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Root recolonization of previous root channels in corn and alfalfa rotations

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Abstract

Distribution of root systems through soils and recolonization of root channels by successive crops are fundamental, though difficult to study, processes of soil ecology. This article reports a minirhizotron (MR) study of corn and alfalfa root systems throughout the soil profile of Kalamazoo loam (fine-loamy, mixed, mesic Typic Hapludalf) monolith lysimeters for a three-year succession of corn, alfalfa and corn. Multiple-date comparisons within and between years were conducted to estimate total root densities in each soil horizon. Root recolonization was assessed by comparing every video frame of paired minirhizotrons, from recordings conducted one growing season apart. Distributions of corn root systems were modified by tillage practices. In 1994, root populations of corn in the Bt_1 horizon peaked 75–90 days after planting (DAP). Numbers of corn roots per m^2 in the Bt_1 horizon were consistently higher for no-tillage (NT) than for conventional tillage (CT) lysimeters, in 1994 and 1996. Distribution of alfalfa roots within the soil profile was not significantly modified by tillage. However, alfalfa root decomposition rates responded to conventional and no-tillage practices and were specific for each soil horizon. Corn root systems growing in soils previously cropped with alfalfa presented similar patterns of root distribution by horizons as that of the previous alfalfa crop. Successive corn root systems did not display similar distribution patterns throughout the soil profile from one growing season to the next. Proportions of roots of the current crop recolonizing root induced macropores (RIMs) of the previous crop averaged 18% for corn after corn, 22% for alfalfa after corn and 41% for corn after alfalfa, across Bt horizons and tillage treatments. In conclusion, distribution of corn root systems appeared to be modified by tillage practices and root recolonization of RIMs was controlled by the preceding crop.

Introduction

Distribution of root systems in the soil profile is an important factor in the determination of water and nutrients available to plants (Kuchembuch and Barber, 1987). Modified distributions of corn (*Zea mays* L.) root systems within the soil profile have been observed under contrasting fertilizer rates (Anderson, 1987; Durieux et al., 1994), irrigation (Robertson et al., 1980), and tillage managements (Anderson, 1987; Bauder et al., 1985; Vepraskas and Wagger, 1990). Development of the corn root system is facilitated at depths where favorable conditions for water, nutrients and soil physical properties merge. Much less

understood is the response of corn root systems to root-induced macropores (RIMs) and associated decomposing root tissues from previous crops which present heterogenous networks for root distribution.

The recolonization of RIMs by developing root systems of crops has been suggested as an important factor influencing root growth and water movement through soils (Smucker et al., 1995). Root colonization of horizons has been reported to be in direct relationship with the number of soil biopores (Wang et al., 1986). Alfalfa (*Medicago sativa* L.) in rotation with corn promoted corn root distribution in the soil profile by creating accessible RIMs for corn root development (Stone et al., 1987). Plants restore substantial amounts of carbon and nitrogen to soils

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through root exudation and decay (Milchunas et al., 1985; Smucker, 1984). The recolonization of recent RIMs and root growth along decaying root tissue have been suggested to contribute to plant nutrition, water uptake and root diseases in both rotation and intercropping systems (Aiken and Smucker, 1996; Smucker, 1993). Carbon inputs from alfalfa root systems to soils were assessed to be five times higher than corn root contributions (Angers, 1992). During the growing season significant amounts of atmospheric fixed nitrogen can be transferred from alfalfa to intercropped plants (Brophy et al., 1987; Ta and Faris, 1987). Consequently, proximity of the roots to a nutrient source, i.e. decaying root tissue, can contribute significantly to plant uptake and nutrition.

Minirhizotron (MR) techniques have been widely used to characterize the distribution of root systems within soil profiles. This non-destructive approach is a unique opportunity for multiple observations throughout the growing season and provides comparative images of roots which can be utilized for determining root turnover (Smucker, 1990). Variations in total root numbers across time have been used to assess root death, turnover, and new root production for multiple soil depth increments or complete horizons (Huang, 1995; Pietola and Smucker, 1995). Specific root turnover can also be assessed by monitoring the temporal succession of root growth in every single recorded video frame along the MR tube (Cheng et al., 1990, 1991). This second technique is more precise but more time consuming. Temporal analyses of root development and decay in individual MR frames have also been used to assess root colonization of RIMs and lines of least resistance (Rasse and Smucker, 1995). Year to year comparison of root dynamics in individual MR frames is limited to MR tubes that can be kept in place for multiple years. Field-installed MR tubes have generally been removed for harvest and tillage operations. Horizontal MR tubes, installed in the wall of monolith lysimeters or access tunnels into the field are appropriate for multiple-year studies (Goins and Russelle, 1996; Lizazo and Ritchie, 1997; Rasse and Smucker, 1995).

