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ROOT DYNAMICS, PRODUCTION AND DISTRIBUTION IN AGROECOSYSTEMS ON THE GEORGIA PIEDMONT USING MINIRHIZOTRONS

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SUMMARY

(1) Growth rates, death rates and distribution of grain sorghum and weed roots in conventional tillage (CT) and no-tillage (NT) plots were measured using the minirhizotron technique. Total root production in the two systems was estimated by combining minirhizotron and soil coring methods.

(2) Most root growth occurred before flowering and most roots died after flowering. The specific root growth rates of both CT and NT were highest at the beginning of the season and then declined. In contrast, the specific root death rates in the two systems were very low during the early season, increased markedly beginning at the early reproductive growth stage, peaked at flowering and declined afterwards.

(3) A root turnover index, the average of the specific growth rate and the specific death rate, was introduced in order to assess the intra-seasonal root turnover or change rate. The root turnover index of NT was higher than that of CT most of the time before flowering and slightly lower than CT after flowering.

(4) No-tillage had higher root density in the upper soil layer (0–5 cm) and in the deep soil layer (below 60 cm), but lower in the middle layer (5–60 cm) compared to CT. The estimated total root production in the top soil layer (0–28.2 cm) was 220 g m^{-2} for NT and 224 g m^{-2} for CT, and was not significantly different between treatments.

INTRODUCTION

Research on plant root systems under field conditions is difficult, because soil limits their accessibility for observation (McMichael & Taylor 1987). Measurement of root production and turnover has been one of the most intractable problems in all terrestrial ecosystems (Fogel 1985; Singh & Coleman 1977). In addition, the most commonly used soil coring method for measuring root production is often subject to serious problems (Singh *et al.* 1984). These problems have been discussed frequently in the recent literature (Vogt *et al.* 1986). Coleman (1985) stated that '... we must have better measurement of changes in root production and intra-season and annual turnover, the crude practice of sequential harvesting of fibrous roots may give erroneous estimates of below-ground production.' Many researchers agree that new methods are needed whereby root production can be estimated without relying solely on biomass data (Huck, Hoogenboom & Peterson 1987; Singh *et al.* 1984; Vogt *et al.* 1986).

Radio-tracer techniques have been used in measuring root production and turnover (Milchunas *et al.* 1985; Singh & Coleman 1973, 1974, 1977; Warembourg & Paul 1977). They have generated interesting and useful information, albeit requiring certain safety procedures, and involving costs, particularly of sample preparation and analytical equipment.

The recently improved minirhizotron technique (Upchurch & Ritchie 1983) is a promising method for use in root production and turnover studies. It is non-destructive

and relatively less labour intensive, and frequent measurements can be done *in situ* with little disturbance to the natural environment. Minirhizotrons have been used in studies of rooting depth (Böhm 1974; Gregory 1979; Bragg, Govi & Cannell 1983; Upchurch & Ritchie 1983), root length density (Bland & Dugas 1988; Sanders & Brown 1978; Upchurch & Ritchie 1983), root dynamics (Gregory 1979; van Noordwijk, Jager & Floris 1985; Hansson & Andren 1987; Eissenstat & Caldwell 1988) and pathological effects on roots (Rush, Upchurch & Gerik 1984). Studies of root production and turnover *in situ* using minirhizotrons are very rare.

In this study, a minirhizotron technique combined with a soil coring method was used to measure growth rates, death rates, turnover rates and distributions of roots along the soil profiles of conventional tillage and no-tillage agroecosystems in the Georgia Piedmont, south-eastern United States. These results are then used to estimate root production in the two systems.

MATERIALS AND METHODS

Site description

Our research was done at the Horseshoe Bend experimental area, near Athens, Georgia, on the Georgia Piedmont. The soil is a well-drained Hiwassee sandy clay loam found on 0–2% slope. Physical and chemical properties of this soil have been summarized elsewhere (Groffman 1985). The area has been under conventional tillage and no-tillage treatments since 1978. A complete site description and management history were given by Groffman, Hendrix & Crossley (1987).

