Growth of Rhizosphere Competent and Incompetent *Fusarium* Species from Corn on Carbon Substrates

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ABSTRACT

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The ability of *Fusarium* isolates that are rhizosphere incompetent or competent on corn to grow on types of carbon common in the rhizosphere was examined in culture. When growth of *Fusarium* species was evaluated on glucose, pectin, carboxymethyl cellulose, microcrystalline cellulose, xylans, or xylose, *F. graminearum* produced a significantly greater hyphal dry weight than did *F. equiseti, F. moniliforme, F. oxysporum, F. proliferatum,* or *F. solani*, whereas *F. graminearum* produced fewer conidia than did the other species. Intraspecific variation in growth occurred among isolates of *F. graminearum, F. oxysporum,* and *F. proliferatum.* When *F. graminearum* was paired with *F. moniliforme, F. oxysporum,* or *F. proliferatum*, the numbers of macroconidia and colony-forming units of *F. graminearum* were lower than those obtained from cultures of *F. graminearum* grown alone. *F. moniliforme, F. oxysporum,* and *F. proliferatum* generally yielded no difference in conidial or colony-forming unit production when in dual culture with *F. graminearum* as when cultured singly. These data suggest that *F. graminearum* is less competitive than or is suppressed by *F. moniliforme, F. oxysporum,* and *F. proliferatum* and, therefore, could not be rhizosphere competent.

Additional keywords: maize, root rot, stalk rot, *Zea mays*.

An organism consistently associated with the rhizosphere is classified as rhizosphere competent (20). Rhizosphere competence has been described as the ability of an organism to colonize the rhizosphere in at least the upper 2 cm of root from an infested seed (1). Plant-produced carbon in the rhizosphere exists in root exudates, mucigel, cell wall residues, and sloughed plant cells (2). Information on the growth of *Fusarium equiseti* (Corda) Sacc., *F. proliferatum* (T. Matsushima) Nirenberg, and nonwilt-producing forms of *F. oxysporum* Schlechtend.:Fr. on cellulose, pectin, and xylans has been reported only briefly (15), whereas substrate utilization by wilt-producing forms of *F. oxysporum*

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has been studied extensively (6,10,11,18,22). Previously, cellulolytic enzymes found in rotted corn stalks were thought to be associated with the presence of *F. moniliforme* J. Sheld. (12) and were identified in culture (21). Little is known about production of cell wall-degrading enzymes by *F. graminearum* Schwabe (21) or its ability to utilize various carbon sources (15). *F. solani* (Mart.) Sacc. has been reported to produce cellulase or pectinase in culture (4,24) and utilize xylose and xylans (13,15).

Several *Fusarium* species were evaluated for rhizosphere competence on corn (*Zea mays* L.), and *F. moniliforme, F. oxysporum, F. solani,* and *F. proliferatum* were rhizosphere competent, whereas *F. graminearum* and *F. equiseti* were not (8,9, 14,16,17). We sought to determine whether differences in rhizosphere colonization (competence/incompetence) could be attributed to the ability of an isolate to utilize in culture various carbon sources present in the rhizosphere. The objectives of this study were to 1) determine whether differences in mycelial dry weight or sporulation exist among the rhizosphere-competent species, *F. moniliforme, F. oxysporum, F. solani,* and *F. proliferatum*, and the incompetent species, *F. equiseti* and *F. graminearum*, on glucose, pectin, and soluble and microcrystalline cellulose; 2) determine whether differences in mycelial dry weight or sporulation exist among *F. oxysporum, F. proliferatum,* and *F. graminearum* on xylans or xylose; 3) determine whether intra-