This article reports the development of alfalfa and corn root systems throughout the soil profile of Kalamazoo loam soil encased in monolith lysimeters for a three-year succession of corn, alfalfa and corn. Distributions of root systems per horizons are compared for conventional tillage (CT) and no-tillage (NT) systems. Root recolonization of RIMs and decaying roots is assessed for corn after corn, alfalfa after corn, and corn after alfalfa, by visually comparing individual video-recorded MR frames over time.

Material and methods

Experimental design and treatments

Four undisturbed monolith lysimeters were installed in a long-term field experiment on a Kalamazoo loam soil (fine-loamy, mixed, mesic Typic Hapludalf) at the Kellogg Biological Station in southwestern Michigan. Soil horizons are a loamy Ap from 0 to 0.26 m which overlays a clay loam Bt_1 from approximately 0.26 to 0.55 m, then a Bt_2 horizon enriched in coarse material from 0.55 to 0.80 m, which is underlain by a coarse glacial outwash parent material. The lysimeters, 1.2×1.8 m of surface area and 2.1 m deep, installed in 1990, are part of a replicated field experiment established in 1986 to investigate N supply and tillage effects on numerous soil and plant interactions. Two lysimeters were installed in conventional tillage (CT) plots and two in no-tillage (NT) plots. All field operations conducted in the lysimeters matched the management of the surrounding plots. No nitrogen fertilizer has been applied since 1991. Conventional tillage lysimeters were manually spaded in the second week of April 1994. No-tillage lysimeters were non-disturbed. Three rows of corn (Pioneer hybrid 3573) were planted at high density in the lysimeters on 6 May 1994 and later thinned to guarantee a uniform plant density matching field conditions of 67 700 seeds per hectare. The corn canopy was continuous across the lysimeter to field interface, with the exception of a 1 m gap over each access door adjoining each lysimeter. Corn was harvested as silage on 23 August 1994. Lysimeters under CT treatment were manually spaded to 20 cm on 29 August 1994. Glyphosate was sprayed on NT lysimeters at rate of 7 L ha^{-1} on 30 August 1994. Alfalfa (Pioneer 5246) was sown in the lysimeters on 1 September 1994. All lysimeters received 112 kg K_2O ha^{-1} and 337 kg ha^{-1} of pellet lime on 7 April 1995. Alfalfa was harvested on 12 June, 22 July and 1 September 1995. Alfalfa was spray-killed on 2 May 1996 with glyphosate at 4.6 L ha^{-1} and (2,4 D) ester at 2.3 L ha^{-1}. Conventional tillage (CT) lysimeters were manually spaded on 8 May 1996. Corn (Pioneer hybrid 3573) was planted in all lysimeters at rates of 67 700 seeds per hectare on 13 May 1996. Corn was harvested as silage on 4 September 1996.
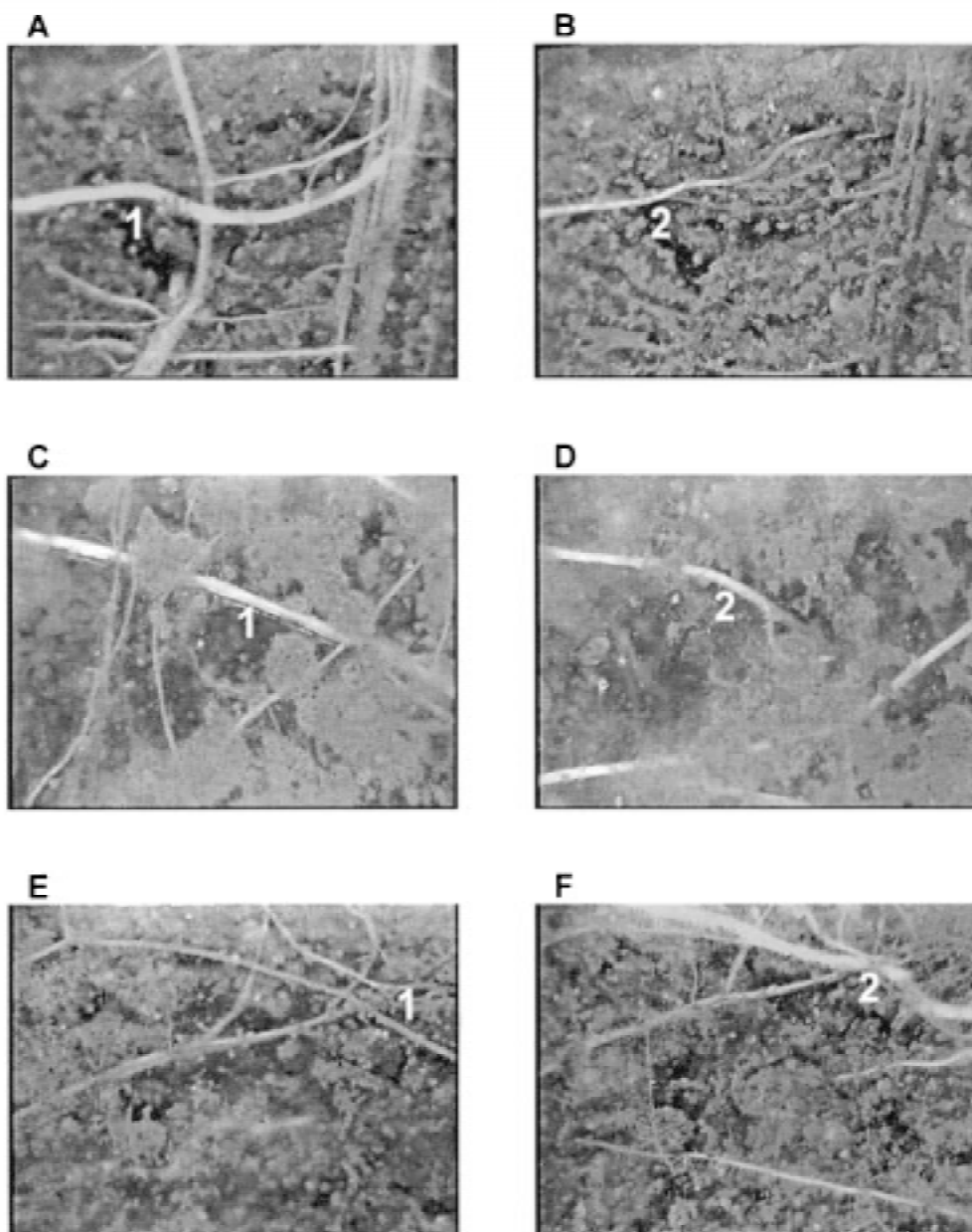
Figure 1. Minirhizotron pictures of corn roots in 1993 (A), corn roots in 1994 (C) and alfalfa roots in 1995 (E), shown decayed at the next growing season and recolonized by corn (B), alfalfa (D) and corn roots (F). 1 = future RIM and 2 = new recolonizing root.

