

# Tillage or no-tillage: Impact on mycorrhizae

Zahangir Kabir

*Department of Land, Air and Water Resources, 1150 Plant and Environmental Sciences Building, University of California, Davis, One Shields Ave., Davis, California 95616, USA (e-mail: kabir@ucdavis.edu). Received 14 October 2003, accepted 9 September 2004.*

Kabir, Z. 2005. **Tillage or no-tillage: Impact on mycorrhizae.** *Can. J. Plant Sci.* **85**: 23–29. Arbuscular mycorrhizal (AM) fungi are ubiquitous in agricultural soils. These fungi play important roles in plant nutrition and soil conservation. The persistence of AM fungi in ecosystems depends on the formation and survival of propagules (e.g., spore, hyphae and colonized roots). While spores are considered to be resistant structure that may be view as “long-term” propagules when viable host plants are not present, hyphae are considered to be the main source of inocula when host plants are present and the soil is not disturbed. Tillage is an integral part of modern agriculture that can modify the physical, chemical and biological properties of a soil. Consequently, tillage practices may also affect AM fungi. The various tillage practices used in the management of soil for maximum crop production may negatively impact the survival of AM fungal propagules. In tilled soil, certain AM species may survive while others may disappear. Because AM fungi are more abundant in the topsoil, deep plowing may dilute their propagules in a greater volume of soil, thereby reducing the level of infection of a plant root. Tillage is particularly detrimental to AM hyphae if the soil is tilled in the fall and the hyphae are detached from the host plant. Under no-till (NT), AM fungi survive better, particularly when they are close to the host crop on which they developed. There is speculation that in NT systems, plants may follow old root channels and potentially encounter more AM fungal propagules than plants growing in soil that has been tilled. Management of AM fungi in NT soil is essential to maximizing benefits to crops. This review reports how tillage practices affect AM fungi species richness, survivability and infectivity, and how conservation tillage can increase AM fungi survival, consequently improving plant phosphorus uptake and soil aggregate stability.

**Key words:** Arbuscular mycorrhizal fungi, conservation tillage, conventional tillage, P uptake, soil aggregate stability, cover crops, crop yield

Kabir, Z. 2005. **Travail ou non-travail du sol : incidence sur les mycorrhizes.** *Can. J. Plant Sci.* **85**: 23–29. Les mycorrhizes à arbuscules (MA) sont des champignons omniprésents dans les sols agricoles. Ces champignons jouent un rôle important pour la nutrition des plantes et la conservation du sol. Leur persistance dans l'écosystème dépend de la formation et de la survie des propagules (les spores, les hyphes et les racines colonisées). Bien que les spores soient considérées comme des propagules « à long terme » à cause de leur résistance en l'absence de plantes hôtes, les hyphes demeurent la principale source d'inoculum quand il y a des plantes hôtes et que le sol n'est pas perturbé. Les labours font partie intégrante des pratiques agricoles modernes et peuvent modifier les propriétés physiques, chimiques et biologiques du sol. De telles pratiques affectent donc aussi les MA. Diverses pratiques employées pour parvenir à la production maximale d'une culture ont une incidence négative sur la survie des propagules des MA. Certaines espèces de champignons survivront dans le sol retourné alors que d'autres périront. Les MA étant plus abondants dans le sol de surface, un labour en profondeur diluera leurs propagules dans un plus grand volume, donc réduira le taux d'infection des racines de la plante hôte. Les labours sont particulièrement néfastes quand le travail s'effectue à l'automne et que les hyphes des MA se détachent de la plante hôte. Les MA survivent mieux avec le non-travail du sol, surtout quand ils se trouvent à proximité de la culture qui a servi à leur développement. On se demande si les plantes n'empruntent pas les anciens canaux radiculaires dans les champs non travaillés, si bien qu'elles trouvent plus de propagules de MA que celles poussant dans un sol travaillé. Une gestion des MA dans le sol non travaillé est essentielle si l'on veut que les cultures en profitent au maximum. La présente étude explique comment les pratiques en matière de travail du sol affectent la richesse des espèces de MA, leur capacité de survie et leur pouvoir infectieux et comment les pratiques de conservation accroissent la survie de ces cryptogames, donc améliorent l'absorption du phosphore par les plantes et la stabilité des agrégats du sol.

**Mots clés:** Mycorrhizes à arbuscules, conservation du sol, travail du sol classique, absorption du P, stabilité des agrégats, cultures abris, rendement des cultures

Tillage, the mechanical manipulation of soil, is a common practice in modern agriculture. Tillage is performed to enhance decomposition of crop residues through physical breakdown and incorporation into soil. Tillage is also used to level soil, prepare seedbeds for planting, and incorporate fertilizers, manures and pesticides. Additionally, it can serve as a method of post-emergence weed control and as a management tool to disrupt or reduce the incidence of diseases and pests. While tillage is necessary in many situations, it may also lead to soil degradation and environmental pollution. There are two main types of tillage systems, conven-

tional (CT) and conservation (at least 30% residue left on the soil surface; Conservation Technology Information Center 1995). The general category of conservation tillage includes specific practices such as no-till (NT), ridge-tillage, reduced tillage (RT), shallow tillage and strip tillage. Reduced tillage systems are characterized by a reduction in the intensity or number of tillage operations compared to CT (generally autumn plowing plus spring disking). In RT sys-

**Abbreviations:** AM, arbuscular mycorrhizal; CT, conventional tillage; NT, no-till; RT, reduced tillage

tems most of the crop residues remain on the soil surface, and the tillage operation is normally done only in spring. Thus, the soil remains undisturbed throughout the winter, as is the case under NT systems. Concerns of environmental degradation through the transport of sediments, nutrients and pesticides from farmlands to surface waters, as well as the need to conserve soil water in dry areas, have prompted a switch to conservation tillage practices. These practices may improve soil physical properties at the macroscopic level, which in turn affects chemical and biological properties of soil at the microscopic level including AM fungi.