The study was begun in spring 1986. Rye (*Secale cereale* L.) was used as a winter cover crop and was mowed and left on the soil surface in no-tillage plots. The conventional tillage plots were moldboard-ploughed in late May to a depth of about 15 cm. Both CT and NT plots received 45 kg ha⁻¹ of nitrogen and 540 kg ha⁻¹ of 0-9-27 NPK fertilizer. Grain sorghum (*Sorghum bicolor* Moench) seeds were drilled with a no-till planter on 17 June with a row spacing of 80 cm. The sorghum seedlings emerged on 22 June, bloomed (50%) on 22 August (61 days after emergence), and physiologically matured on 26 September (96 days after emergence). The experiment used a completely randomized design with three replicates for each tillage treatment.

Minirhizotron method

The transparent minirhizotrons were made of polycarbonate tubing with 3 mm wall thickness and an inside diameter of 51 mm. They were scored on the outside top surface with a 1-mm wide etching along their length, which was cross-etched at each 10-cm interval. Eight minirhizotrons per plot were installed systematically along a transect on a crop row. The installation procedure of Box & Johnson (1987) was followed. Briefly, minirhizotron tubes were installed at 22° from vertical along the direction of the crop row. A 45-mm diameter hole was drilled to 1.7-m depth by a tractor-mounted auger, sizing the hole with a 55-mm outside-diameter bit mounted on a Giddings soil tube (51 mm o.d.). The minirhizotrons had bullet-nosed plugs made of solid polycarbonate glued into the bottom end of the polycarbonate tubing and were pressed into the soil holes with a push rod positioned against the inside centre of the plugs. This installation procedure was necessary to obtain an intimate interface between the wall of the minirhizotron and the soil around it. Exterior surfaces of the tube protruding above the soil surface were wrapped with black plastic electrical tape to prevent light entry into the tube and

subsequent possible adverse effects on root growth (Pearson 1974). The minirhizotrons were kept closed with rubber stoppers except when root recordings were made. All minirhizotrons were installed on 26 June, 4 days after emergence.

Roots intersecting minirhizotrons were observed using a Circon colour video camera, model MV9011, connected to a colour video monitor (a Panasonic colour TV with a 38-mm picture tube) and a video cassette recorder (VCR) model VKP900. The image produced by the camera was observed in the monitor and recorded on a video tape simultaneously. During recording, the camera was moved from the bottom of the tube upwards along the vertical line on the minirhizotron. The moving speed was approximately 3 mm s^{-1} or less, which facilitated observing, counting and tracing of the root image later on. An image recording of a root picture strip of 16 mm actual width on the upper surface of each minirhizotron was obtained after each sampling time. Analysis of the resulting tapes was done in the laboratory on the VCR mentioned above with a 20-inch diagonal, black-and-white, flat screen TV set. Each screen of the live root picture strip was first fixed on the screen through the pause function of the VCR and then the live root was traced on a sheet of clear plastic. The consecutive root picture strip from the first sampling date was obtained in this way. For all the following sampling dates, the same plastic sheet was overlaid on the TV screen and the root picture already on the plastic was compared to that on the screen. Root growth and death incurred during each sampling interval were traced or marked onto the plastic sheet. Any previously recorded root that either became black or disappeared from the picture was recorded as dead at the corresponding date. Different colour pens were used to designate different sampling dates. A planimeter was used to measure root length in each 10-cm depth along the soil profile of each individual minirhizotron. Root length density was obtained using the equation:

$$RLD = L/(AD)$$

where *RLD* is root length density (cm cm^{-3}), *L* is the length reading from the planimeter (cm), *A* is the area of the tube wall measured (cm^2), and *D* is the distance from the outside surface of the tube to the depth of the soil which can be observed in the camera, here 0.2 cm (Atkinson 1985).

Root numbers were counted in the laboratory following the procedure described by Box & Johnson (1987) and converted to root length density using the formula of Upchurch & Ritchie (1983).

Biomass sampling

Above-ground biomass of crop and weeds was harvested by the end of the growing season on 17 November 1986. A quadrat of $0.5 \times 0.5 \text{ m}$ was sampled with the minirhizotron at the centre of the area. All biomass samples were oven-dried (75°C) for at least 5 days and weighed on a balance.