Instrumentation and measurements

Each lysimeter is equipped with a steel access chamber, which is positioned directly along the lysimeter and gives access to one full side of the monolith. Access ports for instrumentation were cut in the stainless steel wall separating the monolith from the access chamber. Horizontal polybutyrate minirhizotron tubes, five per lysimeter, were installed 1 cm below and 6 cm above the respective interfaces of the Bt_1, Bt_2 and C horizons of each lysimeter, directly under the middle of the three corn rows. MR tubes, each with an internal diameter of 5 cm, had a recordable length of 88 cm. No MR tube could be installed in the Ap horizon due to tillage constraints. Though no data were collected

in the Ap horizon, other rhizotron studies have shown that corn root systems usually have their highest root densities at soil depths between 30 and 50 cm (Tan and Fulton, 1985), or in the Bt_1 and Bt_2 horizons of Kalamazoo loam soils (Huang, 1995). Root intersections with the upper surfaces of MR tubes were recorded with a minirhizotron color microvideo camera (Bartz Technology, Santa Barbara, CA) equipped with an index handle (Ferguson and Smucker, 1989). Identical frame positions, 1.35 × 1.8 cm each, were recorded from 1994 to 1996. Two previous recordings in November 1992 and August 1993 were also available for the study. Permanently installed MR tubes presented a background of roots at different stages of decomposition from previous growing seasons. Initial analyses of the May 1994 video images showed that large numbers of corn roots from the previous growing season showed little or no sign of decomposition, and could not be discriminated from newly developing roots. Consequently, new roots of the current crop were counted against the background of roots from the previous crop. Simultaneous observations of two video recordings were completed using two VCR-monitor sets. We compared all root observations in each frame to a reference date, free of new roots. Evaluations of root recolonization rates from current and previous root images were performed on MR tubes located 1 cm below the Ap and Bt_1 horizons of each lysimeter. The C horizon was not analyzed for root recolonization as no roots were observed for NT corn in the C horizon during 1994. Corn root systems in each of the two horizons at their maximum development, i.e. in early August 1994 and 1996, were compared to root systems of the previous crop at their stage of maximum development, i.e. in early August 1993 for corn, and just before spray-killing alfalfa on 2 May 1996. Alfalfa root systems in June 1995 were compared to corn root systems in August 1994. June was chosen for visually evaluating alfalfa root recolonization so that sufficient root extension throughout the Bt horizons was completed without significant root recolonization of alfalfa by itself following root turnover. A new root was considered to recolonize an old root, decaying or residual channel, when the new root grew tangentially, at distances ≤0.5 mm, to the old root location for at least 20% of the observed length of the new root. A new root which grew within the above parameters, and may have occupied more than one old RIM, qualified as one reoccupation unit only. Old root channels were only considered valid if they had been clearly generated or invaded by a root during the previous growing
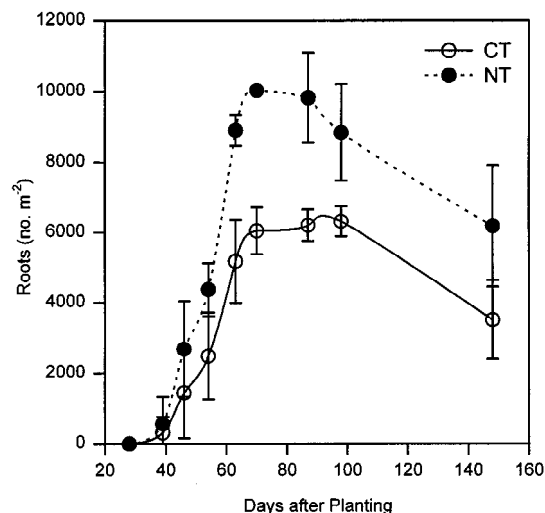