Arbuscular mycorrhizal fungi form symbiotic relationships with plants. In these associations plants provide carbohydrates to the fungi in exchange for mineral nutrients from the fungi. The name “arbuscular” is derived from the characteristic structures, arbuscules, which occur within host-plant cortical cells and are thought to be the primary site for fungus/plant metabolic exchanges (Scannerini and Bonfante-Fasolo 1983; Barea 1991). AM hyphae proliferate externally from colonized roots. The extra-radical hyphae increase the volume of soil that can be exploited for nutrients and make a fundamental bridge between plants and soil. While improved nutrient acquisition is considered to be the primary benefit of the AM symbiosis, other benefits such as protection against root pathogens (Thygesen et al. 2004), improved soil structure (Bethlenfalvay and Barea 1994, Kabir and Koide 2002), increased vegetation in polluted soil (Vivas et al. 2003) and enhanced water use efficiency (Caravaca et al. 2004) can also be gained from the presence of AM fungi.

Arbuscular mycorrhizal fungi are ubiquitous in both natural and agricultural soils. In agricultural field soils up to 50 m of AM hyphae per gram of soil have been observed (Smith and Read 1997) and hyphae can extend more than 9 cm beyond the roots (Camel et al. 1991). Phosphorus is a primary plant nutrient, however, in soil solution the concentration of P is usually very low. Phosphorus is transported to roots from the soil mainly via diffusion, however, the diffusion coefficient of P is very low, about 1/10th of that of K and  $\text{NH}_4$  and 1/100th of that of  $\text{NO}_3$ . Consequently, P is easily depleted in the root zone (Harley 1989). Barber (1995) calculated that since an annual crop's root system occupies less than 1% of the soil volume and since the P depletion zone of the plant root is between 1 and 2 mm in width, theoretically, plant roots should take up only 1–2% of applied P to the soil. In practice, however, plants take up 10–15% of applied P (Brady and Weil 1995). The presence of AM hyphal networks in soil seems to improve efficiency of plant P uptake from the soil. Nonetheless, tillage and other forms of soil disturbance can alter the ability of AM fungi to colonize roots, thereby reducing P uptake. Reducing tillage appears to be an effective means of minimizing AM hyphal network destruction, ensuring optimal plant nutrient uptake, and reducing soil erosion.

From the perspective of sustainable crop production, it is very important to understand the dynamics of AM fungi in agricultural soil as influenced by tillage. The purpose of this paper is to review how soil management practices affect the development of AM fungal associations with crop plants.

## EFFECTS OF SOIL DISTURBANCE ON MYCORRHIZAL FUNCTIONING

### Impacts on AM Fungal Development

Soil disturbance has a negative effect on AM fungi and thereby reduces the benefits to crops and soil quality that are derived from mycorrhizae. Schenk et al. (1982) in Florida, USA, reported an increase of mycorrhizal spores and root colonization on several agronomic crops with minimum tillage compared with conventional tillage. Mulligan et al. (1985) in Michigan, USA, proposed that the negative impact of tillage on root colonization was due to lower root growth of dry bean (*Phaseolus vulgaris* L.) caused by increased soil bulk densities in tilled soils. In contrast, O'Halloran et al. (1986) in eastern Canada found greater root growth but lower P uptake of corn in CT soils, suggesting that the negative effects of tillage were not the result of reduced root growth. O'Halloran et al. (1986) reported that disturbance of previously NT soils decreased early plant growth, P uptake and AM colonization in corn. Their other studies indicated that the effects of soil disturbance did not occur if the AMF had been eradicated by  $\gamma$ -radiation. Furthermore, when a non-mycorrhizal canola plant (O'Halloran et al. 1986) or spinach (Evans and Miller 1988) was grown, soil disturbance did not have any effect on P absorption of those plants. The fungicide Benomyl minimized the effect of soil disturbance on P uptake by corn (Evans and Miller 1988). Collectively, these results indicate that the negative effect of disturbance on P uptake is likely due to impaired AM association.

Extraradical hyphae are thought to be the main source of inoculum in soil (Sylvia 1992) especially when host plants are present and soil is not tilled for crop production. Evans and Miller (1990) in eastern Canada observed that disturbance of root-free soil containing only AM hyphae detached from host plants reduced the AM colonization of corn roots planted later in this soil, and decreased plant growth and nutrient uptake. This suggested that if the AM hyphal network is not disrupted, the next crop will be more rapidly connected to the network and nutrient absorption capacity would be enhanced. Jasper et al. (1989) in Australia found a reduction of AM colonization of clover after soil disturbance and suggested that most of this reduction was due to decreased hyphal viability. However, contrasting results were obtained by McGonigle et al. (1990) in eastern Canada in a study on the effect of soil disturbance on AM colonization and corn growth. Unlike previous studies, decreases in P uptake and plant growth were not accompanied by a decrease in AM colonization. McGonigle et al. (1990) proposed that if AM fungi were an important component of the disturbance effect, it would have to be through the dismantling of a potential though dynamic hyphal network rather than through reduction in the mycorrhizal colonization potential of the soil. The role of extraradical hyphae as principal propagules for AM colonization might be of considerable importance, particularly in cool climates where population of the viable spores in agricultural soils may be extremely low following winter (Dalpé Y., unpublished data; Addy et al. 1997). Most of these early studies suggest that AM were involved in P uptake and were negatively affected by soil disturbance, but conclusive experimentation

was hampered by lack of methodologies to examine AM hyphae directly in the soil. Current research supports this hypothesis and addresses various mechanisms.