Root biomass of crop and weeds was sampled with a hand-driven soil core sampler (5.0 cm i.d.) on the crop row 1 m away from each minirhizotron to a depth of 28.2 cm on 10 September 1986. Each soil core was divided into five segments (0–5.0, 5.0–9.4, 9.4–13.0, 13.0–18.8, 18.8–28.2 cm). The unusual depth distribution was followed to be consistent with other multi-year data sets in our field plots. A total of six soil cores per plot were sampled and bulked together. Soil core samples were then stored in a cool room (2°C), washed with tap water, and hand-sorted for total live roots (intact, white-coloured roots) of both sorghum and weeds from other organic materials within 1 week of sampling. The roots were separated into coarse ($> 1 \text{ mm}$) and fine ($< 1 \text{ mm}$) categories, oven-dried for at

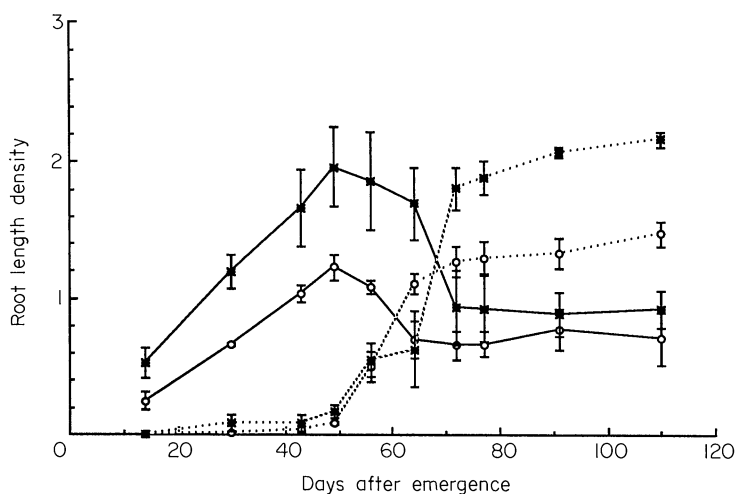


FIG. 1. Root length density (cm cm^{-3}) during the growing season in the 0–28.2 cm soil layer through time. — \times —, live roots of conventional tillage, — \circ —, live root of no-tillage; $\cdots \times \cdots$, dead roots of conventional tillage, $\cdots \circ \cdots$, dead roots of no-tillage; bar = 2 S.E.

least 3 days and weighed on an electronic balance. No attempt was made to separate sorghum roots from weed roots.

Analysis of data

The following parameters of root dynamics were calculated:

$$LR_j = \Sigma(G_j - D_j) \quad (j = 1, 2, 3, \dots);$$

$$DR_j = \Sigma D_j \quad (j = 1, 2, 3, \dots);$$

$$sGr_j = (G_j/t_j)/[(LR_{(j-1)} + LR_j)/2] \quad (j = 1, 2, 3, \dots)$$

$$sDr_j = (D_j/t_j)/[(LR_{(j-1)} + LR_j)/2] \quad (j = 1, 2, 3, \dots)$$

$$TI_j = (sGr_j + sDr_j)/2 \quad (j = 1, 2, 3, \dots)$$

where LR_j is the standing live root-length density at time j ; G_j is the root growth during the time period from time $j-1$ to j ; D_j is the root death during the time $j-1$ to j ; DR_j is the total dead roots produced by time j ; t_j is the time period between $j-1$ and j ; sGr_j is the specific root growth rate at time j ; sDr_j is the specific root death rate at time j ; and TI_j is the root turnover index at time j . All these parameters for root dynamics were calculated and analysed for the 0–28.2 cm soil layer only. Statistical analysis between the two tillage treatments for all the measurements described above was done with a two-tailed t -test.

RESULTS

Most root growth occurred before flowering and most roots died during and after flowering (Fig. 1). The live root-length density of CT in the top soil layer was higher than NT consistently throughout the growing season and dead root density of CT was also significantly higher than NT during the late season.