Figure 2. Corn root demographics in the Bt_1 horizon of conventional tillage (CT) and no-tillage (NT) lysimeters in 1994. Error bars represent standard deviations for $n = 2$.

season (Figure 1). Root channels vacant for more than one year, before root occupation, were not considered to be recolonized. Information for each MR frame consisted of: (1) total root number for the previous growing season, (2) total number of new roots, (3) number of new roots recolonizing decomposing old roots or their associated RIMs of the previous year, (4) number of new roots that were not recolonizing old roots or RIMs of the previous year. These numbers were then calculated and presented in percentage of new roots recolonizing old roots and RIMs.

Soil water contents were estimated by time domain reflectometry (TDR). Probes, inserted at same depths as MR tubes, were composed of two metal rods, 30.5 cm long and 0.5 cm dia., installed horizontally 5 cm apart in the soil profile. Soil water data were collected with a TDR-meter model 1502C (Tektronix Inc, Beaverton, Oregon, U.S.A.). Transformation of TDR readings into volumetric soil water contents was performed using Topp's equation (Topp et al., 1980).

Statistical analyses

A year to year comparison of individual MR tubes in a corn alfalfa rotation was possible because of the horizontal insertions of the MR tubes in monolith lysimeters. The weakness of the design resides in the low replication level due to the very high cost of lysimeter installation. Error bars were represented by standard deviations, as standard errors of duplicated samples can be misleading with respect to the signifi-

cance of mean separation. Averages of two replicates were compared by F-test (SAS institute, 1989) between horizon for similar tillage and year, and between tillage for similar horizon and year.

Results

Corn roots reached the Bt_1 horizon about 35 days after planting (DAP) in 1994 (Figure 2). Root populations of corn in 1994 peaked 75 to 90 DAP in the Bt_1 horizon for both CT and NT treatments (Figure 2). Numbers of corn roots per m^2 in the Bt_1 horizon were consistently greater for NT than CT, in 1994 and 1996 (Figure 3). This increased corn root population under NT in the Bt_1 horizon was statistically significant ($P \leq 0.05$) in summer 1994, despite the limitation of having only two replications. Conventional tillage management appeared to favor corn root colonization into the Bt_2 horizon in 1994 (Figure 3). Corn roots reached the C horizon about 85 DAP in the CT lysimeters in 1994, while no corn roots were observed in the C horizons of NT lysimeters (Figure 3). Corn roots had grown into the C horizons of both tillage treatments by August of 1996, although CT accumulated greater quantities of roots. Considering the overall corn root profile in 1994 and 1996, NT appeared to promote higher root densities in the upper part of the soil profile, while CT induced root growth in deeper horizons. Alfalfa root growth in 1995 and early spring 1996 was not consistently modified by tillage (Figure 3). Alfalfa root populations peaked in May 1996, just before the spray-killing of the crop.

Maximum development of corn roots in the top Bt_1 horizons by August were compared to lowest soil water contents reached before 1 July in that soil layer, for the 1994 to 1996 growing seasons (Figure 4). A significant correlation ($r^2 = 0.92$) was observed between corn root populations and soil water contents during dry periods of 1994. Higher soil water contents retained in the soil profile during dry periods resulted in greater root populations later in the growing season. The Bt_1 horizons of NT treatments retained higher soil water contents than the same horizons of the two CT lysimeters in 1994 (Figure 4). In 1995 for alfalfa and 1996 for corn, correlations between total roots and minimum soil water contents were non significant ($n = 4$), however a positive trend between these two variables was observed. Combined data for corn in 1994 and 1996 revealed a pronounced ($r^2 = 0.88$, $P \leq$

Table 1. Correlations of total root numbers observed for the same minirhizotron tubes across both tillage treatments and horizons, among crops grown for four consecutive growing seasons from 1993 to 1996

	Corn (Aug 93)	Corn (Aug 94)	Alfalfa (June 95)	Corn (Aug 96)
Corn (Aug 93)	1	−0.01	0.51	0.43
Corn (Aug 94)		1	0.11	0.21
Alfalfa (June 95)			1	0.84**
Corn (Aug 96)				1