### Impacts on AM Fungal Community Composition

In a research field (Kabir et al. 1997a, 1998a) in Quebec, Canada, the AM species diversity in a soil under 12 yr of CT practice was significantly lower than that of the NT soil (unpublished data). Hamel et al. (1994) in Quebec, Canada, reported the disappearance of *Gigaspora margarita* and *G. caledonium* 3 yr after plowing and putting a previously uncultivated field into cultivation. Similarly, Boddington and Dodd (2000) observed a decrease in AM fungal species richness in tilled soil, relative to untilled soil, growing *Gliricidia sepium* in Indonesia; *Scutellospora* sp. disappeared after soil disturbance. Significantly more AM spores were also observed by Jansa et al. (2002) in soil growing wheat under NT than under CT in Switzerland. Jansa et al. (2003) also found that *Scutellospora* was more dominant in low-tillage fields, whereas *Glomus* was dominant in highly tilled fields. Douds et al. (1995) found more *G. occultum*-like spores under NT corn-soybean-wheat rotations and more *G. etunicatum*-like and other *Glomus* spp. spores in soils under cultivation in Pennsylvania, USA. Sieverding (1991) observed that *G. scitillans* was sporulating earlier and was able to produce more spores than other AM species in plowed soils in Columbia. The author reported that 75% of the spores in plowed soils were belonging to *G. scitillans* while this species accounted for only 5% of the total spores in NT soils. This suggests that tillage practices may select AM fungi with certain characteristics and eliminate others. For example, soil disturbance created by tillage may favor fast-growing species that might be less mutualistic and less efficient in improving host plant nutrients uptake (Johnson and Pflieger 1992).

### Differentiating Effects of Disturbance on Nutrient Acquisition and AM Functioning

The most dramatic effect of AM fungal proliferation in the soil is an increase in P absorption by the host plants (Koide 1991). Phosphorus is found in very low concentration in the soil solution as it has a high affinity for fixation onto soil minerals (Lambert et al. 1984). The distribution of nutrients, especially P, in the soil profile is affected by tillage intensity (Dick 1983) and thus may impact P availability to crop roots. Research on the importance of soil disturbance on AM colonization has been inconsistent, but P absorption by plants in disturbed soil has always been lower than those grown in undisturbed soil (Miller 2000). This indicates the importance of the AM hyphal network in potential tillage operations.

Kabir et al. (1998a) in Quebec, Canada, found that in a sandy loam soil P concentration in corn plants growing under NT and RT was greater than under CT at the 12- to 14-leaf and silking stages. At the grain filling stage, however, plant P concentration was greater only under NT, and the difference between P concentrations obtained under CT and RT had disappeared. In another year in the same soil, NT increased P concentration in the corn plant only at the 12-

to 14-leaf stage. In the clay soil, however, P concentration was greater under NT both at the 12- to 14-leaf and the silking stage. These results are in accordance with those of O'Halloran (1982) who also observed higher P absorption by corn in a NT system. McGonigle and Miller (1993), in eastern Canada, observed that corn shoot P concentrations were significantly greater under NT and RT than under CT. In addition to P, Kabir et al. (1998a) found that Zn and Cu concentrations in corn plants were sometimes significantly greater under NT than under CT plots. A similar effect of soil disturbance on Zn and Cu was also observed for corn in pot studies (McGonigle and Miller 1996). Mozafar et al. (2000) reported that the concentrations of P, Zn and Cu in corn and those of P, K, Mn and Zn in wheat grown in Switzerland were greater in plants under NT than under CT at most of their sampling dates. While NT systems allow for greater nutrient uptake, in certain circumstances, crop yields are reduced with NT. Thus the relatively minor economical benefits that derived from improved nutrient acquisition are therefore, often dwarfed by the losses in crop yield. However, considering the cost and benefit ratio, one could argue that the profitability of NT is similar to CT even though yields are reduced under NT. Furthermore, considering soil health and the environment, growing crops in an NT system far outweigh any short-term benefit of CT systems.

### Relationships among Soil Disturbance, AM Fungi and Aggregate Stability

Soil structure quality and aggregate stability in agricultural fields are influenced by agricultural practices. Tillage gradually reduces aggregate stability making soil more vulnerable to wind and water erosion. Arbuscular mycorrhizal fungi make direct contributions to aggregation and aggregate stability (Bethlenfalvay and Barea 1994; Kabir and Koide 2000, 2002) and therefore play an important role in soil conservation. AM hyphae have been positively correlated with soil aggregate stability (Kabir and Koide 2002). Because AM hyphal networks remain intact in NT soils, the density of active hyphae is greater than under CT soils (Kabir et al. 1997a). Hence, the importance of AM fungi for aggregation is greater in NT than in CT systems. Tisdall (1991) speculated that extracellular polysaccharides of fungi and bacteria provide a cementing agent for aggregates. Wright and Upadhyaya (1996) discovered "glomalin", a glycoprotein on the surface of active AM hyphae, which appears to act as a cementing agent for soil particles. The more abundant AM mycelium under NT may lead to a more abundant production of glomalin under NT than CT. In contrast, in CT regimes, disruption of the hyphal network due to tillage operations, would likely lead to reduced glomalin production and reduced aggregate stability. For example, Bethlenfalvay and Barea (1994) found an isolate of *Glomus mosseae*, which improved soil aggregation by 50% when associated with pea, in a yellow clay-loam soil, and by 400% in a gray silt-loam soil. Wright et al. (1999) reported that both aggregate stability and total glomalin were greater under NT than under CT in the top 0 to 5 cm of the soil. They also found that when soil was collected from the grassland adjacent to the tillage experiment, the structure of the top 0–10 cm of the grassland