The specific root growth rates (sGr) ($\% \text{ day}^{-1}$) of CT and NT in the top soil layer (0–28.2 cm) showed declining trends through the growing season (Fig. 2). The sGr differed

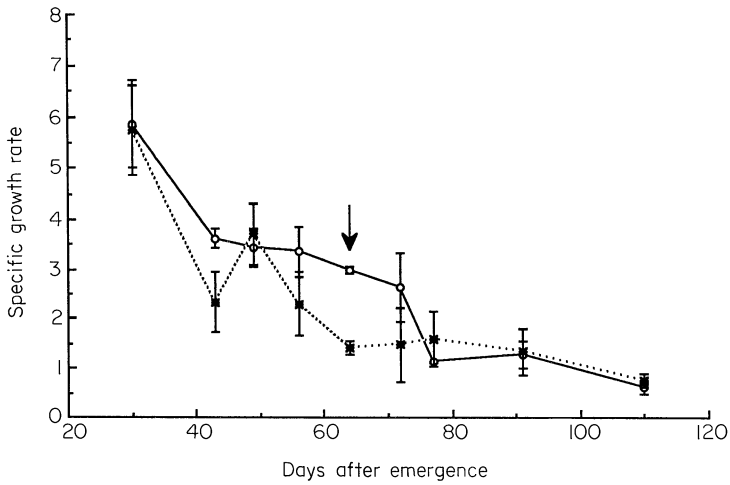


FIG. 2. Specific root growth ($\% \text{ day}^{-1}$) of conventional tillage ($\cdot \cdot \cdot \times \cdot \cdot \cdot$) and no-tillage ($\text{—}\circ\text{—}$) through time. The arrow indicates the time point at which the two treatments were significantly different at $P < 0.05$; bar = 2 S.E.

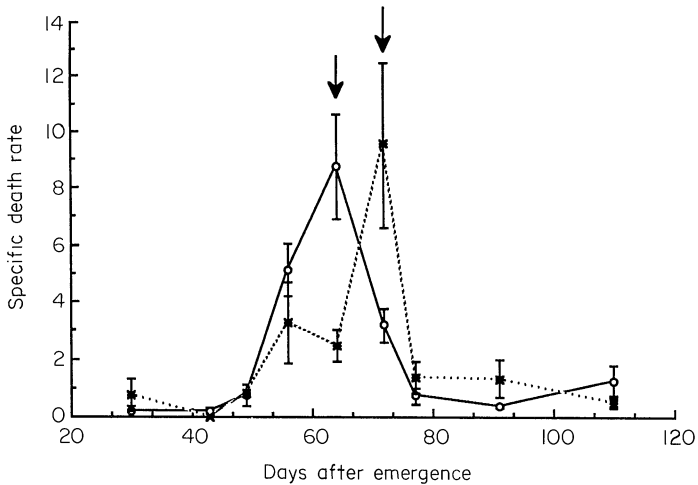


FIG. 3. Specific root death rate ($\% \text{ day}^{-1}$) of conventional tillage ($\cdot \cdot \cdot \times \cdot \cdot \cdot$) and no-tillage ($\text{—}\circ\text{—}$) through time. The arrows indicate the time points at which the two treatments were significantly different at $P < 0.05$; bar = 2 S.E.

between CT and NT mainly in the early season (significant at $\alpha = 0.05$ on one date) when root growth was predominant for both tillage systems, and disappeared after flowering. The specific root death rates (sDr) ($\% \text{ day}^{-1}$) of CT and NT in the top soil layer both increased markedly, beginning at the early reproductive growth stage, peaking at flowering, and declining afterwards (Fig. 3). The difference of sDr between CT and NT showed a contrary pattern. The sDr of NT was higher than CT from 56 to 65 days after

