Plant and Soil 180: 139–146, 1996.

Influence of compaction from wheel traffic and tillage on arbuscular mycorrhizae infection and nutrient uptake by *Zea mays*

James A. Entry[1], D. Wayne Reeves[2], Eric Mudd[1], William J. Lee[1], Elizabeth Guertal[1] and Randy L. Raper[2]
[1]*Department of Agronomy and Soils, 202 Funchess Hall, Auburn University, AL 36849-5412, USA* and* [2]*National Soil Dynamics Laboratory, Agricultural Research Service, US Department of Agriculture, PO Box 3439, Auburn, AL 36831-3439, USA*

Received 30 August 1995. Accepted in revised form 4 January 1996

Key words: arbuscular mycorrhizae, compaction, tillage, nutrient concentration

Abstract

Interactive effects of seven years of compaction due to wheel traffic and tillage on root density, formation of arbuscular mycorrhizae, above-ground biomass, nutrient uptake and yield of corn (*Zea mays* L.) were measured on a coastal plain soil in eastern Alabama, USA. Tillage and soil compaction treatments initiated in 1987 were: 1) soil compaction from tractor traffic with conventional tillage (**C,CT**), 2) no soil compaction from tractor traffic with conventional tillage (**NC,CT**), 3) soil compaction from tractor traffic with no-tillage (**C,NT**), and, 4) no soil compaction from tractor traffic with no-tillage (**NC,NT**). The study was arranged as a split plot design with compaction from wheel traffic as main plots and tillage as subplots. The experiment had four replications. In May (49 days after planting) and June, (79 days after planting), root biomass and root biomass infected with arbuscular mycorrhizae was higher in treatments that received the NC,NT treatment than the other three treatments. In June and July (109 days after planting), corn plants that received C,CT treatment had less above-ground biomass, root biomass and root biomass infected with mycorrhizae than the other three treatments. Within compacted treatments, plants that received no-tillage had greater root biomass and root biomass infected with mycorrhizae in May and June than plants that received conventional tillage. Corn plants in no-tillage treatments had higher root biomass and root biomass infected with mycorrhizae than those in conventional tillage. After 7 years of treatment on a sandy Southeastern soil, the interactive effects of tillage and compaction from wheel traffic reduced root biomass and root biomass infected with mycorrhizae but did not affect plant nutrient concentration and yield.

Introduction

Agricultural production systems in the southeastern United States include intensive tillage for seedbed preparation, incorporation of fertilizer and weed control. Nutrients are retained to a greater degree in no-till and conservation tillage systems because soil organic matter and soil microorganisms are less disturbed than in plowed systems. No-till systems promote C accumulation at the soil surface due to lack of incorporation of crop residues. Wood and Edwards (1992) found that organic C and N were 67% and 66% higher, respectively, in the top 10 cm of soil when soybean (*Glycine max* L. Merr.), wheat (*Triticum aestivum* L.) and corn (*Zea mays* L.) were grown under a no-till rather than a conventionally tilled system. Wood et al. (1991) found that initiation of no-till resulted in higher soil organic carbon, soil organic N and less NO_3-N in the top 40 cm of soil. In the 40 to 180 cm depths less NO_3-N was found in the no-till system indicating that no-till farming may reduce NO_3 losses below the root zone. The availability of soil nutrients was greater under conservation tillage than under conventional tillage system on an Appalachian Plateau soil in northeast Alabama (Edwards et al., 1992). Hargrove (1985) and Follett and Peterson (1988) reported greater extractable Ca, Mg,

* FAX No: + 1205 8443945

P, Mg and Zn in the surface soils of no-till agronomic systems than conventionally tilled systems.

Intensive tillage can exacerbate soil compaction from wheel traffic. Increasing size and weight of farm tractors is causing increasing compaction of soils throughout the United States. Soils of the Southern Coastal Plain often require annual subsoiling to destroy compacted zones that form just below the plow layer as a result of previous tillage operations (Raper et al., 1994; Reeves and Touchton, 1986). Soil compaction resulting from wheel traffic leads to decreased soil structure and porosity, decreased water content at field capacity, increased soil erosion and ultimately reduced yield and quality of crops by impeding root growth (Soane, 1990). Soils in no-tillage systems withstood the negative impacts of wheel induced compaction better than conventional tillage (Reeves et al., 1992; Voorhees and Lindstrom, 1984).