soil was more stable than that of the cultivated soil after several years under NT and 4 yr under CT. The production of glomalin was also greater in the grassland than under NT. Collectively, these results indicate that activities of AM fungi are greater in NT than CT, and when mycotrophic plants are present, leading to greater hyphal densities, glomalin production, and aggregate stability.

### OPTIMIZING THE AM FUNGAL BENEFIT VIA CHANGES IN CROPPING SYSTEMS

#### Tillage Practices

Some AM fungi are capable of free-living growth after the death of their host plant (Tommerup and Abbott 1981). However, questions remain concerning how long the hyphae remain viable in the absence of a living host plant, and how soil disturbance may affect the survivability of these AM hyphae especially in the field condition when different tillage operations take place.

Experiments were undertaken to determine effects of the timing of tillage on the survival of AM hyphae (Kabir et al. 1997a). In these experiments, fall tillage severely reduced AM hyphal viability, but spring tillage had little effect on AM hyphal viability. This research revealed that timing of tillage is critical to the survival of AM hyphae. McGonigle et al. (1990) reported that as the number of tillage operations is increased, AM fungal benefits to host plants are gradually decreased. Kabir et al. (1997a) concluded that the reduction of the AM fungal benefits is due to the reduction of viable AM hyphae. McGonigle and Miller (1999) demonstrated that extraradical AM hyphae, which overwintered in the field remained viable as inoculum in spring and that disturbance of these hyphae in spring reduced colonization and P uptake in the following crop.

For row crops, the influences of tillage on AM development are likely related to spatial and temporal distributions of the AM fungi. Kabir et al. (1998a) studied AM fungal distributions under CT, RT and NT corn. The greatest seasonal fluctuation of hyphal density was observed under the row, where a sharp increase occurred at the silking stage and decreased thereafter. The least variation and least overall hyphal densities were observed between the rows.

Densities of total and metabolically active hyphae were greatest directly in the crop row and decreased with distance from the row. About half of the hyphae were observed in the row in both soils, whereas less than 20% of hyphae were observed between the two rows in both clay and sandy loam soils (Kabir et al. 1998a), again suggesting a prevalence of AM hyphae in the row. Plants growing near the previous year's row are likely to receive more benefits from AM fungi than plants growing between the two rows. For example, ridge tillage near the previous year's row could increase the benefits of AM fungi to the crops. Hyphal densities in the row were greater under NT than under CT, but between rows there was no difference between NT and CT. Mulligan et al. (1985) observed that excessive secondary tillage reduced AM colonization of *Phaseolus vulgaris* L. Mycorrhizal root colonization of corn growing in NT and ridge till plots was greater than that in CT plots (McGonigle and Miller 1993).

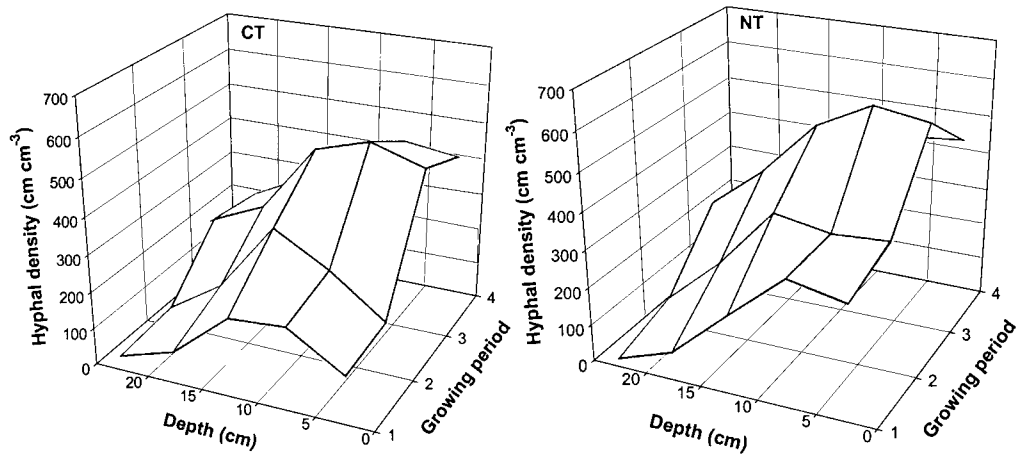
The vertical distribution is also influenced by tillage practices (Kabir et al. 1998b). Mycorrhizal growth was measured within the top 0–25 cm of soil in NT and CT fields under corn cultivation. Arbuscular mycorrhizal hyphae and spores were more abundant in the top 0- to 15-cm layer of the soil profile and decreased dramatically below this depth. Similar results were reported for AM spores by An et al. (1990) in Kentucky, USA, under soybean, and by Smith (1978) in an Australian wheat field under NT and CT operations. This suggests that tilling the soil to a depth of 15 cm would affect most of the AM fungi and that plowing below this depth would dilute the AM propagules in the zone of seedling establishment.