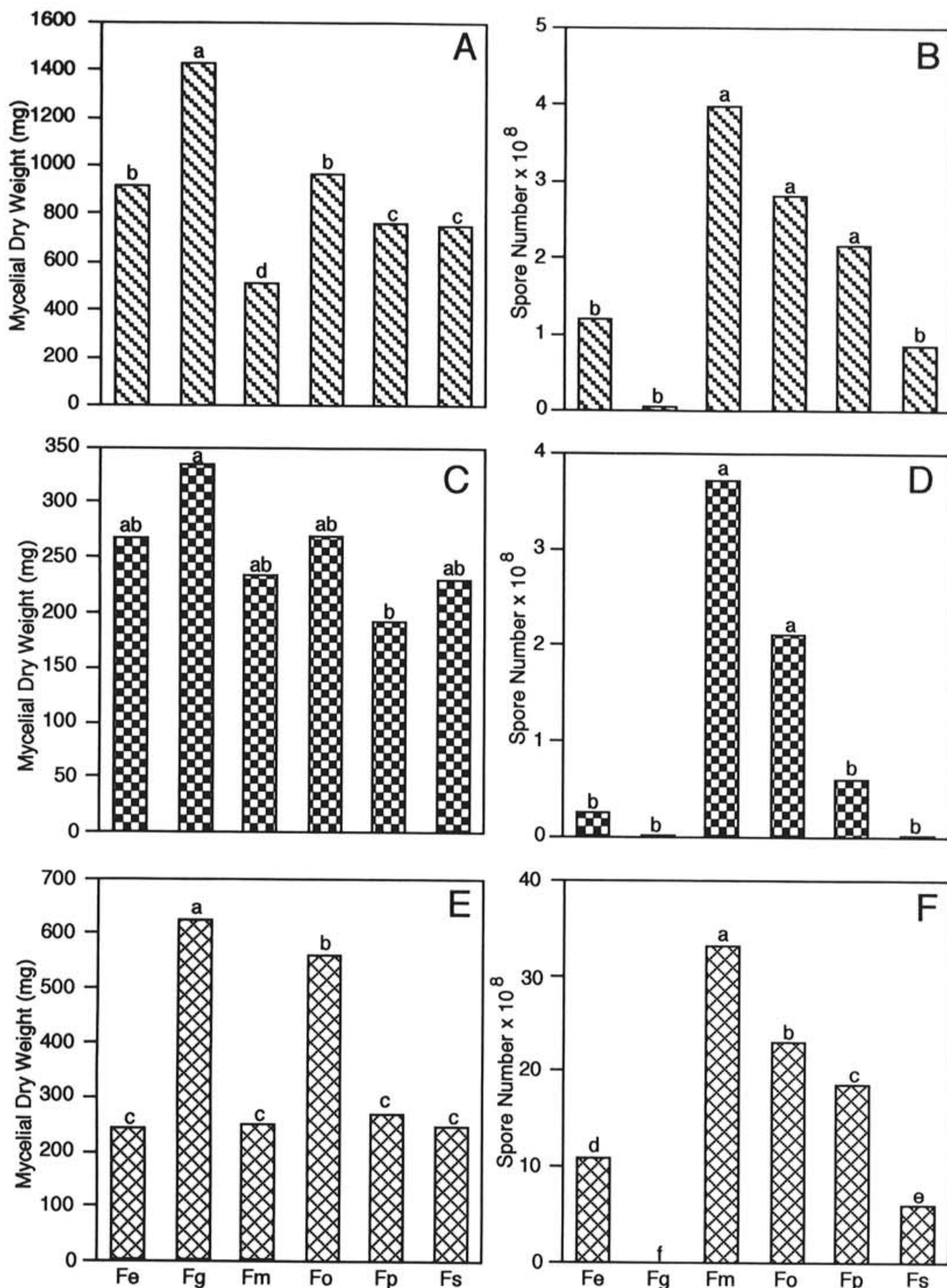

Fig. 1. Mycelial dry weight of six isolates of *Fusarium* after 12 days in liquid medium containing **A,** microcrystalline cellulose, **C,** glucose, and **E,** pectin and production of macro- and microconidia in liquid medium containing **B,** microcrystalline cellulose, **D,** glucose, and **F,** pectin. Fe = *F. equiseti*, Fg = *F. graminearum*, Fm = *F. moniliforme*, Fo = *F. oxysporum*, Fp = *F. proliferatum*, and Fs = *F. solani*. Numbers represent mean per flask and are based on three flasks per isolate per run (nine flasks per isolate). Bars labeled with the same letters are not significantly different ($P = 0.05$) according to Tukey's W statistic.

specific variation in mycelial dry weight or sporulation exist among isolates of *F. oxysporum, F. proliferatum,* and *F. graminearum* on pectin or microcrystalline cellulose; and 4) examine competition between species by evaluating sporulation and yield of colony-forming units (cfu) by respective *Fusarium* isolates when *F. graminearum* was paired with *F. moniliforme, F. oxysporum,* or *F. proliferatum.*

MATERIALS AND METHODS

All fungi used in this study were isolated in Minnesota. The isolate of *F. equiseti* (E1) was from a corn root. The *F. moniliforme* (M1) and *F. solani* (S1) isolates were from corn stalks. Five isolates of *F. graminearum* (G1–G5), four *F. oxysporum* (O1–O4), and four *F. proliferatum* (P1–P4) isolates were included. Isolates G1, G5, O1, P1, and P4 were from corn roots. Isolates G4, O3, and P3 were from corn stalks. Isolates G2, G3, and O4 were from wheat roots. Isolate O2 was from field soil, and P2 was from a corn kernel.

