# Mycorrhizae: Possible Explanation for Yield Decline with Continuous Corn and Soybean

Nancy Collins Johnson,* Philip J. Copeland, R. Kent Crookston, and F. L. Pfleger

## ABSTRACT

**Earlier studies showed that mycorrhizal fungi selectively proliferate in soils cropped in monoculture to corn (*Zea mays* L.) or soybean [*Glycine max* (L.) Merr.]. This study evaluated whether the dominant mycorrhizal fungi, based on spore numbers present in soil, affected growth and nutrient uptake of the following crop. Plots at two locations in Minnesota with a continuous corn or continuous soybean history were planted to both corn and soybean. The relationship between spore numbers of proliferating species of mycorrhizal fungi and crop yield and nutrient concentrations were assessed using simple correlation analysis. Spore populations of mycorrhizal fungi which proliferated in corn were generally negatively correlated with the yield and tissue mineral concentrations of corn, but were positively correlated with the yield and tissue mineral concentrations of soybean. Spore populations of soybean proliferators exhibited the reciprocal relationship, although less clearly. We suggest that, compared to other fungi, proliferating VAM fungal species may be less beneficial (or perhaps detrimental) to the crop in which they proliferate. We propose a mechanism to explain how vesicular-arbuscular mycorrhizal (VAM) fungi could cause yield depressions associated with monoculture, and outline research needed to test this hypothesis.**

YIELDS OF CROPS generally decline over time in continuous monoculture. Crop rotation is an established practice to optimize yields, but the actual mechanisms responsible for the positive effects of rotation are not fully understood. Several workers have suggested that the interaction of rotation and crop yield is at a microbiological level (Shipton, 1977; Turco et al., 1990).

Most crops form symbiotic associations with VAM fungi. These fungi are obligate symbionts that produce persistent soil-borne spores. Below-ground crop residues contain these spores along with fragments of hyphae and moribund VAM roots, all of which may serve as infective propagules for VAM fungal colonization of the following crop.

Hyphae of VAM fungi extend into the soil more extensively than root hairs and can enhance the absorption of immobile nutrients (Rhodes and Gerdemann, 1975). Mycorrhizae are generally recognized for their importance in P uptake, but they also may improve uptake of immoble micronutrients such as Cu and Zn (Lambert et al., 1979; Pacovsky, 1986). The VAM fungi have been shown to improve crop yields, even when P fertility of soils does not appear to limit plant growth (Medina et al., 1988).

The fungi that form VAM associations are a diverse group of over 144 species. Species, and even isolates within species, vary greatly in their effects on plants ranging from mutualistic to neutral to pathogenic (e.g. Carling and Brown, 1980; Modjo and Hendrix, 1986; Bethlenfalvay et al., 1989). Furthermore, VAM fungal species vary in their ability to proliferate in different crop species (Schenck and Kinloch, 1980); and, although VAM fungi are typically considered to be generalists, there is increasing evidence that some degree of specificity exists between VAM fungi and plants (Rosendahl et al., 1990).

We recently studied VAM fungal populations in a crop rotation experiment at Waseca and Lamberton, MN (Johnson et al., 1991). In that study, we observed distinctly different VAM fungal communities in field plots with continuous corn and continuous soybean cropping histories. At Waseca, *Glomus aggregatum* Schneck & Smith emend. Koske, *G. leptotichum* Schneck & Smith, and *G. occultum* Walker were significantly ($p \leq 0.05$) more abundant in plots with a corn history, whereas spores of *G. microcarpum* Tul. & Tul. were significantly more abundant in plots with a soybean history. Furthermore, densities of *G. mosseae* (Nicol. & Gerd.) Gerd. & Trappe tended ($p \leq 0.07$) to be higher in plots with a corn history and *G. claroideum* Schenck & Smith tended ($p \leq 0.09$) to be more abundant in plots with a soybean history. At Lamberton, *G. albidum* Walker & Rhodes, *G. mosseae,* and *G. occultum* were significantly more abundant in plots with a corn history than in plots with a soybean history.

Since VAM fungi differ in their effects on plants, the composition of communities of VAM fungi could affect nutrient uptake and consequently crop yields (Schenck et al., 1989). The present study examines the relationship between spore abundances of individual VAM fungal species and the yields and tissue mineral concentrations of corn and soybean to evaluate the possibility that mycorrhizae may be involved in the yield decline associated with continuous cropping. We also propose a mechanism to explain how mycorrhizae could cause such yield depressions and outline research needed to test this hypothesis.