Although soil physical properties as affected by tillage and wheel traffic have been independently researched, the interactive effects of residue management and traffic induced compaction on mycorrhizal colonization of plant roots and nutrient uptake have not been investigated. Previous studies on this site have shown that compaction from wheel traffic and conventional tillage interacted to decrease soil strength, soil moisture and plant N uptake efficiency while increasing N losses from the plant-soil system compared to no compaction from wheel traffic in a no-tillage system (Reeves et al., 1992; Torbert and Reeves, 1994, 1995). The objective of this research was to determine the interactive effects of tillage and compaction due to wheel traffic on root density, soil microbial biomass, arbuscular mycorrhizae, nutrient uptake and yield of corn.

Materials and methods

Field procedures

The site is located at the E V Smith Alabama Agricultural Experiment Station Research Farm near Montgomery, Alabama, USA (32° 24.5'N, 85° 57'W). Tillage and compaction treatments have been implemented since 1987 on a Norfolk loamy sand (fine, loamy, siliceous, thermic Typic Kandiudult). Treatments were: 1) soil compaction from tractor traffic with conventional tillage (**C,CT**), 2) no soil compaction from tractor traffic with conventional tillage (**NC,CT**), 3) soil compaction from tractor traffic with no-tillage (**C,NT**), and, 4) no soil compaction from tractor traffic with no-tillage (**NC,NT**). The study was arranged as a split plot design with compaction from wheel traffic as main plots and tillage system as subplots. The experiment had four replications. Soil compaction and tillage treatments were imposed on a corn (*Zea mays* L.) - soybean (*Glycine max* (L.) Merr.) rotation with a winter cover crop of crimson clover (*Trifolium incarnatum* L.) system.

Field operations

Soybeans were grown in 1993, followed by a winter crimson clover cover crop, with corn grown in the summer of 1994. Plots were 21.3 m long × 6.1 m wide. In all years field operations were carried out using an experimental wide-frame tractive vehicle that spans the entire width of the research plots and performs field operations without applying traffic to the plots (Monroe and Burt, 1989). A 4.6 Mg tractor was utilized to compact the soil on wheel-traffic treatments (Reeves et al., 1992). During the fall the tractor was driven over the plots to simulate planting of the cover crop and any required fertilizer applications. The tractor was driven in trafficked plots in the spring/summer to simulate four-row field preparations and planting.

The cover crop was drilled on 2 November 1993 and in spring of 1994, sprayed with glyphosate, N-(*phosphonomethyl*) glycine (0.46 kg ai ha^{-1}) and 2,4-DB [2,4-*dichlorophenoxy*)*butyric acid*) to kill the cover crop. The conventional tillage treatment occurred on 5 April, six days before corn planting and wheel-traffic were applied. The tillage operation involved two trips with a disk to 12–14 cm depth, followed by one trip with a field cultivator. Corn was planted 11 April 1994 in 75-cm rows at a seeding rate of 59,000 seeds ha^{-1}, and the stand later thinned to 49,400 plants ha^{-1}. After planting, wheel-traffic was applied to compact plots the same day. On 13 April 1994 (2 days after planting), 33 kg S ha^{-1}, 25 kg K ha^{-1}, 15 kg Mg ha^{-1}, 10 kg P ha^{-1}, 6 kg Zn ha^{-1} and 3 kg B ha^{-1} was applied to all plots. On April 27, (16 days after planting), 168 kg N ha^{-1} was applied to all plots.

Soil moisture

One set of 6 mm diameter parallel paired stainless steel rods were installed to 40-cm depth in the tracked middle position of each plot at corn tassel emergence. A Tektronix 1502B TDR (Tektronix Inc., Beaverton, OR) cable tester was used to measure soil water using time domain reflectometery (TDR) (Topp and Davis, 1985). Soil moisture was taken 9 times over a 35 day period at 65, 70, 75, 80, 85, 87, 90, 99 and 100 days after planting.

Sample analysis

All measurements or samples were taken in row-middles. and measurements made in trafficked plots were taken in row-middles that had received wheel-traffic. Soil bulk density measurements were made using the core method described by Blake and Hartage (1986) on April, 12 1993. Organic C and total N were determined on soil samples collected in May of 1994. Soil samples were dried at 55 °C for 48 hr and ground to pass a 1-mm sieve. Soil C was analyzed using dry ashing methods described in Nelson and Sommers (1982) and total plant N was analyzed using methods described in Yeomans and Bremmner (1991) on a LECO CHN-600 analyzer (LECO Corp., St. Joseph, MI). Soil organic C analysis was made with a LECO CHN-600 analyzer (LECO Corp., St. Joseph, MI).