Isolates were purified by the single-conidium or hyphal-tip methods and stored at 5 C on silica gel (23). Isolates were grown on potato-dextrose agar (PDA) (7) under fluorescent lamps (three General Electric or Sylvania 40-W tubes) supplemented with black light (one Sylvania 40-W tube, BLB series) for a 12-h photoperiod at 24 C. Inoculum was increased by placing plugs (5 mm diameter) of cultures growing on PDA into Difco (Difco Laboratories, Detroit) potato-dextrose broth (PDB). Liquid cultures were incubated at 24 C on a rotary shaker (60 rpm) with no direct lighting.

Conidia of all *Fusarium* species were collected by filtering 12- to 16-day-old PDB cultures through sterile glass wool, counted with a hemacytometer, and adjusted to 10^5 cfu/ml of sterile distilled water. Liquid cultures of *F. graminearum* were placed under 12-h photoperiod conditions (described above) for 72 h to induce production of macroconidia.

Carbon sources tested were microcrystalline cellulose (Sigma cell type 20, Sigma Chemical Co., St. Louis), carboxymethyl cellulose (Sigma medium viscosity), pectin (Sigma citrus), xylans (Sigma oat spelts), D(+)-xylose, and glucose. One gram of each carbon source was mixed with 50 ml of Czapek-Dox salt solution (7) in flasks. The medium was autoclaved (121 C), and 0.5 ml of inoculum of a single species was added to each flask, except in the competition studies. For the competition studies, *F. graminearum* inoculum was produced on PDA because of sparse spore production in PDB culture; a 4-mm^2 section of PDA colonized by the fungus was used as inoculum.

Flasks were placed on a rotary shaker (60 rpm) at 24 C. Entire flasks were sampled 12 days after *Fusarium* was added, except in the competition study, these flasks were sampled on day 16. Mycelial mats were collected on glass wool and rinsed with distilled water until the effluent ran clear. Filtrates and the first 100 ml of effluent were combined, and conidia were counted with a hemacytometer. Mycelial mats were dried at 24 C for at least 72 h and weighed.

For competition studies with two *Fusarium* species in a single flask, colony-forming units were determined 16 days after the cultures were started. Mycelia and macroconidia of each *Fusarium* species could not be distinguished reliably from the other *Fusarium* species in the flask, so minced contents of each flask were diluted and placed onto media suitable for identification of *Fusarium* species. Flasks containing a single species were included in each sampling to provide a measurement of the sampling procedure's effect on the number of colony-forming units for each *Fusarium* species. The contents of each flask were minced for 30 s at 12,000 rpm on a Brinkman Kinematica AG Polytron (Kinematica Ag, Littau, Switzerland). The number of colony-forming units was determined through a dilution series suspended in 0.12% water agar. Molten but cooled, acidified PDA (20 ml) was poured over 1 ml of propagule suspension in a petri dish, and the contents of the dishes were mixed with a gentle swirling motion. Petri dishes were sealed in plastic bags and incubated at 24 C. After 8 days, the colonies were identified and counted.

Experimental design and data analysis. A randomized complete block design was used in the experiments. The area of the rotary shaker area was divided into three blocks. Three replicates (flasks) for each isolate and medium were used in each of three trials of each experiment. Treatment means were calculated for each isolate and medium in each trial. Means were calculated from combined trials (total nine flasks per species combination and medium) if effects of trial were not significant ($P = 0.05$). Independent variables and their interactive forms were tested for significant ($P = 0.05$) effects on means by an analysis of variance (19), and means were compared with Tukey's W statistic.