** Significant at $P \leq 0.01$.

Table 2. Proportion of new roots recolonizing RIMs along decomposed roots from the previous growing season, for 1994 (corn after corn), 1995 (alfalfa after corn), and 1996 (corn after alfalfa)

Tillage	Horizon	Corn (94) after corn (93) %	Alfalfa (95) after corn (94) %	Corn (96) after alfalfa (95) %
CT	Bt_1	9.3 (4.1)[a]	15.5 (0.7)	45.0 (10.1)
	Bt_2	16.5 (6.8)	30.5 (13.4)	37.8 (2.6)
NT	Bt_1	16.4 (12.7)	21.4 (2.6)	35.6 (4.5)
	Bt_2	29.6 (7.8)	22.0 (9.0)	43.8 (1.3)
Averages		18.0	22.4	40.6

[a] Standard deviations for two replicates.

0.001) correlation between total roots and minimum soil water contents.

Root distributions for each crop within the soil profiles, represented by the total number of roots for each individual MR tube, were correlated for the 1993–1996 growing seasons (Table 1). Distribution of corn root systems (1996) were significantly correlated to the distribution of the previous alfalfa root systems (1995). No spatial correlation was observed between the distributions of root systems for corn (1994) following corn (1993), and alfalfa (1995) following corn (1994).