Kabir and O'Halloran (unpublished data) observed lower hyphal density under CT than under NT in the top 0- to 15-cm soil depth at the early stage of corn growth (5- to 6-leaf stage), in the 0- to 10-cm depth at the 10- to 12-leaf stage, and in the 0- to 5-cm depth at the silking stage (Fig. 1). These differences disappeared at maturity. The number of AM spores was significantly greater in NT than in CT in the top 0- to 10-cm of soil through the 10- to 12-leaf stage, but tillage effects differences disappeared at the silking stage (Fig. 2). The negative effects of soil disturbance on AM hyphae and spores changed over time under CT soil and are ephemeral. Hyphal densities gradually increased from the 5- to 6-leaf stage to the silking stage of corn and decreased thereafter. The distribution of spores, however, did not follow the same seasonality as the hyphal densities under both tillage systems. The number of spores gradually increased up to plant maturity, indicating that spores are the final product of the AM fungal growth cycle (Fig. 2).

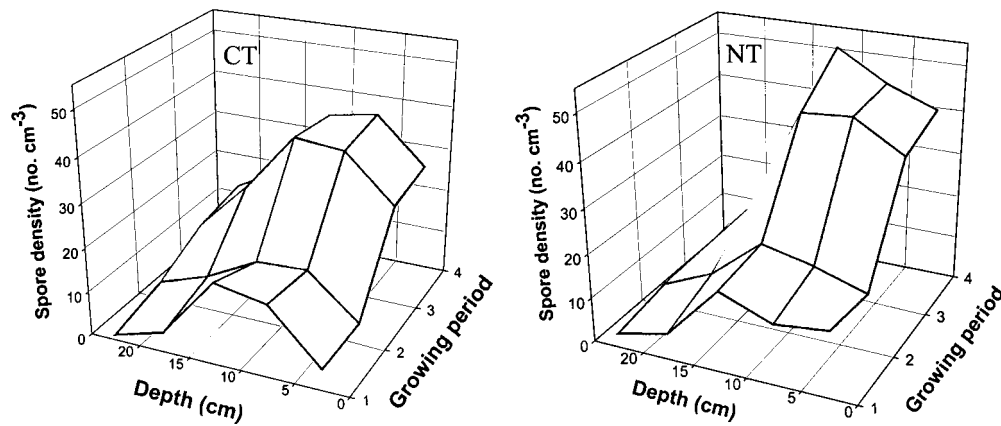
#### Cover Crops

Since AM fungi are biotrophic, viability of AM hyphae gradually decreases in the absence of host plants such as during a fallow, even in NT systems. Arbuscular mycorrhizal hyphal survival and inoculum potential depends on the presence of the host plants during the fallow period. Harinikumar and Bagyaraj (1988) in India reported 40% reduction of AM inoculum in field soil after leaving the land fallow for one season. Long-fallow periods (more than a year) in northern Australia were associated with a decline in mycorrhizal colonization and AM sporulation in various crops (Thompson 1987). This reduction in AM fungal inoculum may be exacerbated by adverse winter conditions (Kabir et al. 1997a). In a NT system in eastern Canada, winter alone caused a reduction of approximately 31 and 40% of total and metabolic active hyphae, respectively (Kabir et al. 1997b).

It is important to maintain the level of AM inoculum in soil over winter to maximize the benefits of AM fungi on the following crop. Mycotrophic cover crops capable of surviving freezing winter conditions may help maintain the AM inoculum potential in soil. Whereas a mycorrhizal cover crop may improve P uptake and eventually increase crop yield, a non-mycorrhizal cover crop in the cropping schedule of a NT or CT systems may reduce propagules of AM fungi in the soil. An experiment was conducted by Kabir and Koide (unpublished) in Pennsylvania, USA, to verify the effect of growing mycorrhizal and non-mycorrhizal cover crops over winter in NT system. At 31 d after planti-



**Fig. 1.** Seasonal and vertical distribution of mycorrhizal hyphae in four corn-growing periods: 5- to 6-leaf stage (1), 10- to 12-leaf stage (2), silking stage (3), and mature stage (4) in conventional (CT) and no tillage (NT) systems.



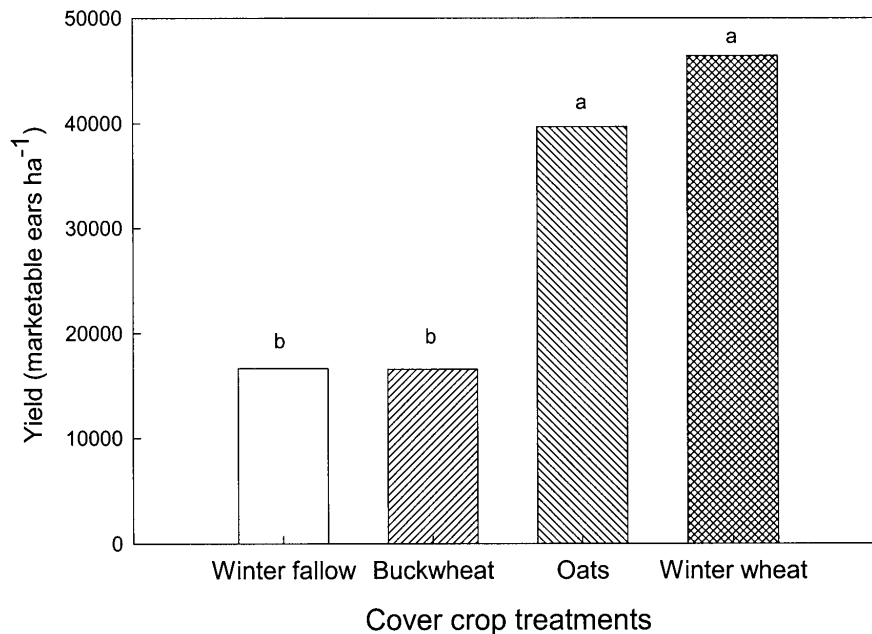
**Fig. 2.** Seasonal and vertical distribution of mycorrhizal spores in four corn-growing periods: 5- to 6-leaf stage (1), 10- to 12-leaf stage (2), silking stage (3), and mature stage (4) in conventional (CT) and no tillage (NT) systems.