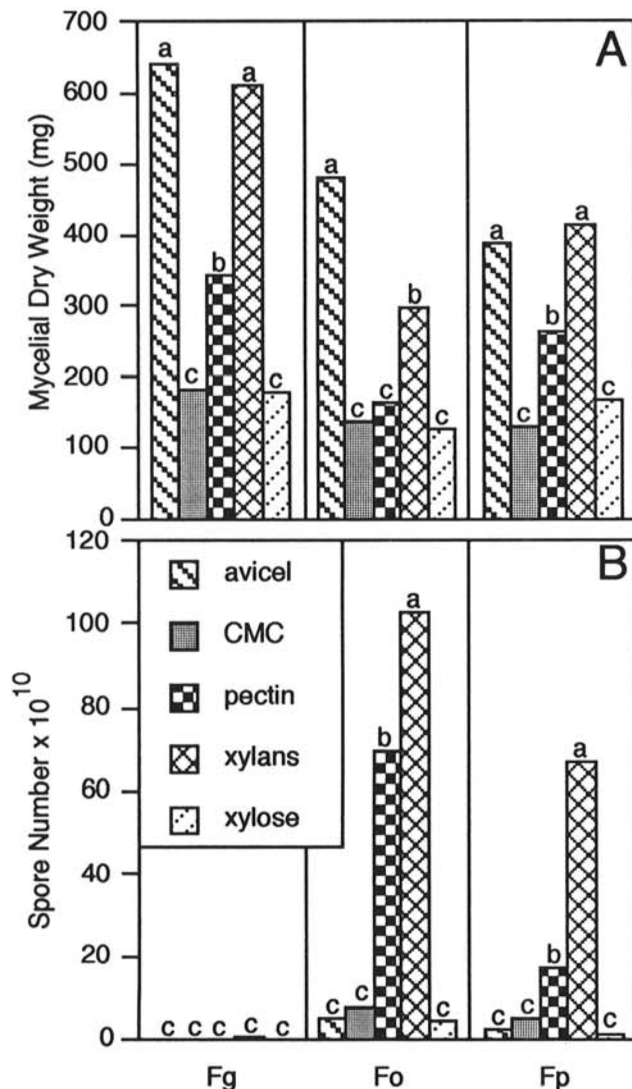

Fig. 2. A, Mycelial dry weight and **B,** macro- and microconidia of *Fusarium graminearum* (Fg), *F. oxysporum* (Fo), and *F. proliferatum* (Fp) grown 12 days in liquid medium containing microcrystalline cellulose (avicel), carboxymethyl cellulose (CMC), pectin, xylans, or xylose. Numbers represent mean per flask and are based on three flasks per isolate per run (nine flasks per isolate). Bars labeled with the same letters are not significantly different ($P = 0.05$) according to Tukey's W statistic.

RESULTS

For each experiment, effect of run was not significant, and in all three runs, we found similar values of mycelial dry weights and spore numbers for each species, as well as similar relative differences; therefore, overall means are presented for these studies.

Mycelial dry weight and sporulation. *F. graminearum* grown on a medium containing microcrystalline cellulose yielded the greatest mycelial dry weight (Fig. 1A), followed by *F. oxysporum* and *F. equiseti. F. moniliforme* yielded the lowest mycelial dry weight, whereas *F. solani* and *F. proliferatum* yielded dry weights

significantly ($P = 0.05$) greater than that of *F. moniliforme*. When the substrate contained glucose, *F. graminearum* yielded a significantly greater mycelial dry weight than *F. proliferatum* (Fig. 1C). The dry weights of the other four species were not significantly different from each other or from *F. graminearum*. When grown on pectin (Fig. 1E), *F. graminearum* produced the greatest mycelial dry weight, followed by *F. oxysporum*; the mycelial dry weights of the other four species did not differ significantly from each other.

The isolates of *Fusarium* species included in this study generally produced the greatest number of conidia when grown on pectin (Fig. 1F) compared to microcrystalline cellulose (Fig. 1B) or glucose (Fig. 1D). *F. moniliforme* yielded a greater number of conidia than did the other five species on all three substrates. On microcrystalline cellulose, *F. moniliforme* produced the greatest number of conidia, but numbers did not differ significantly ($P = 0.05$) from *F. oxysporum* or *F. proliferatum* (Fig. 1B). Sporulation by these three species was significantly greater than sporulation by *F. equiseti, F. graminearum,* or *F. solani*. On glucose, *F. moniliforme* yielded the greatest number of conidia, but the number was not significantly different from that produced by *F. oxysporum* (Fig. 1D). Sporulation of these two species was significantly greater than sporulation by the other four species. Significantly fewer conidia were produced in decreasing numbers by *F. oxysporum, F. proliferatum, F. equiseti, F. solani,* and *F. graminearum*, respectively, on pectin compared to *F. moniliforme* (Fig. 1F). Isolate-medium interactions were statistically significant for mycelial dry weight and sporulation but constituted a small portion of the model sum of squares.

Mycelial dry weight and sporulation on xylans and xylose. Mycelial dry weights for *F. graminearum, F. oxysporum,* and *F. proliferatum* were significantly greater ($P = 0.05$) on microcrystalline cellulose and xylans than on pectin, carboxymethyl cellulose, or xylose (Fig. 2A). Sporulation by *F. graminearum* was almost nonexistent in all five media tested (Fig. 2B). Sporulation by either *F. oxysporum* or *F. proliferatum* was greatest on xylans relative to the other media; ample sporulation was associated with pectin, whereas sporulation was sparse with microcrystalline cellulose, carboxymethyl cellulose, or xylose substrates. Isolate-medium interactions were statistically significant for mycelial dry weight and sporulation but constituted a small portion of the model sum of squares.