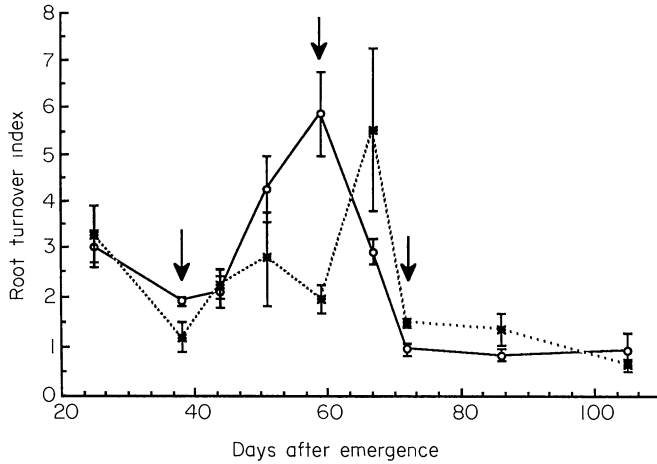


FIG. 4. Root turnover index (% day⁻¹), average of specific growth rate and specific death rate, of conventional tillage (· · · × · · ·) and no-tillage (—○—) through time. The arrow indicates the time point at which the treatments were significantly different at $P < 0.05$; bar = 2 S.E.

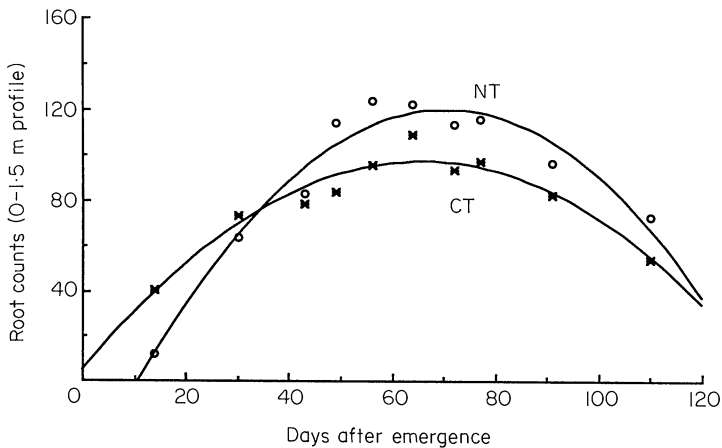


FIG. 5. Root counts along the 1.5-m soil profiles of conventional tillage (CT) and no-tillage (NT) through time (total counts per minirhizotron of 1.5 by 150 cm observing area). Day 0 = 22 June. Quadratic regression equation for NT, $y = -47.5 + 4.7x + 0.034x^2$ ($r = 0.98$); for CT, $y = 4.4 + 2.8x - 0.021x^2$ ($r = 0.96$); y = root counts, x = days after emergence.

emergence (significant at $\alpha = 0.05$ on one sampling date), whereas the sDr of CT was higher than NT 72 days after emergence (significant on one sampling date). The root turnover index (average of sGr and sDr) of CT and NT showed a similar pattern to that of sDr alone (Fig. 4). The root turnover index of NT was higher than CT most of the time before flowering, and CT was slightly higher than NT after flowering.

There was a quadratic relationship between live root counts and days after emergence, with peaks at about 70 days after emergence ($r = 0.976$ for NT, $r = 0.961$ for CT) (Fig. 5).