ng sweet corn, root colonization and shoot P content of the plants were significantly greater in mycorrhizal cover cropped (oats and winter wheat) plots than in fallow plots or non-mycorrhizal cover cropped (buckwheat) plots. This indicates that the mycorrhizal cover crop increased or maintained AM fungal inoculum in soil. Accordingly, sweet corn shoot dry weight (14 and 31 days after planting) and plant height (87 d after planting) were significantly greater in the mycorrhizal cover cropped plots. Similarly, sweet corn yield was also greater in the mycorrhizal cover cropped plots than in the fallow or non-mycorrhizal cover cropped plots (Fig. 3). Boswell et al. (1998) and Kabir and Koide (2000) demonstrated that mycotrophic winter cover cropping with wheat or dandelion increased subsequent sweet corn yield. Kabir and Koide (2002) observed that either single or mixed mycotrophic cover crops increased the following cash crop's P status, and plant P status positively correlated with vegetative growth, reproductive maturity and yield of sweet corn. These results suggest that management of indigenous AM fungi is important to maintain or improve AM fungal

propagules by using cover crops for succeeding crops improvement either under NT or CT operations.

## CONCLUSIONS

Conventional tillage practices reduce AM hyphal survival and proliferation thus reducing benefits of the symbiosis to associated plants and soils. Under temperate climates, it is beneficial to optimize survival of AM hyphae from fall to spring often in the absence of a living host plant. Fall tillage has been shown to adversely affect hyphal viability and host plant benefits in the following year. Reduced tillage or ridge tillage systems have less negative effects than CT on the abundance of AM propagules because tillage operation in these systems are performed in the spring and AM fungi remain intact throughout the winter. In my studies the greatest amounts of hyphae were found in the crop rows and hyphal abundance decreased logarithmically to the inter-row, suggesting that growing crops close to the previous years' rows optimizes AM fungal benefits. Arbuscular mycorrhizal fungi were abundant in the upper 15 cm of the soil irrespective of tillage practices suggesting that



**Fig. 3.** Marketable sweet corn ear production growing in mycorrhizal cover crops (oats and winter wheat), non-mycorrhizal cover crop (buckwheat) and winter NT fallow. Different letter indicate a significant ( $P < 0.05$ ) difference between the treatment means.

deep plowing (<15 cm) would dilute the AM propagules into a greater volume of soil. Inoculum dilution, however, is not the main mechanism for the tillage effect since researchers have found that colonization is not always decreased by soil disturbance, although nutrient uptake is usually reduced. Since AM fungi are biotrophic, the combination of fallowing and tillage substantially reduces the density of AM infective propagules (Kabir et al. 1999). This problem is aggravated by adverse weather conditions. More research is needed to define the interactive effects of soil disturbance and fallowing, especially for field and vegetable crops other than corn. No-tillage along with mycotrophic winter cover crops improves AM hyphal densities and inoculum potential, which subsequently stabilizes soil and increases crop yield (Boswell et al. 1998; Kabir and Koide 2000, 2002). By introducing a mycotrophic cover crop after fall tillage, it may be possible to increase the benefits of AM fungi in CT systems as well.

#### ACKNOWLEDGMENTS

This paper was presented at a Joint Symposium of The Canadian Society of Agronomy, the Canadian Society of Soil Science and the Fourth International Conference on Mycorrhizae held in Montreal, QC, 11 August 2003. I gratefully acknowledge the financial support from the International Conference on Mycorrhizae for attendance at the symposium and the Canadian Society of Agronomy for publication costs. I would like to thank Tom Forge, C. Hamel, K. Reed and anonymous reviewers for their valuable suggestions and criticisms to improve the manuscript.

**Addy, H. D., Miller, M. H. and Peterson, R. L. 1997.** Infectivity of the propagules associated with extraradical mycelia of two AM fungi following winter freezing. *New Phytol.* **135**: 745–753.

**An, Z.-Q., Grove, J. H., Hendrix, J. W., Hershman, D. E. and Henson, G. T. 1990.** Vertical distribution of endogonaceous mycorrhizal fungi associated with soybean, as affected by soil fumigation. *Soil Biol. Biochem.* **22**: 715–719.

**Barber, S. A. 1995.** Soil nutrient bioavailability — A mechanistic approach. John Wiley & Sons, New York, NY. pp. 49–84.

**Barea, J. M. 1991.** Vesicular-arbuscular mycorrhizas as modifiers of soil fertility. *Adv. Soil Sci.* **15**: 1–40.

**Bethlenfalvay, G. J. and Barea, J. M. 1994.** Mycorrhizae in sustainable agriculture. I. Effects on seed yield and soil aggregation. *Am. J. Alt. Agric.* **9**: 157–161.