Variability within species. No significant differences ($P = 0.05$) occurred in dry weights of mycelia grown on pectin (Fig. 3A) or in sporulation on cellulose (Fig. 3B) by isolates of *F. oxysporum* (O1–O4) or *F. proliferatum* (P1–P4). There was variation among isolates of both species in sporulation on pectin and among mycelial dry weights of *F. oxysporum* isolates on cellulose. Some *F. graminearum* isolates produced significantly greater mycelial dry weights on cellulose than on pectin, but the number of spores produced by these isolates was negligible on both media. Some interaction terms were significant for both mycelial dry weight and sporulation. Interaction terms that were statistically significant for mycelial dry weight include: medium-species (17% of model sum of squares), medium-isolate (3% of model sum of squares), and medium-species-isolate (4% of model sum of squares). Interaction terms that were statistically significant for sporulation include: medium-species (18% of model sum of

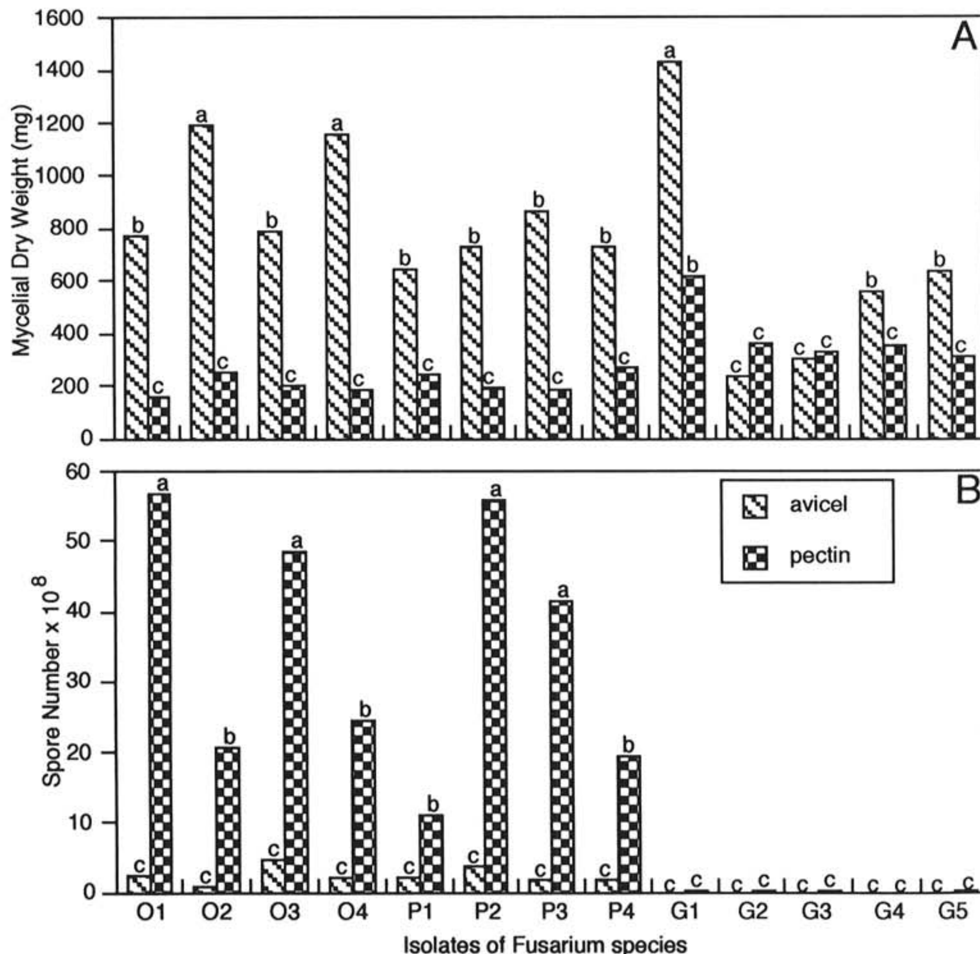

Fig. 3. Variability in **A,** mycelial dry weight and **B,** macro- and microconidia among isolates of *Fusarium oxysporum* (O1–O4), *F. proliferatum* (P1–P4), and *F. graminearum* (G1–G5) grown 12 days in liquid medium containing microcrystalline cellulose (avicel) or pectin. Numbers represent mean per flask and are based on three flasks per isolate per run (nine flasks per isolate). Bars labeled with the same letters are not significantly different ($P = 0.05$) according to Tukey's W statistic.

squares), medium-isolate (5% of model sum of squares), and medium-species-isolate (7% of model sum of squares).

Dual cultures. There was no significant ($P = 0.05$) effect on number of macroconidia produced by *F. graminearum* on cellulose incubated in dual culture with any of the other three *Fusarium* species compared to *F. graminearum* incubated alone (Fig. 4A). Conidial production by *F. graminearum* was significantly suppressed when the fungus was paired with *F. moniliforme* on pectin but not when paired with either *F. oxysporum* or *F. proliferatum* (Fig. 4C). Production of macroconidia by *F. graminearum* was significantly lower on xylans (Fig. 4E) when *F. graminearum* was grown with the other three species of *Fusarium* compared to *F. graminearum* incubated alone.