## MATERIALS AND METHODS

This study was conducted in 1988 as part of a long-term, corn-soybean rotation experiment at the University of Minnesota's Waseca and Lamberton Agricultural Experiment Stations. Corn and soybean were each grown continuously, and in rotation, in experimental plots arranged in a randomized complete block design and replicated four times. Details of the experimental design can be found in Crookston et al. (1991).

We examined four different cropping sequences: continuous corn, continuous soybean, first-year corn (following 5 yr of soybean), and first-year soybean (following 5 yr of corn). This design allowed us to examine corn grown in soils with VAM fungal communities characteristic of a corn history (continuous corn) and a soybean history (first-year corn). Similarly, we could examine soybean grown in soils with VAM fungi characteristic of a soybean history (continuous soybean) and a corn history (first-year soybean).

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N.C. Johnson, 212 Spruce Street, Santa Fe, NM 87501; P.J. Copeland and R.K. Crookston, Dep. of Agronomy and Plant Genetics, Univ. of Minnesota, St. Paul, MN 55108; and F.L. Pfleger, Dep. of Plant Pathology, Univ. of MN, St. Paul, MN 55108. Contribution of the Minnesota Agric. Exp. Stn. Journal no. 19,078. Received 15 May 1991. *Corresponding author.

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Table 1. Yield of grain and dry matter and tissue concentration of P, Cu, Zn for corn and soybean grown in soils with a soybean history (SH) or a corn history (CH) at Waseca and Lamberton ($n = 4$).

| | | Yield of | | | | | | Concentration of | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Grain | | | Dry matter | | | P | | | Cu | | | Zn | | |
| Crop | Site | SH | CH | SE‡ | SH | CH | SE | SH | CH | SE | SH | CH | SE | SH | CH | SE |
| | | Mg/ha | | | g/plant | | | g/Kg | | | mg/Kg | | | mg/Kg | | |
| Corn | Waseca | 6.0 | 4.6† | 0.8 | 94 | 78† | 10 | 2.1 | 1.9† | 0.09 | 5.6 | 5.2 | 0.5 | 31 | 26† | 3.0 |
| | Lamberton | 6.2 | 5.3* | 0.3 | 109 | 96* | 5 | 1.9 | 1.9 | 0.2 | 5.7 | 4.9 | 1.0 | 24 | 25 | 1.5 |
| Soybean | Waseca | 1.9 | 2.2* | 0.2 | 6.4 | 6.4 | 0.9 | 2.7 | 3.1* | 0.05 | 5.7 | 8.4* | 0.5 | 29 | 31 | 2.2 |
| | Lamberton | 1.9 | 2.1 | 0.2 | 7.9 | 7.4 | 1.4 | 2.6 | 2.6 | 0.2 | 7.0 | 8.5* | 0.2 | 29 | 27 | 2.1 |

†,* mean pairs are significantly different by *t*-test at $P \leq 0.10$ and $P \leq 0.05$ respectively.
‡ SE = root mean square error.

Shoot samples were collected at silking in corn and at the R3 stage in soybean (Fehr and Caviness, 1980). Ten plants were randomly selected from each plot from rows adjacent to yield rows. Samples were dried at 60 °C for 72 hours and ground in a Wiley mill to pass through a 1-mm screen. Shoot concentration of P, Zn, and Cu was determined by inductively-coupled plasma emission spectroscopy. Plots were harvested by a plot combine and grain yields determined from two or three yield rows, according to location (Crookston et al., 1991). Three weeks after crop emergence composite soil samples were taken from each plot by collecting two cores (15 cm deep by 2-cm diam.) about 2.5 cm from the stems of four corn or soybean seedlings. Spores were extracted from 25 g of air-dried soil, counted and identified to species as described in Johnson et al. (1991).

Two sample *t*-tests were used to compare mean grain yield, dry matter yield, and mineral concentration in continuous vs. first-year crops. Spore counts were normalized using a $\ln(x+1)$ transformation, and simple linear correlation analysis was used to determine the degree of association of spore densities with crop yields or nutrient concentrations.