**Boddington, C. L. and Dodd, J. C. 2000.** The effects of agricultural practices on the development of indigenous arbuscular mycorrhizal fungi. I. Field studies in an Indonesian ultisol. *Plant Soil* **218**: 137–144.

**Boswell, E. P., Koide, R. T., Shumway, D. L. and Addy H. D. 1998.** Winter wheat cover cropping, VA mycorrhizal fungi and maize growth and yield. *Agric. Ecosyst. Environ.* **67**: 55–65.

**Brady, N. C. and Weil, R. R. 1995.** The nature and properties of soils. Prentice Hall, Upper Saddle River, NJ. pp. 328–568.

**Camel, S. B., Reyes-Soils, M. G., Ferrera-Cerrato, R., Franson, R.L., Brown, M. S. and Bethlenfalvay, G. J. 1991.** The growth of mycorrhizal mycelia through bulk soil. *Soil Sci. Soc. Am. J.* **58**: 389–393.

**Caravaca, F., Figueroa, D., Barea, J. M., Azcon-Aguilar, C., Roldan, A. 2004.** Effect of mycorrhizal inoculation on nutrient acquisition, gas exchange, and nitrate reductase activity of two Mediterranean-autochthonous shrub species under drought stress. *J. Plant Nutr.* **27**: 57–74.

**Conservation Technology Information Center. 1995.** Survey guide: National crop residue management guide. West Lafayette, IN.

**Dick, W. A. 1983.** Organic carbon, nitrogen and phosphorus concentrations and pH in soil profiles as affected by tillage intensity. *Soil Sci. Soc. Am. J.* **47**: 102–107.