Colony-forming units were based on conidia and mycelial fragments and were calculated as the mean number of colonies per flask determined by dilution plating. Numbers of colony-forming units of *F. graminearum* were significantly ($P = 0.05$) less when the fungus was incubated in culture with *F. moniliforme, F. oxysporum,* or *F. proliferatum* on cellulose (Fig. 4B), pectin (Fig. 4D), or xylans (Fig. 4F) relative to the numbers that resulted when *F. graminearum* was incubated alone.

No significant ($P = 0.05$) suppression in number of spores produced by *F. oxysporum* was observed when this species was cultured with *F. graminearum* on cellulose (Fig. 5A) relative to a pure culture of *F. oxysporum*. Total numbers of macroconidia and microconidia produced by *F. oxysporum* were significantly

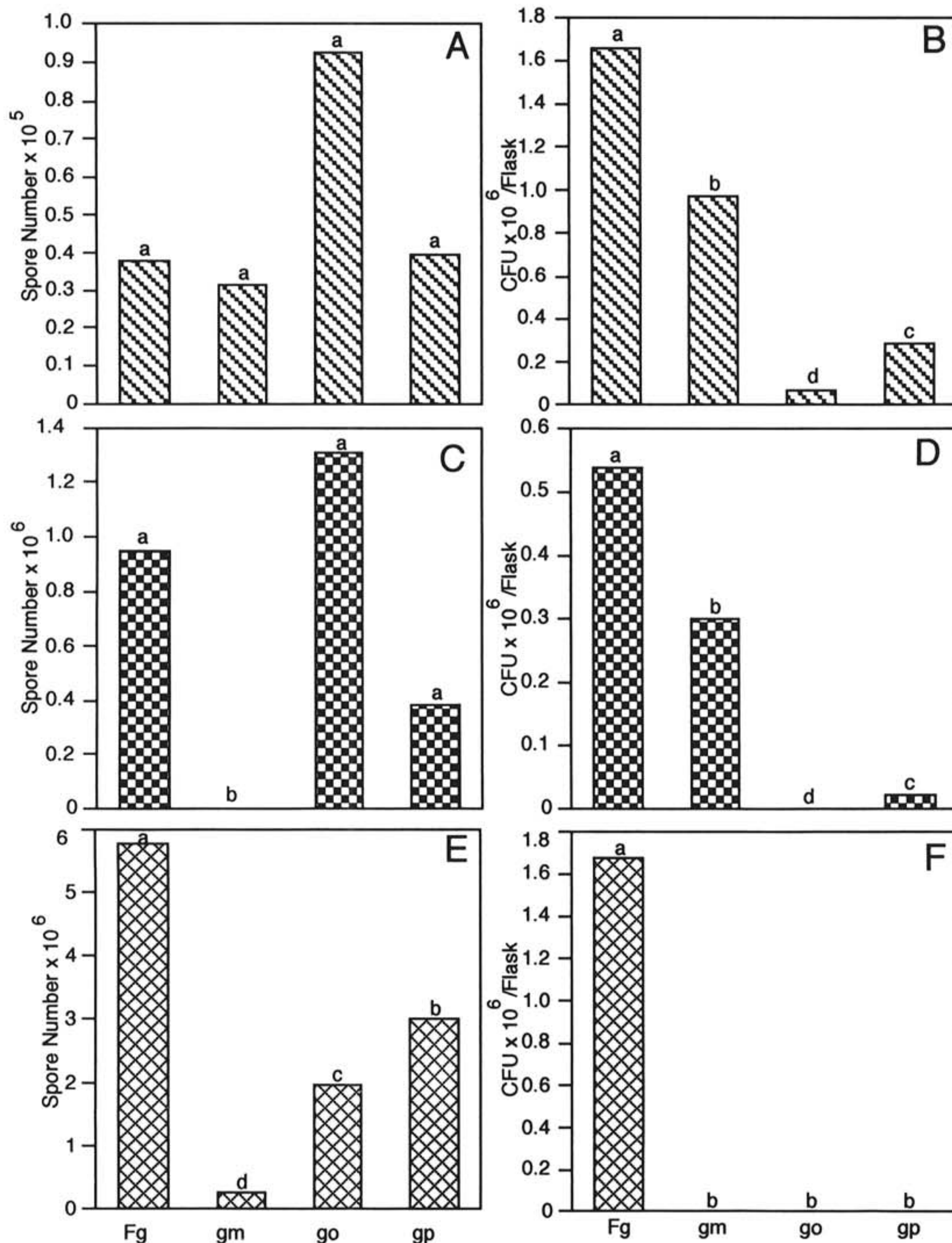

Fig. 4. Macroconidia produced by *Fusarium graminearum* (Fg) grown 16 days singly or paired with *F. moniliforme* (gm), *F. oxysporum* (go), or *F. proliferatum* (gp) in liquid medium containing **A,** cellulose, **C,** pectin, and **E,** xylans and colony-forming units (CFU) of *F. graminearum* when grown 16 days singly or paired with the other *Fusarium* species in liquid medium containing **B,** cellulose, **D,** pectin, or **F,** xylans. Numbers represent mean per flask and are based on three flasks per isolate per run (nine flasks per isolate combination). Bars labeled with the same letters are not significantly different ($P = 0.05$) according to Tukey's W statistic.

lower when *F. oxysporum* was mixed with *F. graminearum* and grown on pectin (Fig. 5C) or xylans (Fig. 5E) compared to growth of *F. oxysporum* alone. There was no significant difference in production of macroconidia and microconidia by *F. moniliforme* or *F. proliferatum* when either species was grown in dual culture with *F. graminearum* compared to *F. moniliforme* or *F. proliferatum* grown alone on cellulose (Fig. 5A), pectin (Fig. 5C), or xylans (Fig. 5E).

When *F. moniliforme* was grown in dual culture with *F. graminearum*, numbers of colony-forming units of *F. moniliforme* were significantly ($P = 0.05$) greater than the numbers of colony-forming units produced when *F. moniliforme* was grown alone on cellulose (Fig. 5B) or pectin (Fig. 5D). There was no significant difference between the number of colony-forming units of *F. moniliforme* grown on xylans singly or in dual culture with *F. graminearum* (Fig. 5F). Similarly, there were no significant differences in the number of colony-forming units of *F. oxysporum* or *F. proliferatum* grown in dual culture with *F. graminearum* compared to the number of colony-forming units produced by *F. oxysporum* or *F. proliferatum* grown singly on cellulose (Fig. 5B), pectin (Fig. 5D), or xylans (Fig. 5F). Isolate-medium interactions were statistically significant for both sporulation and