## RESULTS

At both sites, grain and dry matter yields were significantly higher in corn with a soybean history rather than a corn history. Furthermore, at Waseca, tissue concentrations of P and Zn were higher in corn with a soybean history than a corn history (Table 1). At Waseca, grain yield and tissue concentrations of P and Cu were significantly greater in soybean with a corn history rather than a soybean history. Soybean at Lamberton also contained higher concentrations of Cu when following corn rather than soybean (Table 1).

Spore abundance of the Waseca corn proliferators (*G. aggregatum, G. leptotichum, G. mosseae,* and *G. occultum*) tended to be negatively associated with the yields and mineral concentrations of corn and positively associated with grain yield and mineral concentration of soybean (Table 2). In contrast, the abundance of soybean proliferators (*G. claroideum* and *G. microcarpum*) were negatively related to P, Cu and Zn concentrations of soybean (Table 2).

At Lamberton, spore abundances of two of the three corn proliferators (*G. mosseae,* and *G. occultum*) were negatively correlated with the dry matter yield and Zn concentration of corn, and all three corn proliferators tended to be positively correlated with the dry matter yield and Cu concentration of soybean (Table 3).

## DISCUSSION

Continuous monocultures of both corn and soybean generally had lower yields and tissue concentrations of P, Cu, and Zn than first-year crops. Mycorrhizae are known to influence tissue concentrations of P, Cu, and Zn in both corn (Swaminathan and Verma, 1979; Fairchild and Miller, 1988) and soybean (Ross and Harper, 1970; Pacovsky, 1986). Furthermore, Pacovsky et al. (1986) found significantly different Cu and Zn concentrations in sorghum (*Sorghum bicolor* L.) and soybean colonized by four different *Glomus* species.

It is possible that soybean and corn responses to

Table 2. Correlation coefficients of corn and soybean yields and tissue concentrations of P, Cu, and Zn with spore abundances of six VAM fungal species from Waseca. Each coefficient represents the association between spore numbers and the growth or mineral concentrations of continuous and first-year corn or soybean ($n = 8$).

| | Yield of | | | | Concentration of | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Dry matter | | Grain | | Tissue P | | Tissue Cu | | Tissue Zn | |
| Fungal species | Soybean | Corn | Soybean | Corn | Soybean | Corn | Soybean | Corn | Soybean | Corn |
| corn proliferators | | | | | | | | | | |
| *G. aggregatum* | +0.20 | −0.74* | +0.58 | −0.43 | +0.17 | −0.34 | +0.53 | −0.52 | +0.44 | −0.24 |
| *G. leptotichum* | −0.14 | −0.82** | +0.64† | −0.73* | +0.86** | −0.39 | +0.84** | −0.64† | +0.09 | −0.06 |
| *G. mosseae* | −0.0003 | −0.71* | +0.37 | −0.86** | +0.41 | −0.37 | +0.69* | −0.54 | +0.34 | +0.35 |
| *G. occultum* | −0.11 | −0.66† | +0.45 | −0.31 | +0.75* | −0.87** | +0.80** | −0.38 | +0.71* | −0.60† |
| soybean proliferators | | | | | | | | | | |
| *G. claroideum* | −0.15 | −0.24 | −0.46 | −0.17 | −0.70* | +0.12 | −0.66† | −0.52 | −0.64† | −0.11 |
| *G. microcarpum* | −0.01 | +0.28 | −0.47 | +0.18 | −0.76* | +0.19 | −0.76* | +0.62† | −0.71* | −0.26 |

†,*,** correlations are significant at $p \leq 0.10$, 0.05, and 0.01 respectively.

**Table 3. Correlation coefficients of corn and soybean yields and tissue concentrations of P, Cu, and Zn with spore abundances of three VAM fungal species from Lamberton. Each coefficient represents the association between spore numbers and the growth or mineral concentrations of continuous and first-year corn or soybean ($n = 8$).**

| | Yield of | | | | Concentration of | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Dry matter | | Grain | | Tissue P | | Tissue Cu | | Tissue Zn | |
| Fungal species | Soybean | Corn | Soybean | Corn | Soybean | Corn | Soybean | Corn | Soybean | Corn |
| corn proliferators | | | | | | | | | | |
| *G. albidum* | +0.74* | −0.18 | +0.56 | −0.19 | +0.09 | −0.40 | +0.74* | +0.34 | −0.47 | −0.06 |
| *G. mosseae* | +0.38 | −0.72* | −0.23 | −0.57 | −0.02 | −0.47 | +0.23 | −0.07 | −0.25 | −0.51 |
| *G. occultum* | +0.34 | −0.60† | +0.62† | −0.31 | +0.08 | +0.03 | +0.47 | −0.44 | −0.44 | −0.69* |