Root recolonization of RIMs, which appeared as open channels and decomposed roots, were analyzed within the individual MR frames. These data showed cropping sequence-related patterns for the three years of study (Table 2). Root recolonization percentages did not consistently differ between tillage treatments. Except for CT corn 96, consistently higher root recolonization percentages were observed in the Bt_2 than in the Bt_1 horizons. No significant differences in root reoccupation were observed between horizons. Corn roots recolonizing previous corn RIMs averaged 18% in 1994. Alfalfa root recolonization of previous corn RIMs averaged 22% in 1995. However, 41% of the
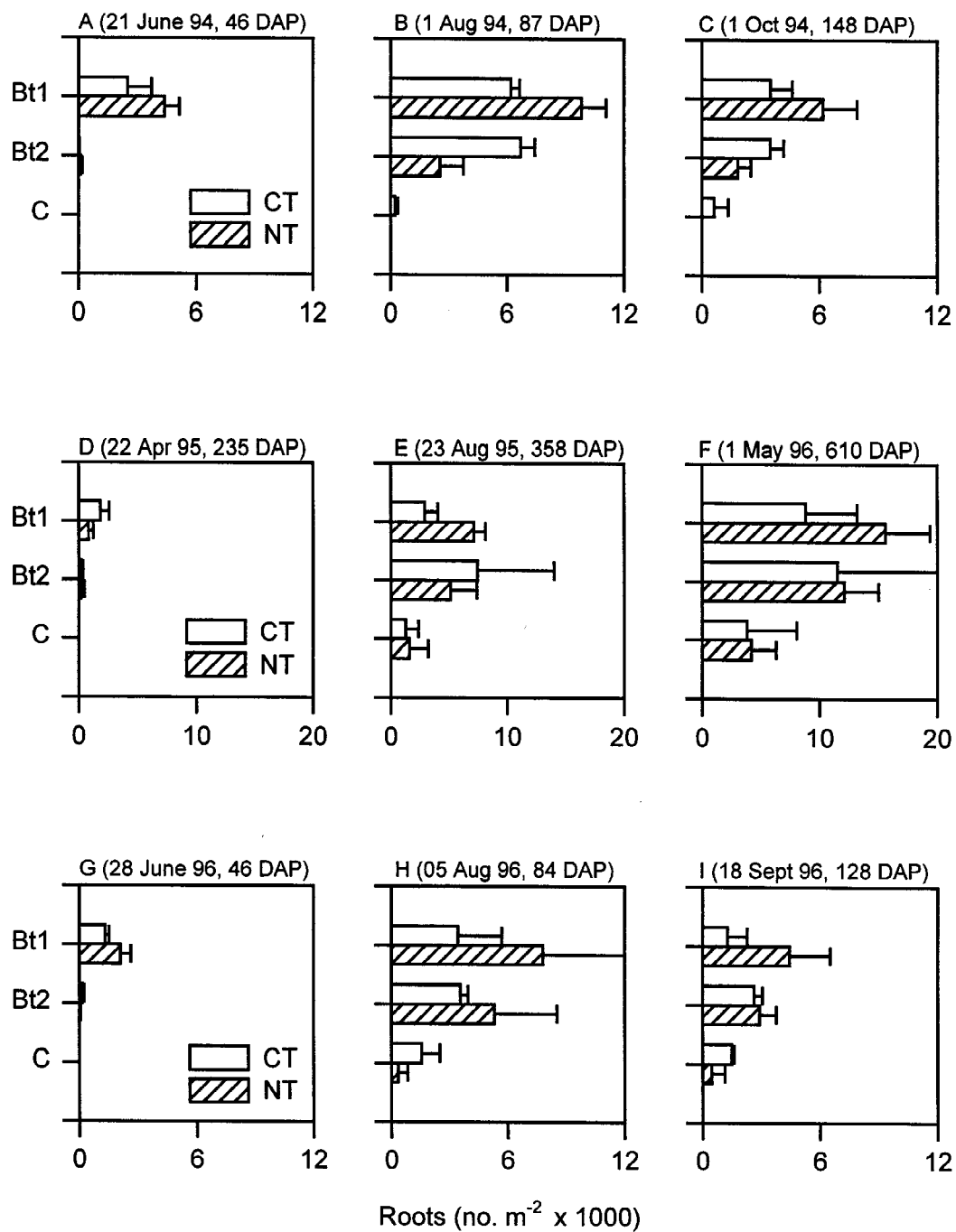
Figure 3. Root demographics per horizon observed at different days after planting (DAP) of crops in conventional tillage (CT) and no-tillage (NT) lysimeters for corn 1994 (A, B, C), alfalfa 1995 and 1996 (D, E, F), and corn 1996 (G, H, I). Error bars represent standard deviations for $n = 2$.
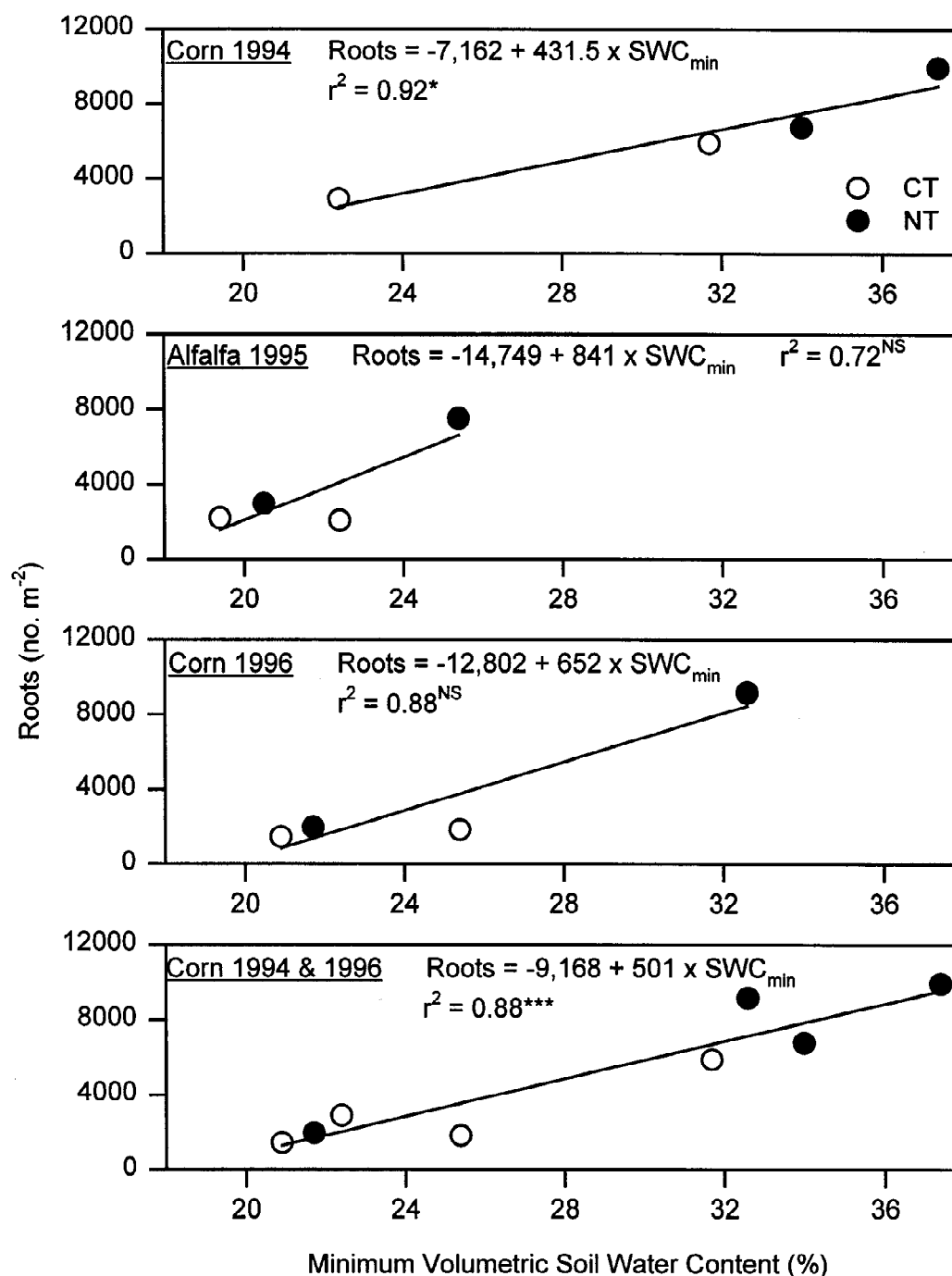
Figure 4. Correlation between minimum volumetric soil water contents (SWCmin) reached before 1 July and root numbers observed in August of the same year, in the upper Bt_1 horizon of conventional tillage (CT) and no-tillage (NT) lysimeters. *, *** Significant at $P \leq 0.05$ and $P \leq$ 0.001, respectively.