- Douds, D. D., Glaves, L. and Janke, R. R. 1995.** Effects of tillage and farming system upon populations and distribution of vesicular-arbuscular mycorrhizal fungi. *Agric. Ecosyst. Environ.* **52**: 111–118.
- Evans, D. G. and Miller, M. H. 1988.** Vesicular-arbuscular mycorrhizas and the soil — disturbance induced reduction of nutrients absorption in maize. I. Casual relations. *New Phytol.* **110**: 67–74.
- Evans, D. G. and Miller, M. H. 1990.** The role of external mycelial network in the effect of soil disturbance upon vesicular-arbuscular colonization of maize. *New Phytol.* **114**: 65–71
- Hamel, C., Dalpé, Y., Lapierre, C., Simard, R. R. and Smith, D. L. 1994.** Composition of the vesicular-arbuscular fungi population in an old meadow as affected by pH, phosphate and soil disturbance. *Agric. Ecosyst. Environ.* **49**: 223–231.
- Harinikumar, D. M. and Bagyaraj, D. J. 1988.** Effect of crop rotation on native vesicular-arbuscular mycorrhizal propagules in soil. *Plant Soil.* **110**: 77–80.
- Harley, J. L. 1989.** The significance of mycorrhiza. *Mycol. Res.* **92**: 129–139.
- Jansa, J., Mozafar, A., Anken, T., Ruh, R., Sanders, I. R., Frossard, E. 2002.** Diversity and structure of AMF communities as affected by tillage in a temperate soil. *Mycorrhiza* **12**: 225–234.
- Jansa, J., Mozafar, A., Kuhn, G., Anken, T., Ruh, R., Sanders, I. R., Frossard, E. 2003.** Soil tillage affects the community structure of mycorrhizal fungi in maize roots. *Ecol. Appl.* **13**: 1164–1176.
- Johnson, N. C. and Pflieger, F. L. 1992.** Vesicular-arbuscular mycorrhizae and cultural stress. Pages 71–100 in G. J. Bethlenfalvay and R. G. Linderman, eds. *Mycorrhizae in sustainable agriculture*. ASA, Madison, WI.
- Jasper, D. A., Abbott, L. K. and Robson, A. D. 1989.** Soil disturbance reduces the infectivity of external hyphae of VA mycorrhizal fungi. *New Phytol.* **112**: 93–99.
- Kabir, Z. and Koide, R. T. 2000.** The effects of dandelion or a cover crop on mycorrhizal inoculum potential, soil aggregation and yield of maize. *Agric. Ecosyst. Environ.* **78**: 167–174.
- Kabir, Z. and Koide, R. T. 2002.** Mixed cover crops, mycorrhizal fungi, soil properties and sweet corn yield. *Plant Soil* **238**: 205–215.
- Kabir, Z., O'Halloran, I. P., Fyles, J. W. and Hamel, C. 1997a.** Seasonal changes of arbuscular mycorrhizal fungi as affected by tillage practices and fertilization: I. hyphal density and mycorrhizal root colonization. *Plant Soil* **192**: 285–293.
- Kabir, Z., O'Halloran, I. P. and Hamel, C. 1997b.** Overwinter survival of arbuscular mycorrhizal hyphae is favored by attachment to roots but diminished by disturbance. *Mycorrhiza* **7**: 197–200.
- Kabir, Z., O'Halloran, I. P., Fyles, J. W. and Hamel, C. 1998a.** Dynamics of the mycorrhizal symbiosis of corn: effect of host physiology, tillage practice and fertilization on spatial distribution of extraradical hyphae in the field. *Agric. Ecosyst. Environ.* **68**: 151–163.
- Kabir, Z., O'Halloran, I. P., Widden, P. and Hamel, C. 1998b.** Vertical distribution of arbuscular mycorrhizal fungi under corn (*Zea mays* L.) in no-till and conventional tillage systems. *Mycorrhiza* **8**: 53–55.
- Kabir, Z., O'Halloran, I. P. and Hamel, C. 1999.** Combined effects of soil disturbance and fallowing on plant and fungal components of mycorrhizal corn (*Zea mays* L.). *Soil Biol. Biochem.* **31**: 307–314.
- Koide, R. T. 1991.** Nutrient supply, nutrient demand and plant response to mycorrhizal infection. *New Phytol.* **117**: 365–381.
- Lambert, D. H., Baku, D. E. and Cote, H. J. 1984.** The role of mycorrhizae in the interactions of phosphorus with zinc, copper, and other elements. *Soil Sci. Soc. Am. J.* **43**: 976–980.
- McGonigle, T. P., Evans, D. G. and Miller, M. H. 1990.** Effect of degree of soil disturbance on mycorrhizal colonization and phosphorus absorption by maize in growth chamber and field experiment. *New Phytol.* **116**: 629–636.
- McGonigle, T. P. and Miller, M. H. 1993.** Mycorrhizal development and phosphorus absorption in maize under conventional and reduced tillage. *Soil Sci. Soc. Am. J.* **57**: 1002–1006.
- McGonigle, T. P. and Miller, M. H. 1996.** Development of fungi below ground in association with plants growing in disturbed and undisturbed soils. *Soil Biol. Biochem.* **28**: 263–269.
- McGonigle, T. P. and Miller, M. H. 1999.** Winter survival of extraradical hyphae and spores of arbuscular mycorrhizal fungi in the field. *Appl. Soil Ecol.* **12**: 41–50.
- Miller, M. H. 2000.** Arbuscular mycorrhizae and the phosphorus nutrition of maize: A review of Guelph studies. *Can. J. Plant Sci.* **80**: 47–52.
- Mozafar, A., Anken, T., Ruh, R. and Frossard, E. 2000.** Tillage intensity, mycorrhizal and nonmycorrhizal fungi, and nutrient concentrations in maize, wheat, and canola. *Agron. J.* **92**: 1117–1124.
- Mulligan, M. F., Smucker, A. J. M. and Safir, G. F. 1985.** Tillage modifications of dry edible bean root colonization by VAM fungi. *Agron. J.* **77**: 140–144.
- O'Halloran, I. P. 1982.** M. Sc. Thesis, Department of Land Resource Science, University of Guelph, Guelph, ON.
- O'Halloran, I. P., Miller, M. H. and Arnold, G. 1986.** Absorption of P by corn (*Zea mays* L.) as influenced by soil disturbance. *Can. J. Soil Sci.* **66**: 287–302.
- Scannerini, S. and Bonfante-Fasolo, P. 1983.** Ultrastructure analysis of mycorrhizal associations. *Can. J. Bot.* **61**: 917–943.
- Schenk, N. C., Smith, G. S., Mitchell, D. J. and Gallaher, R. N. 1982.** Minimum tillage effects on the incidence of beneficial mycorrhizal fungi on agronomic crops. *Florida Sci.* **45** (Suppl.): 8.
- Sieverding, E. 1991.** Vesicular-arbuscular management in tropical agrosystems. Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Dag Hammarskjöld-Weg 1+2, Postfach 5180, 6236 Eschborn 1, Federal Republic of Germany.
- Smith, T. F. 1978.** A note on the effect of soil tillage on the frequency and vertical distribution of spores of vesicular-arbuscular endophytes. *Aust. J. Soil Res.* **16**: 359–361.
- Smith, S. E. and Read, D. J. 1997.** *Mycorrhizal symbiosis*. Academic Press, London, UK.
- Sylvia, D. M. 1992.** Quantification of external hyphae of vesicular arbuscular mycorrhizal fungi. Pages 53–65 in J. R. Norris, D. J. Read, and A. K. Varma, eds. *Methods in microbiology*. Vol. 24. Academic Press, London, UK.
- Tisdall J. M. 1991.** Fungal hyphae and structural stability of soil. *Aust. J. Soil Res.* **29**: 729–743.
- Thompson, J. P. 1987.** Decline of vesicular-arbuscular mycorrhizae in long fallow disorder of field crops and its expression in phosphorus deficiency of sunflower. *Aust. J. Agril. Res.* **38**: 847–867.
- Tommerup, I. C. and Abbott, L. K. 1981.** Prolong survival and viability of VA mycorrhizal hyphae after root death. *Soil Biol. Biochem.* **13**: 431–433.
- Thygesen, K., Larsen, J. and Bodker, L. 2004.** Arbuscular mycorrhizal fungi reduce development of pea root-rot caused by *Aphanomyces euteiches* using oospores as pathogen inoculum. *Eur. J. Plant Pathol.* **110**: 411–419
- Vivas, A., Voros, A., Biro, B., Barea, J. M., Ruiz-Lozano, J. M. and Azcon, R. 2003.** Beneficial effects of indigenous Cd-tolerant and Cd-sensitive *Glomus mosseae* associated with a Cd-adapted strain of *Brevibacillus* sp in improving plant tolerance to Cd contamination. *Appl. Soil Ecol.* **24**: 177–186.
- Wright, S. F. and Upadhyaya, A. 1996.** Extraction of an abundant and unusual protein from soil and comparison with hyphal protein of arbuscular mycorrhizal fungi. *Soil Sci.* **161**: 575–586.
- Wright, S. F., Starr, J. L. and Paltineanu, I. C. 1999.** Changes in aggregate stability and concentration of glomalin during tillage management transition. *Soil Sci. Soc. Am. J.* **63**: 1825–1829.