†,* correlations are significant at $p \leq 0.10$ and 0.05 respectively.

cropping sequence were not independent of the responses of the VAM fungal community to cropping sequence. Only experimental tests can establish a causal relationship between yield decline and population densities of VAM fungal species, but our correlative findings support the hypothesis that a shift in the composition of the VAM fungal community may have contributed to the yield decline associated with continuous cropping.

The following conceptual model summarizes a mechanism for this effect.

1. Continuous cropping selects for the most rapidly growing and sporulating VAM fungal species.
2. These fungi provision their own growth at the expense of their plant symbionts and are therefore either inferior mutualists, or perhaps even parasitic, compared to nonproliferating species of VAM fungi.
3. Over time, crop vigor declines in monoculture because populations of detrimental species increase and populations of beneficial species decrease in the VAM fungal community.
4. Interruption of a monoculture (rotation) reduces the relative abundance of detrimental fungi, and increases the relative abundance of beneficial fungi.

This hypothesis should be experimentally tested by individually assessing the effects of proliferating fungal species (and isolates) on crop physiology and yield. Furthermore, each of the four premises listed above must be examined carefully in order to thoroughly test the hypothesis. Current research techniques are sufficient to adequately test some, but not all aspects of these premises.

Spore populations are an indirect measure of the VAM fungal community. We assumed that early season spore abundances of different VAM fungal species were proportional to root colonization by these VAM fungi throughout the growing season. This may or may not have been a valid assumption since VAM fungal species are known to vary in the amount of spores they produce relative to the biomass of their thallus (Gianinazzi-Pearson et al., 1985). There is currently no method to assess the validity of this assumption in field studies. Future research designs may circumvent this limitation through the use of recently developed serological (Wright and Morton, 1989) techniques that permit the identification of VAM fungi within root systems.

The experimental plots at Waseca were kept weed-free, whereas both the corn and soybean plots at Lamberton were rather heavily infested with foxtail [*Setaria faberi* Herrm., *S. leutescens* (Weigel) F. T. Hubb, and *S. viridis* (L.) P. Beauv.]. This may explain why a single species, *G. aggregatum*, dominated both cropping histories at Lamberton (Johnson et al., 1991) and also why the Lamberton correlations were less often statistically significant than the Waseca correlations.

Our hypothesis assumes that detrimental VAM fungi are the direct causes of yield decline. Host-fungus competition for C has been suggested as a cause of growth depressions in mycorrhizal plants (Buwalda and Goh, 1982); however, alternative explanations are also plausible. For instance, it is possible that mycorrhizal fungi are not directly causing crop decline but are simply vectors of, or concomitant with, other agents of decline. Cooper (1975) showed that the soil microorganisms added with a crushed spore mycorrhizal inoculum reduced the growth of *Solanum* and *Leptospermum*. Similarly, Hall (1984) found glass-wool-filtered washings of VAM fungal inocula reduced the growth of white clover (*Trifolium repens* L.).

Additionally, other soil microorganisms acting as antagonists may influence the composition of the VAM fungal community, so the VAM fungal species that dominate a certain cropping system may not be the most rapidly growing species, but rather, the species most resistant to microbial attack (Ross and Ruttencutter, 1977; Kitt et al., 1987). Detrimental effects of soil microorganisms on VAM fungi may be manifest in host plants. For example, Hetrick et al. (1988) showed that nonsterile soil reduced the growth of big bluestem grass (*Andropogon gerardii* Vitman) by reducing VAM colonization of its roots. The exact nature of these microbial agents remains unclear and future research should be directed at their elucidation.

The rotation effect is most certainly caused by many interacting factors. We hypothesize that mycorrhizae are but one of these factors, and that through crop rotation, a farmer may be inadvertently managing the VAM fungal community so that the most beneficial fungal species are more common than less beneficial (or detrimental) species.

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