Table 3. Correlations between the proportion of new root recolonization, i.e. number of new roots recolonizing RIMs divided by the total numbers of new roots, and the number of old roots from the previous growing season. Correlations conducted for $n = 8$, across 2 horizons and 2 tillages for 2 replicated lysimeters

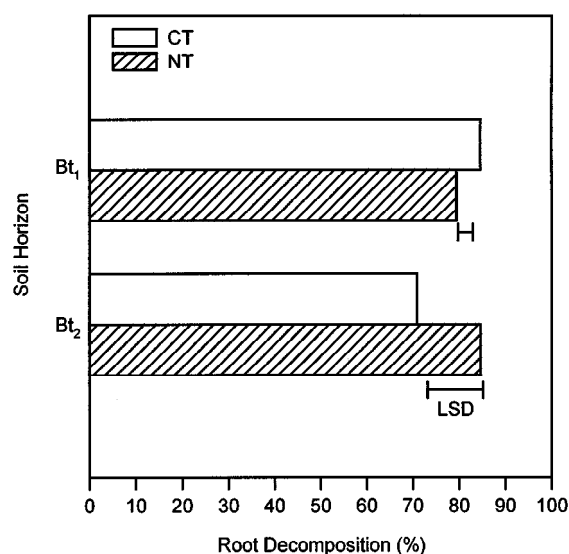| Number of old roots	Proportion of new root recolonization		
	1994 (corn)	1995 (alfalfa)	1996 (corn)
Nov. 93 (corn)	0.83*		
Aug. 94 (corn)		0.75*	
Aug. 95 (alfalfa)			0.26

* Significant at $P \leq 0.05$.

Figure 5. Alfalfa root decomposition from 1 May to 5 August 1996, in Bt_1 and Bt_2 horizons of conventional tillage (CT) and no-tillage (NT) monolith lysimeters.

corn roots recolonized alfalfa RIMs in 1996 (Table 2). The percentage of new roots recolonizing RIMs, across tillage treatments and horizons, was significantly correlated to root populations of the year before, for corn (1994) after corn (1993) and alfalfa (1995) after corn (1994) (Table 3). However, no significant correlation was observed between alfalfa root populations in 1995 and proportion of corn roots recolonizing alfalfa RIMs in 1996 (Table 3).

Alfalfa root decomposition rates were assessed, following a spray-killing on 2 May 1996, for the period from 1 May to 5 August 1996 (Figure 5). Alfalfa root populations on 5 August 1995 were estimated by counting total root numbers and subtracting corn root populations, the difference consisting of undecayed alfalfa roots. Between 70 and 84% of alfalfa roots ap-

peared decomposed on MR frames three months after spray-killing the crop. Alfalfa roots in the Bt_1 horizon were significantly more decomposed in CT than in NT lysimeters, while the opposite was true in the Bt_2 horizon (Figure 5).

Discussion

Maximum length of the corn root system has been reported to occur around 80 DAP (Barber, 1986; Huang, 1995), remain relatively constant for two weeks and then decline rapidly (Mengel and Barber, 1974). In our study, maximum corn root development in the Bt_1 horizon of Kalamazoo loam soils appeared concomitant with maximum corn root length throughout the entire profile. This minirhizotron study presented a similar time sequence for corn root development as was previously reported by destructive root extraction studies (Barber, 1986; Mengel and Barber, 1974). Greater corn root proliferation in the Bt_1 horizon of the NT treatment than in the CT treatment concur with previous studies reporting that preferential accumulations of corn roots occur in the top Ap horizon of NT *versus* CT soils (Anderson, 1987; Bauder et al., 1985; Newell and Wilhelm, 1987). In a previous study at the same location, Huang (1995) observed greater corn root densities in the Ap horizons of Kalamazoo loam soils under NT compared to CT treatments. The same author also reported decreased corn root densities in the C horizon of NT *versus* CT plots, one year out of two.

Significant correlations between corn root populations and minimum soil water contents suggest that corn root populations in the Bt_1 horizon of Kalamazoo loam soils respond negatively to soil water deficits experienced earlier in the growing season. These findings concur with studies reporting that irrigated corn developed greater root populations in the upper part of the soil profile than non-irrigated corn, while roots of non-irrigated corn developed similar to higher populations at depths greater than 30 cm (Newell and Wilhelm, 1987; Robertson et al., 1980). Maximum root populations measured in this study were not significantly correlated to minimum soil water contents in the Bt_2 and C_1 horizons before early July. Minimal correlations may have resulted from small variations in soil water contents of the Bt_2 and C_1 horizons.