Grain yield was determined by hand harvesting from the middle 4 rows of each plot at maturity. Three randomly selected corn plants from each plot were cut at ground level on the 30th day in May, June and July (49, 79 and 109 days after planting), dried at 70 °C for 96 hr and weighed to determine above-ground biomass. To estimate nutrient concentration, at each sampling prior to tasseling the uppermost fully expanded leaf was collected from 10 corn plants on each plot. After tasseling the earleaf was sampled. To estimate nutrient uptake corn plants sampled to determine above-ground biomass were used to determine nutrient uptake. Uppermost leaves and whole plant tissues were dried and tissue was ground to pass 1.0 mm^2. A 0.5 g subsample was ashed at 525 °C in a muffle furnace, ash was dissolved in 10% HNO_3, brought to a 50 mL volume and analyzed for B, Ca, Cu, fe, Mg, K, P, and Zn with a Jarrell-Ash inductively coupled plasma spectrophotometer. Total N was analyzed using LECO CHN-600 analyzer (LECO Corp., St. Joseph, MI). Nutrient concentration is equivalent to nutrients contained in 1 g of the uppermost earleaf corn tissue at the specified sampling time. Nutrient uptake was calculated as the average nutrient contained in 5, 1.000 g samples multiplied by the total weight of that plant on July 30 (109 days after planting).

Soil samples were collected on the same days as above-ground biomass for determination of root biomass, percentage of roots colonized by mycorrhizae and microbial biomass C. Root weight per volume of soil was determined by driving a 7 cm diameter × 8.5 cm long core into the soil. Three soil cores were randomly taken from row middles from the center 3 rows of each plot on the 30th day of May, June, July 1995 (49, 79 and 109 days after planting). The soil core, including soil and roots, was removed. Soil was then sieved to pass a 1 mm opening, roots were collected and washed 3 times with tap and 3 times with distilled water. Roots were dried at 80 °C and weighed.

Soil samples for microbial biomass C determination were stored for less than 12 h, at less than 5 °C before and after being sieved through a 2 mm screen, two 50 g subsamples were taken from each sample, one $CHCl_3$ fumigated for 24 h, and the other used as a control. Both samples were extracted with 50 mL 0.5 *M* K_2SO_4 immediately following fumigation (Vance et al., 1987). A thirty mL aliquot of each extract was transferred into diffusion tubes and evaporated to 5 mL. After adding 2-mL of 2 *N* H_2SO_4 samples, shaken for 1 h, and dichromate digested (Snyder and Trofymow, 1984). A vial (15 mm × 5 mm) containing 1 mL 1 *N* NaOH was used to capture CO_2-C liberated. Organic C was determined by titrating the remaining NaOH with 2 *N* HCl and the 0.45 factor was used to convert the fraction of C extracted to microbial biomass carbon.

Mycorrhizal infection

Three cores from each plot were taken as described above on the 30th day of May, June and July (49, 79 and 109 days after planting). Roots were removed from cores and washed three times with distilled H_2O. Three roots were selected randomly from each core, cut to 3.0 cm and cleared by placing them in a solution of 10% (w/v) KOH. The solution and roots were then placed in a microwave oven for 5 min. Roots were then placed in a solution of 0.05% trypan blue in lactoglycerol for 24 hr. (Phillips and Hayman, 1970). Roots were observed under 100 × on a microscope and percentage of root area infected root was using the slide length technique described in Giovannetti and Mosse (1980). Root biomass infected with mycorrhizae = % root area infected with mycorrhizae × root length /2.

Statistical analysis

All dependent variables were tested for normality with univariate procedures. Data were then analyzed by means of two way analysis of variance procedures for a split plot design with Statistical Analysis Systems.

The analysis of variance indicated that the interactive effects of compaction from wheel traffic and tillage on bulk density, aboveground biomass, root biomass, and P, K, Ca, Mn, and Fe uptake by corn plants were significant at $\alpha = 0.05$; therefore interactions must be considered in treatment comparisons (Saedcecor and Cochran, 1980). Contrasts on preplanned comparisons among individual treatment means were determined using the Least Square Means test. Differences were judged significant at $\alpha = 0.05$. Residuals were equally distributed with constant variances.