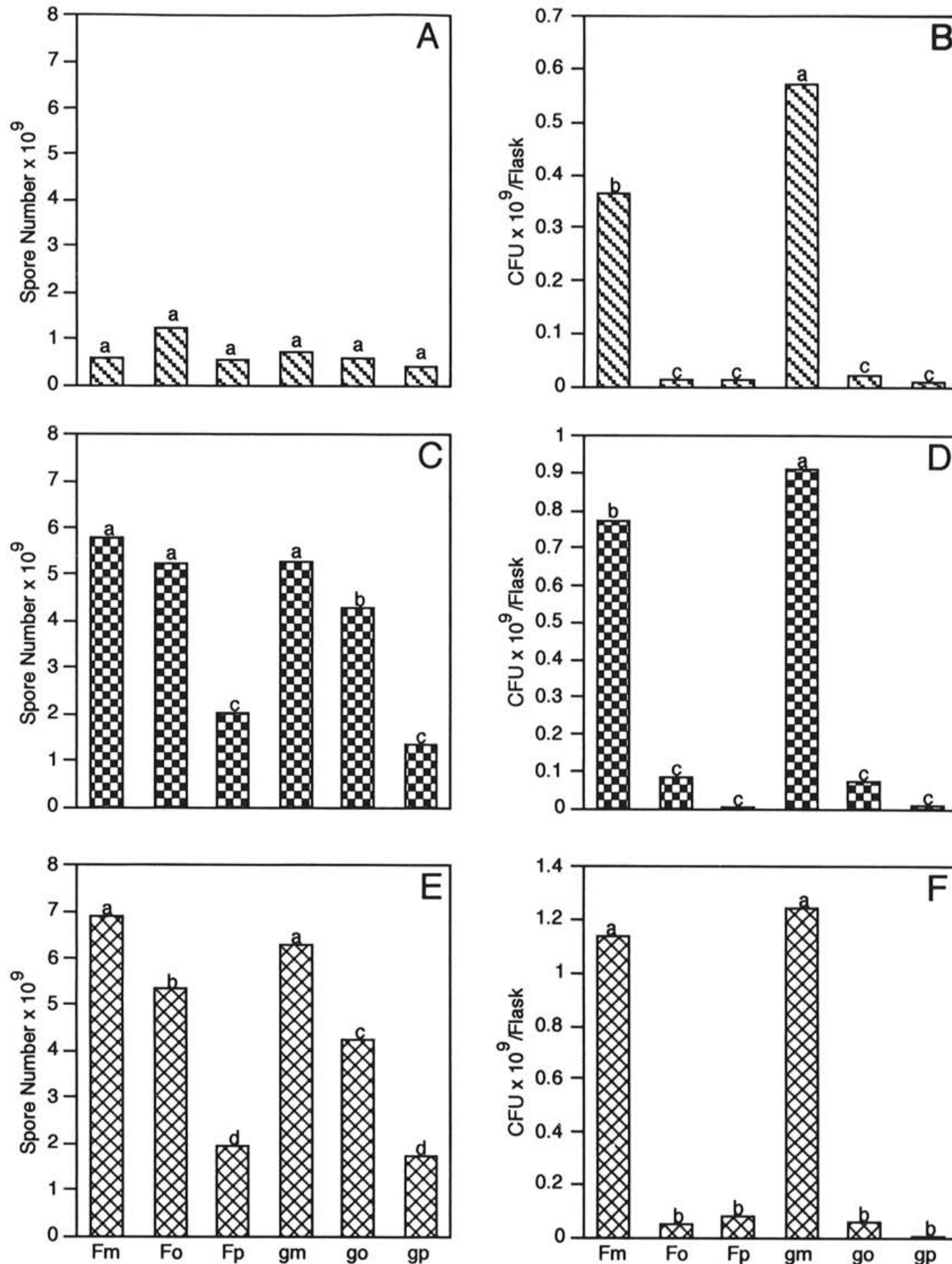

Fig. 5. Macroconidia and/or microconidia produced by *Fusarium moniliforme* (Fm, gm), *F. oxysporum* (Fo, go), or *F. proliferatum* (Fp, gp) grown 16 days singly or paired, respectively, with *F. graminearum* in liquid medium containing **A**, microcrystalline cellulose, **C**, pectin, and **E**, xylans and number of colony-forming units (CFU) of the same fungi when grown 16 days in liquid medium containing **B**, cellulose, **D**, pectin, or **F**, xylans. Numbers represent mean per flask and are based on three flasks per isolate per run (nine flasks per isolate combination). Bars labeled with the same letters are not significantly different ($P = 0.05$) according to Tukey's W statistic.

number of colony-forming units but constituted a small portion of the model sum of squares.

DISCUSSION

We are the first to report in-vitro utilization of various carbon sources by *F. equiseti, F. proliferatum,* and nonwilt-producing forms of *F. oxysporum* (14,15). In our study, rhizosphere-competent isolates of *F. moniliforme, F. oxysporum, F. proliferatum,* and *F. solani* did not utilize cellulose, pectin, or xylans to a greater degree than the rhizosphere-incompetent *F. equiseti* or *F. graminearum. F. graminearum*, a poor colonizer of the rhizosphere of corn (16,17), produced greater mycelial dry weights relative to those by other *Fusarium* species. Conclusions about behavior of *Fusarium* species are tempered by the fact that isolates within species differ from each other. This was demonstrated by the variability among isolates of *F. graminearum, F. oxysporum,* and *F. proliferatum* in growth on cellulose and pectin.