In contrast to corn, alfalfa root populations did not significantly respond to tillage management. Over the three-year period, fine root populations in the soil pro-

file were the greatest in Spring 1996. This burst in alfalfa fine root development in the spring has been reported by several authors (Jones, 1943; Pietola and Smucker, 1995; Rechel et al., 1990). Alfalfa root colonization of the soil profile was less responsive to soil water deficits than corn root systems.

Development of corn root systems within the soil profile was positively affected by the root distribution of the previous alfalfa crop. This effect was observed at two levels, both at the sub-horizon level, i.e. root populations above and below horizon interfaces (Table 1), and at the individual root level (Table 2). It is important to carefully interpret differences observed among RIMs recolonization patterns to infer the proper conclusions. Each individual MR video frame, 1.80 cm × 1.35 cm, has a diagonal of 2.25 cm. Consequently, individual MR frames can intercept linearly growing roots on a maximum length of 2.25 cm. Root recolonization figures represent the number of new root segments with a maximum length of 2.25 cm which follow previous RIMs on at least 20% of the visible length of the new root. Consequently, every 2.25 cm segment of corn root had a probability greater than 40% of partially recolonizing RIMs along decomposing roots established by a previous alfalfa crop. Corn root recolonization in 1996 of decaying root channels and RIMs of the previous alfalfa crop (1995) were 2.7-fold greater than corn root recolonization in 1994 of decaying root channels and RIMs of a previous corn crop (1993). Although seasonal modifications on root growth may have influenced the magnitude of the results somewhat, seasonal by previous crop effects can only be separated by future studies involving simultaneous factorial experiments. These results also assume that root recolonizations of RIMs at the surfaces of MR tubes are parallel to recolonization values in the bulk soil (Majdi et al., 1992; Upchurch and Ritchie, 1983). Although this study does not prove that the MR tube surface could enhance or discourage root recolonization, there was no evidence which inferred that different crop root systems would respond differently towards root recolonization at MR surfaces compared to the bulk soil. Consequently, this study suggests that corn roots recolonized RIMs and decomposing roots of alfalfa to a much greater extent than did corn roots following corn. Root recolonization of RIMs by successive crops potentially influences: (1) access of root systems to different parts of the soil profile, (2) plant absorption of mineralization products from decaying root tissue, (3) root contacts with pathogenetic microbial communities, (4) movement of water through

soils, and (5) nitrate leaching. The low percentage of corn root recolonization in 1994, following corn (1993), suggests that RIMs recolonization is not beneficial to same species successions. This observation supports the hypothesis proposed by Smucker (1993) that root growth and clustering within RIMs of the same species increases the potential for root disease.

Preferential corn root recolonization of alfalfa RIMs can result from either root encounters of alfalfa RIMs or other mechanisms of preferential root recolonization. Corn root recolonization of alfalfa RIMs resulted primarily from other mechanisms associated with root recolonization, because recolonization percentages could not be directly related to the number of available sites, i.e. RIMs and decaying roots (Table 3). The absence of a significant correlation between corn root recolonization (96) and previous alfalfa root populations (95) suggests that corn root recolonization of alfalfa RIMs did not exclusively depend upon random encounters or overlapping of total root and RIM numbers but were also affected by selective RIM properties. Alfalfa root ages varied from a couple of days to more than a year old, and therefore different root decomposition stages were in progress when the alfalfa crop was spray-killed. Corn was planted immediately afterwards. Corn roots might have recolonized only certain types of alfalfa roots having reached a certain stage of decomposition. Differential decomposition rates of alfalfa roots were induced by tillage (Figure 5). This supports the hypothesis that associated factors within RIMs (e.g., ions, diseases, gases, pore size distributions, and associated water deficits in July) were involved in determining root recolonization rates. Our reported root recolonization of RIMs is supported, in part, by the positive influences of earthworm channels which stimulate the growth of disease-free roots (Stephens and Daroven, 1997). Stone et al. (1987) also reported that alfalfa RIMs favor corn root penetration into soils. In contrast, it has been observed that large biopores (>1 mm) can be detrimental to plant growth (Passioura and Stirzaker, 1993), and that few corn roots would develop in biopores of dimensions greater than their own radius (Logsdon and Allmaras, 1991). While enhanced root recolonization by corn following alfalfa could result from appropriate pore size distribution and increased water and nutrient availability, reduced root recolonization for corn following corn could be attributed to increased pathogenetic activities. Therefore, we conclude that apparently greater corn root recolonization of alfalfa RIMs may be one

factor which significantly contributes to the positive rotation effect associated with corn following alfalfa.

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