Results

Soil bulk density was higher in treatments that received compaction from wheel traffic, regardless of tillage method (Table 1). Soil C and total N in the 0–10 and 10–20 cm depths, did not differ with compaction or tillage method. Soil C and N averaged 4.97 g and 0.63 kg soil^{-1} respectively in 0–10 cm depth and 3.45 and 0.46 g kg soil^{-1} respectively in 10–20 cm depth. Aboveground biomass of corn in May was greater in soils that did not receive compaction from wheel traffic regardless of tillage treatment (Table 1). In June and July, corn plants that received C,CT treatment had less above-ground biomass than the other three treatments. Tillage or compaction treatments did not affect soil microbial biomass which averaged 0.48 g C kg soil^{-1} in the 0–10 cm depth over June and July.

Compaction from wheel traffic and tillage did not affect the percentage root area infected with arbuscular mycorrhizae. In May and June, root biomass and root biomass infected with mycorrhizae was higher in the NC,NT treatment than the other three treatments (Table 2). Plants from plots that received the C,CT treatment had less root biomass and root biomass infected with mycorrhizae than the other three treatments. Within compaction from wheel traffic treatments, plants in no-tillage had more root biomass and root biomass infected with mycorrhizae than plants in conventional tillage. In July, within compaction from wheel traffic treatments, corn plants in no-tillage had higher root biomass and root biomass infected with mycorrhizae than plants receiving conventional tillage.

Tillage and compaction from wheel traffic treatments did not affect N, P, K, Ca, Mg, Mn, Fe, Cu, B and Zn concentration in upper most ear leaves. The uppermost ear leaves to the tassel contained 41 g N, 5.2 g P, 18.6 g K, 5.6 g Ca, 4.0 g Mg, 69 mg Mn, 156 mg Fe, 4 μg Cu, 59 μg B and 9 μg Zn kg^{-1}. Tillage and compaction from wheel traffic did not affect the amount of N, Cu, B or Zn uptake of corn plants (Table 3). Phosphorus uptake was highest when in plants that received NC,NT treatment and lowest in corn plants that received the C,CT treatment. Potassium uptake was highest when corn plants received the no tillage treatments, regardless of whether compaction from wheel traffic was applied. Calcium uptake was highest in corn plants that did not receive compaction from wheel traffic, regardless of tillage practice. Manganese and Fe uptake was lowest when corn plants received the C,CT treatment compared to the other three treatments.

Soil water maintained in traffic middles for the 35 day period beginning at tasseling was greater in treatments that received compaction from wheel traffic that those that did not receive compaction (Fig.1). This was especially true for the compaction from wheel traffic with conventional tillage treatment. There was a traffic by tillage interaction in that, within compaction from wheel traffic treatments, soil water content was generally higher in the conventionally tilled treatment than in the no-till treatments. However, in the absence of compaction from wheel traffic, soil water content was generally higher, especially after rainfall events, in no-tillage treatments as compared to conventional tillage treatments. This is likely due to less run-off and/or greater infiltration in no-till treatments following heavy rainfall events. This can be seen in Figure 1 following the rainfall events 86 to 88 days after planting.

Discussion

Although the interaction of soil compaction from wheel traffic and conventional tillage resulted in less root biomass, root biomass infected with arbuscular mycorrhizae and above ground biomass there was no difference in nutrient concentration or grain yield of corn plants. Other studies have found that no-till systems have resulted in higher yields than conventionally tilled systems. Van Doren et al. (1976), Hargrove (1985), Dick et al. (1991) and Maskina et al. (1994) found that no-till systems yielded from 10 to 20% more corn than comparable conventionally tilled systems. Edwards et al. (1988) found that corn yields in a no-till system were 30% lower than in a conventional tillage system in the first year of their study; however in the following 3 years corn, soybean and wheat yields were higher when grown in a no-till than a con-

Table 1. Influence of compaction from wheel traffic and tillage on bulk density and aboveground biomass of *Zea mays*

Treatment	Bulk density 3–8 cm (g cm^3)	Aboveground biomass (g/plant) May	June	July
Compaction from wheel traffic with conventional tillage	1.61 a	35.3 b	131.0 b	307.5 b
No compaction from wheel traffic with conventional tillage	1.32 b	48.9 a	202.5 a	353.6 a
Compaction from wheel traffic with no tillage	1.62 a	31.6 b	172.7 a	362.8 a
No compaction from wheel traffic with no tillage	1.36 b	39.8 a	183.4 a	370 8 a

In each column, values followed by the same letter are not significantly different as determined by the Least Square Means Test ($p \leq 0.05$).

