early September, when it was isolated more frequently in stalks than in roots of the same plant. Some root infection may lead to stalk infection early in the season, but by the beginning of September it appears that inoculum must also have originated from crop refuse and become airborne. Lukezic and Kaiser (10) reported air dispersal of *F. roseum* 'Gibbosum,' and Nelson et al (13) detected airborne propagules of *F. roseum* 'Culmorum,' 'Gibbosum,' and 'Graminearum.' The relatively low incidence of *F. roseum* 'Graminearum' in stalks may be attributed to our examination of symptom-free plants. Had we isolated from plants showing symptoms of stalk rot, we might have found a much higher incidence of Graminearum, as was reported in 1957 by DeVay et al (3) in Minnesota.

F. oxysporum was found frequently in roots but rarely in stalks only. When it was isolated from stalks, it also was isolated from roots, but we do not know if the fungus was of the same strain.

The relationship between root and stalk infection is not clear. Perhaps too few root samples were assayed to detect all *Fusarium* spp. Brace roots might have served as means of entrance for *Fusarium* into stalks, but this was not investigated. Also, clones of *Fusarium* spp. may be more adapted to either soil or aerial environments.

As the season progressed, some species occurred less frequently in stalks and others became more common. The overall percentage of stalks colonized increased, and as many as four or five species occupied a tissue fragment by the end of the season. The incidence of stalks infected by a single species decreased later in the season. It is possible that *F. moniliforme* in stalks may be influenced by other *Fusarium* spp. because its occurrence decreased as that of other *Fusarium* spp. increased. Other species of *Fusarium* appeared to be more tolerant of coinfecting species, occupied different niches, or inhabited the same or contiguous tissues without inhibition or competition. We did not observe synergism among species or a pronounced sequence of infection. However, other organisms may play earlier roles in colonization. For example, *Pythium* spp. or *Pyrenochaeta terrestris* may be the pioneer inhabitants of roots, and these fungi are followed by *Fusarium* spp. or other fungi. Work by Young and Kucharek (27) suggests that communities of fungi function in succession in corn plants, although organisms may differ from season to season (4,9). The decrease in number of stalks colonized by *Fusarium* spp. at the end of the season probably occurred as tissues died, were consumed by fungi, or were recolonized by more competitive saprophytes with greater

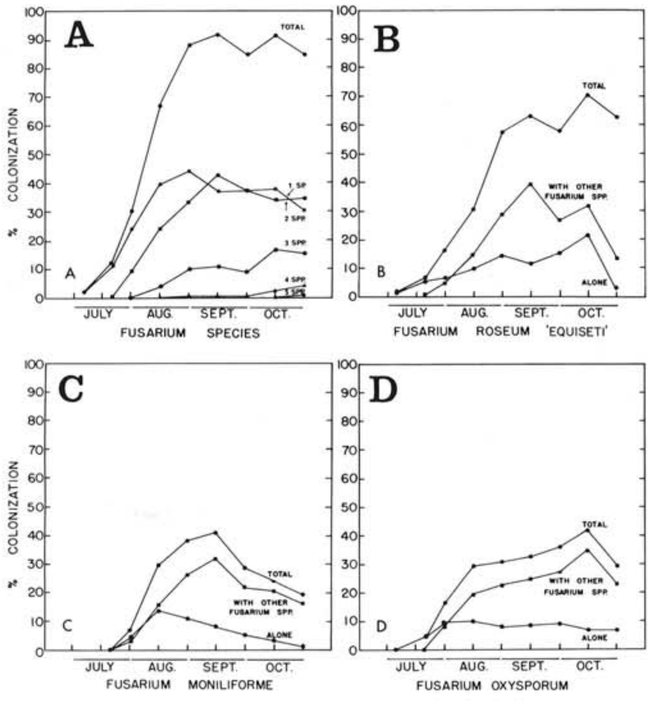

Fig. 7. Incidence of cornstalks infected with one or more *Fusarium* spp. in 1974–1975: **A**, numbers of species per stalk; **B**, percentage of stalks colonized by *F. roseum* 'Equiseti' alone or with other species; **C**, percent of stalks colonized by *F. moniliforme* alone or with other species; and **D**, percent of stalks colonized by *F. oxysporum* alone or with other species. Each point represents the average number of isolations from 240 root systems and the average isolations from 600 cornstalks.

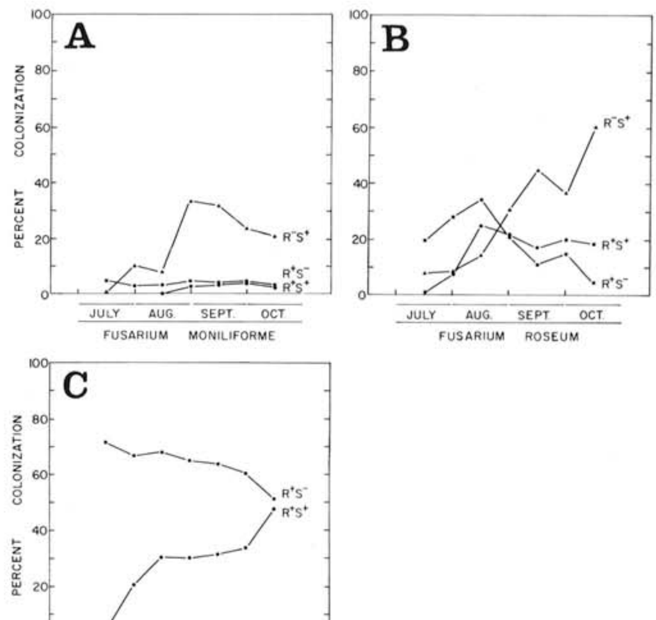

Fig. 8. Incidence of corn plants where only stalks (R^-S^+), only roots (R^+S^-), or both roots and stalks (R^+S^+) were colonized in 1974–1975 by: **A**, *Fusarium moniliforme*; **B**, *F. roseum*; and **C**, *F. oxysporum*. Each point represents the average number of isolations from 240 corn plants.

tolerances for a reduced water potential.

The *Fusarium* spp. overwintering in stalks on the ground were those that produce chlamydospores. *F. moniliforme* was not isolated from the crop debris on the soil surface, but it is reported to overwinter in buried crop debris as thickened hyphae (14,15).

The three hybrids used differed in root lodging ratings and were presumed to differ also in stalk rot susceptibility. They were colonized similarly by all *Fusarium* spp. except *F. moniliforme*. Stalks of Minhybrid 508 (moderately resistant to root lodging) were colonized or infected more frequently by *F. moniliforme* than were the other two Minhybrids. Whether corn hybrids selected over many generations for resistance to *F. roseum* 'Graminearum' without consideration of resistance to *F. moniliforme* could have resulted in hybrids more susceptible to the latter is open to conjecture.

There were seasonal differences in stalk infection in Minnesota. For example, over a 5-yr period, *F. moniliforme* colonized 21–93%, and *F. roseum* colonized 24–86% of stalks from 1973 to 1977 (9). However, in the 2 yr of the present study, results were not this variable. The variation might be related to differences in location as well as season.

In conclusion, it is likely that after anthesis most if not all stalks are naturally infected or colonized internally by one or more species of *Fusarium* and other fungi, without apparent symptoms of stalk rot, and that damage from these fungi depends on the degree of stress subsequently imposed on the plant by the environment.

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