The fact that the isolate-medium (or species-medium) interaction term was statistically significant for mycelial dry weight and sporulation attests to the fact that there is variation among *Fusarium* species in our studies. Generally, mycelial dry weights were greater on microcrystalline cellulose and xylans compared to other carbon sources, but mycelial dry weights did not all increase proportionally. Sporulation was generally greater on xylans and pectin compared to other carbon substrates studied, but sporulations by *F. graminearum* remained relatively unchanged regardless of the carbon source.

The competitive ability of a fungus or its suppression by *F. moniliforme, F. oxysporum,* or *F. proliferatum* may influence its establishment in the rhizosphere, whether the fungus is a pathogen or a rhizosphere saprophyte. Competition among soil microorganisms has been regarded, in part, as competition for substrate (3,5). In our tests, *F. moniliforme, F. oxysporum,* and *F. proliferatum* appear to have a greater competitive ability than, or to suppress, *F. graminearum* when grown in dual cultures on cellulose, pectin, or xylans. Spore production and numbers of colony-forming units of these three fungi were not significantly less in the presence of *F. graminearum* than when grown singly. *F. graminearum*, however, generally did not produce as many spores or colony-forming units when grown in dual cultures with any of the other three fungi on the three carbon sources. Moreover, previous work in a growth chamber (14,16) showed that when corn kernels infested with *F. graminearum* were planted in soil infested with either *F. oxysporum* or *F. proliferatum*, the extent of colonization of the primary root by *F. graminearum* was less than the colonization found in noninfested, pasteurized soil. The poor competitive ability of *F. graminearum* or its suppression by other *Fusarium* species in vitro may indicate putative rhizosphere incompetence or reliance on pathogenesis to become established in the host.

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