Table 2. Influence of compaction from wheel traffic and tillage on root biomass per unit volume and root biomass mycorrhizal infection of *Zea mays*

Treatment	Root biomass (mg 1000 cm^{-3} soil)			Root biomass infection[z]		
	May	June	July	May	June	July
Compaction from wheel traffic with conventional tillage	2.22 d[y]	1.99 d	1.96 d	2.04 d	1.75 d	1.90 d
No compaction from wheel traffic with conventional tillage	3.74 c	3.11 c	2.96 b	3.44 c	2.83 c	2.75 c
Compaction from wheel traffic with no tillage	6.16 b	8.09 b	7.69 a	5.65 b	7.28 b	6.76 b
No compaction from wheel traffic with no tillage	9.21 a	12.09 a	7.97 a	8.36 a	10.88 a	7.33 a

[z] g root infected with arbuscular mycorrhizae/1000 cm^3 soil.
[y] In each column, values followed by the same letter are not significantly different as determined by the Least Square Means Test ($p \leq 0.05$).

Table 3. Nutrient uptake (kg ha^{-1}) of *Zea mays* as affected by compaction from wheel traffic and tillage

Treatment	N	P	K	Ca	Mg	Mn	Fe	Cu	B	Zn
Compaction from wheel traffic with conventional tillage	156 a[z]	20.3 c	139.4 b	50.2 b	48.0 a	0.76 b	1.69 b	0.09 a	0.09 a	0.25 a
No compaction from wheel traffic with tillage	157 a	23.6 b	156.4 b	62.3 a	63.0 a	1.16 a	2.22 a	0.10 a	0.08 a	0.27 a
Compaction from wheel traffic with no tillage	153 a	23.0 b	180.9 a	53.9 b	50.5 a	1.18 a	2.02 a	0.10 a	0.07 a	0.21 a
No compaction from wheel traffic with no tillage	152 a	31.5 a	182.7 a	65.0 a	49.9 a	0.97 ab	1.84 b	0.12 a	0.09 a	0.23 a

[z]In each column, values followed by the same letter are not significantly different as determined by the least square means test ($p \leq 0.05$).

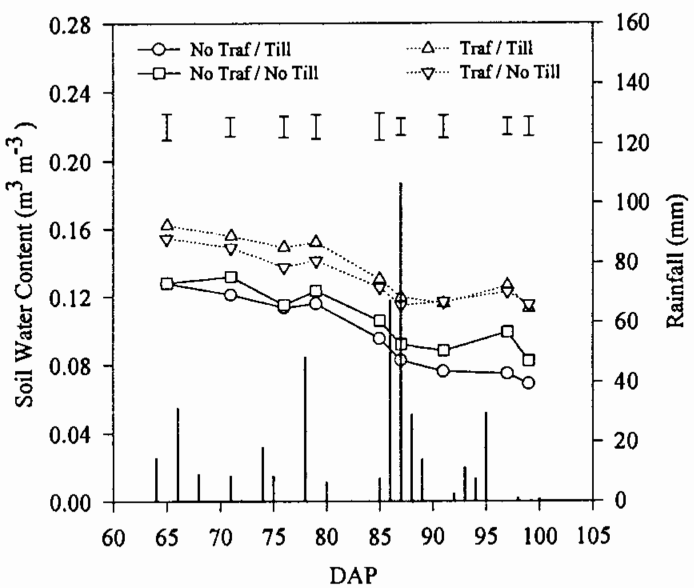

Figure 1. Rainfall and volumetric soil water content from trafficked mid-row position of corn during a 35 day period beginning at tass emergence as affected by compaction from wheel traffic and tillage systems. DAP – Days after planting.

ventional tillage system. According to Bandell (1983), 3 to 6 years are required for corn yields from no-till to equal the yield of corn in conventional tillage systems; after this time yields from no-till consistently exceed-

ed those under conventional tillage. In a 20 year stud average corn yields from a conventional tillage sy tem were higher than corn yields from a no-till syste during the first 7 years, but yields from corn grown i

no-till systems were consistently higher than in conventionally tilled systems after those 7 years (Ismail et al., 1994).

We found that tillage and compaction from tractor traffic treatments had no effect on soil microbial biomass. These results are not consistent with several other studies. Soil microbial biomass averaged 37% higher in the top 7.5 cm of soil in no-tillage systems than in conventionally tilled systems at 7 sites in the midwestern United States (Doran, 1987). Linn and Doran (1984) found higher populations of anaerobic bacteria in the top 7.5 cm of soil in no-till systems than in conventionally tilled systems. Beare et al. (1992) found that active fungal and bacterial biomasses were 2.2 to 2.7 times higher in no-till systems than in conventionally tilled systems. These tillage systems were implemented in sandy soils in a summer-mesic climate; they may not have been in place long enough for soil to accumulate substantial quantities of organic materials to result in elevated microbial biomass to a 10 cm depth.

Tillage and compaction from tractor traffic treatments had no effect on mycorrhizal infection of corn roots. Other studies have found that crop rotation and tillage affect populations and distribution of mycorrhizal fungi in soil and mycorrhizal formation of plants. McGonigle and Miller (1993) reported higher arbuscular mycorrhizal infection in corn early in the growing season (8–9 leaf stage) under no-till systems than moldboard plowing systems. Douds et al. (1995) found that no-tillage soybean and corn systems resulted in higher populations of *Glomus occultum*, but that conventional tillage resulted in greater numbers of *Glomus etunicatum* and *Glomus* spp. spores in the soil. Abbott and Robson (1991) found that there were more arbuscular mycorrhizal fungi spores in the top 8 cm of no-till soils the conventionally tilled soils; however conventionally tilled soils had greater amounts of arbuscular mycorrhizal fungi spores at the 8–15 cm soil depth than no-till soils. In this study, we did not sample corn plots until 49 days after planting (15–20 leaf stage). Although conventional tillage operations increase the numbers of arbuscular mycorrhizal spores in the soil, results of this study suggest, that after 7 years of compaction from wheel traffic with conventional tillage, sufficient mycorrhizal structures associated with dead roots from the previous crop and/or sufficient numbers of spores are present in the soil to fully colonize corn roots.

After 7 years of treatment the interactive effects of tillage and compaction due to wheel traffic seem to have little effect on microbial biomass, root area infected with arbuscular mycorrhize and nutrient concentration of corn plants. However, compaction substantially reduced root biomass and root biomass infected with arbuscular mycorrhizae which most likely lead to lower above-ground plant biomass. These results agree with those of Reeves et al. (1992): no-till systems withstand the detrimental effects of compaction from wheel traffic better than conventional tillage systems. Conservation or no-tillage is the main soil conservation method that most producers can readily implement to reduce erosion. Longer term studies than this one have found not only higher crop yields, but also increased soil carbon and nutrient concentrations. Maximizing soil carbon content and nutrient availability using conservation tillage practices will increase soil quality and thus long-term sustainability of agricultural ecosystems while minimizing soil erosion and other environmental problems due to agricultural production.

References

Abbott L K and Robson A D 1991 Field management of VA mycorrhizal fungi. *In* The Rhizosphere and Plant Growth. Eds. D L Keister and P B Cregan. pp 355–362. Kluwer Academic Publishers, Dordrecht.

Bandel V A 1983 No-tillage for corn- Effects of fertilizer practices and time. Better Crops Plant Food 67, 23–25.

Beare M H, Parmelee R W, Hendrix P F and Cheng W 1992 Microbial and faunal interactions and effects on litter nitrogen and decomposition in agroecosystems. Ecol. Monogr. 62, 569–591.

Blake G R and Hartage K H 1986. Bulk density. *In* Methods of Soil Analysis, Part 1. Ed. A Klute. pp 364–366. American Society of Agronomy, Madison, WI, USA.

Dick W A, McCoy E L, Edwards W M and Lal R 1991 Continuous application of no-tillage to Ohio soils. Agron. J. 83, 65–73.

Doran J W 1980 Soil microbial and biochemical changes associated with reduced tillage. Soil Sci. Soc. Am. J. 44, 765–771.

Douds D D, Galvez L, Janke R R and Wagoner P 1995 Effect of tillage and farming system upon populations and distribution of vesicular-arbuscular mycorrhizal fungi. Agric. Ecosys. Environ. 52, 111–118.

Edwards J H, Thurlow D L and Easton J T 1992 Influence of tillage and crop rotation on yields of corn, soybean and wheat. Agron. J. 80, 76–80.

Edwards J H, Thurlow D L and Easton J T 1988 Influence of tillage and crop rotation on yields of corn, soybean and wheat. Agron. J. 80, 76–80.

Follett R F, Gupta S C and Hunt P G 1987 Conservation practice: relation to the management of plant nutrients for crop production. *In* Soil Fertility and Organic Matter as critical Components of Production Systems. Ed. R F Follett. pp 19–51. SSSA special publ. 19. Soil Science Society of America, Madison, WI, USA.

Follett R F and Peterson G A 1988 Surface soil nutrient distribution as affected by wheat fallow tillage systems. Soil Sci. Soc. Am. J. 52, 141–147.

Giovannetti M and Mosse B 1980 An evaluation of techniques for measuring vesicular arbuscular mycorrhizal infection in roots. New Phytol. 84, 489–500.
Hargrove W L 1985 Influence of tillage on nutrient uptake and yield of corn. Agron. J. 77, 763–768.
Ismail I, Belvins R L and Frye W W 1994 Long term no-tillage effects on soil properties and continuous corn yields. Soil Sci. Soc. Am. J. 58, 216–220.
Leibieg A, Jones A J, Mielke L N and Doran J W 1993 Controlled wheel traffic effects on soil properties in ridge tillage. Soil Sci. Soc. Am. J. 57, 1061–1066.
Linn D M and Doran J W 1984 Aerobie and anaerobic microbial populations in no-till and plowed soils. Soil Sci. Soc. Am. J. 48, 794–799.
Maskina M S, Power J F, Doran J W and Wilhelm W W 1993 Residual effects of no-till crop residues on corn yield and nitrogen uptake. Soil Sci. Soc. Am. J. 57, 1555–1560.
McGonigle T P and Miller M H 1993 Mycorrhizal development and phosphorus absorption by maize under conventional and reduced tillage. Soil Sei. Soc. Am. J. 57, 1002–1006.
Monroe G E and Burt E C 1989 Wide frame tractive vechile for controlled-traffic researeh. Appl. Eng. Agric. 5, 40–43.
Nelson D W and Sommers L E 1982 Total carbon, organic carbon and organic matter. *In* Methods of Soil Analysis, Part 2. Chemical and Microbiological Properties. Eds. A L Page, R H Miller and D R Keeney. pp 539–577. American Society of Agronomy, Madison, WI, USA.
Phillips J M and Hayman D S 1970 Improved procedures for elearing roots and staining parasitic and vesicular arbuscular mycorrhizal fungi for rapid assessment of infection. Trans. Br. Mycol. Soe. 55, 158–160.
Raper R L, Reeves, D W, Burt E C and Torbert H A 1994 Conservation tillage and traffic effects on soil conditions. Trans. ASAE 37, 763–768.
Rhoton F E, Bruce R R, Buehring N W, Elkins G B, Langdale C W and Tyler D D 1993 Chemical and physical characteristics of four soil types under conventional and no tillage systems. Soil Till. Res. 28, 51–61.
Reeves D W, Rogers H H, Droppers J A, Prior S A and Powell J B 1992 Wheel-traffie effects on corn as influenced by tillage system. Soil Till. Res. 23, 177–192.
Reeves D W and Touchton J T 1986 Subsoiling for nitrogen applications to corn grown in a conservation tillage system. Agron. J. 78, 921–926.
Snedecor W G and Cochran W G 1980 Statistical Methods. 7th ed. Iowa State University Press, Ames, Iowa, USA. 354 p.
Snyder J D and Trofymow J A 1984 A rapid accurate wet oxidation diffusion procedure for determining organic and inorganie carbon in plant and soil samples. Commun. Soil Sci. Plant Anal. 15, 587–597.
Soane B D 1990 The role of organic matter in soil compactability: a review of some practical aspects. Soil Till. Res. 16, 179–201.
Topp G C and Davis J L 1985 Measurement of soil water using time-domain reflectometery (TDR) : A field evaluation. Soil Sci. Soc. Am. J. 49, 19–24.
Torbert H A and Reeves D W 1995 Traffic and residue management systems: effects on fate of fertilizer N in corn. Soil Till. Res. 33, 197–213.
Torbert H A and Reeves D W 1994 Fertilizer nitrogen requirements for cotton production as affected by tillage and traffie. Soil Sci. Soc. Am. J. 58, 1146–1423.
Van Doren D M, Tripplet G and Henery J E 1976 Influence of long-term tillage, crop rotation and soil type eombinations on corn yield. Soil. Sci. Soc. Am. J. 40, 100–105.
Vance E D, Brookes P C and Jenkinson D S 1987 An extraction method for measuring soil mierobial biomass C. Soil Biol. Biochem. 19, 703–707.
Voorhees W B and Lindstrom M J 1984 Long term effects of tillage method on soil tilth independent of wheel traffic. Soil Sci. Soc. Am. J. 48, 152–156.
Wood C W and Edwards J H 1992 Agroecosystem management effects on soil carbon and nitrogen. Agric. Ecosys. Environ. 39, 123–138.
Wood C W, Westfall D G and Peterson G A 1991 Soil carbon and nitrogen changes on initiation of a no-till cropping system. Soil Sci. Soc. Am. J. 55, 470–476.
Yeomans J C and Bremner J M 1991 Carbon and nitrogen analysis of soils by automated combustion techniques. Commun. Soil Sci. Plant Anal. 22, 843–850.

Section editor: J H Graham

Plant and Soil 180: 147–158, 1996.

Spatial distribution of ectomycorrhizal mats in coniferous forests of the Pacific Northwest, USA

Robert P. Griffiths[1], Gay A. Bradshaw[2], Barbara Marks[1] and George W. Lienkaemper[2]
[1]*Department of Forest Science, Oregon State University, Corvallis, OR 97331, USA*[*] *and* [2]*Forestry Sciences Laboratory, Pacific Northwest Research Station, USDA Forest Service, 3200 Jefferson Way, Corvallis, OR 97331, USA*

Received 15 May 1995. Accepted in revised form 20 December 1995

Key words: ectomycorrhizal mats, geographic information system, geostatistical analysis, spatial patterns

Abstract

Ectomycorrhizal mats in forest soils have a wide global distribution and have been noted as potentially important elements in forest soil nutrient cycling. To elucidate the relationship between ectomycorrhizal mats and their environment, we undertook field studies and spatial analyses of mat distributions at different spatial scales.

We used two experimental approaches to study mat-forming ectomycorrhizal fungi in coniferous forests of the Pacific Northwest in the United States. In the first approach, ectomycorrhizal mats and other forest floor features were mapped in 2 × 10 m plots and digitized into a geographical information system (GIS) for spatial pattern analysis. In order to examine larger-scale phenomena, a second approach involving other sites was taken; soil cores were taken along 30-m transects, and distance to the closest living potential host tree was calculated for each core.

Mat patterns were studied at two scales: (1) within-stand level (i.e. variability attributed to distribution of other mat species, forest floor attributes, and understory vegetation); and (2) stand level (i.e. variability expressed along a successional gradient). Mat distribution was influenced by: (1) the proximity of one mat to another; (2) the distance from the mat to the closest living tree; (3) the density of living trees in a stand; and (4) the successional stage of the stand.

Although GIS analysis indicated that mats of different morphologies did not physically overlap, there was a tendency for clustering of mats. No apparent correlations were observed between forest floor features and mats located within the 2 × 10 m grids. On the scale of tens of meters, mats decreased with distance from the closest potential host tree. Spatial patterns of mat distributions in harvested sites suggest that these mats may persist at least 2 years after their host trees have been cut. For *Gautieria* mats, total mat area, size, and frequency differed with stand age.

This study has demonstrated the importance of both spatial scaling and forest stand age when the natural distribution of mycorrhizal fungi is examined. Results suggest the need for mat research directed at higher-order scales (e.g. stand and watershed) that will provide accurate information for managing forests to ensure their survival and normal function.

Introduction

Ectomycorrhizal fungi play an important role in preserving species diversity by providing host trees with necessary nutrients from mineral soil and soil organic matter (Read, 1993). Some ectomycorrhizal fungi form dense, visible mats commonly found in the litter layers and upper soil horizons of forest soils throughout the world (Castellano, 1988). This study examines mat-forming ectomycorrhizal fungi such as those in the genera *Gautieria* and *Hysterangium*, which produce hypogeous sporocarps (truffle fruiting bodies). These mats alter the chemical and physical properties of forest soil, producing localized habitats for unique assemblages of soil organisms (Cromack et

[*] FAX No: + 15037371393