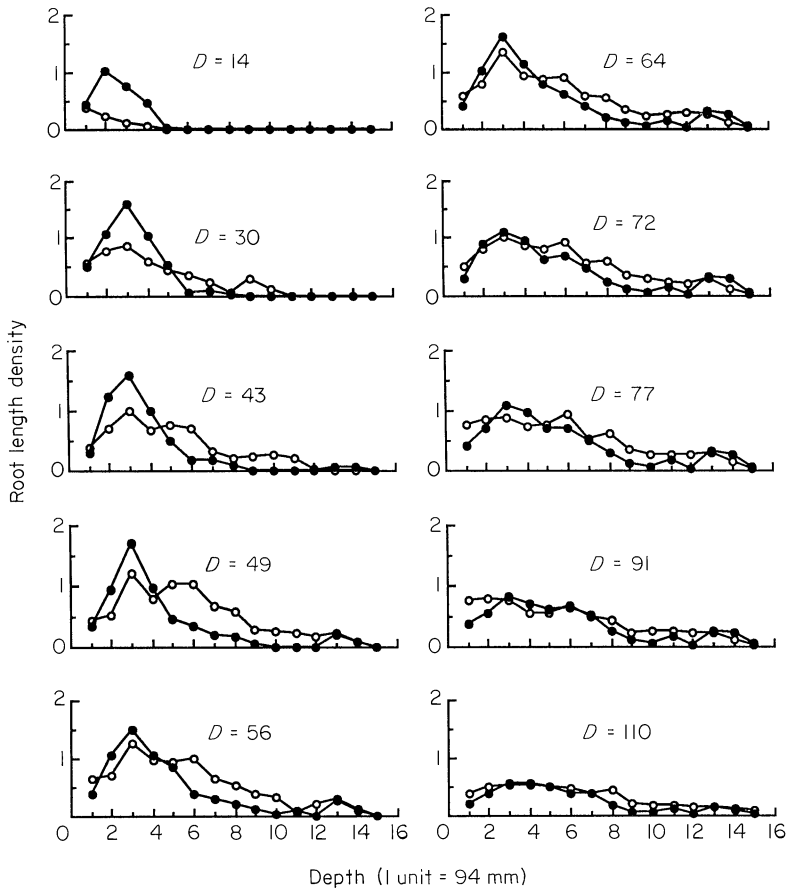


FIG. 6. Distribution of live root-length densities along the soil profiles (sixteen depths) of conventional tillage (—●—) and no-tillage (—○—) at ten different sampling dates. D = number of days after emergence.

The live root-length density of NT at depth 1 was consistently higher than CT except for the first sampling date and mostly lower than CT at depths 2, 3 and 4 except for the last three sampling dates (Fig. 6). Interestingly, the live root-length density of NT was consistently higher than CT in the deep soil profile below depth 60 cm.

Soil core data indicated that the fine live root-biomass density (FLRBD) of NT was significantly ($\alpha = 0.05$) higher than that of CT in the upper surface soil layer (0–5 cm), but lower than CT in the 5–28.2 cm soil layers (Fig. 7). This pattern was similar to that of live root density from root counts of minirhizotron. A negative exponential distribution of fine root biomass density along the 0–28.2 cm profile was observed for both CT and NT ($r = 0.978$ for CT, $r = 0.968$ for NT).

No correlation existed between soil core measurements and live root counts from the minirhizotrons and between soil core data and the hand tracing data from the minirhizotrons. However, the root-length densities produced from hand tracing of the video tape from the minirhizotrons did have a significant ($r = 0.66$, $P < 0.01$) linear

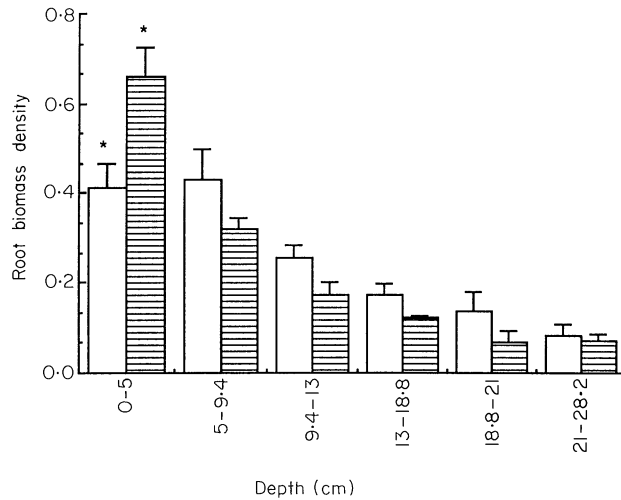


FIG. 7. Distribution of fine live root-biomass densities (kg m^{-3}) of conventional tillage (CT) (□) and no-tillage (NT) (▨) on one sampling date (77 days after emergence). Bars with asterisks indicate a significant difference ($P < 0.05$) between the two treatments. Negative exponential regression of the fine live root-biomass density with depth indicates $r = 0.98$ for CT and $r = 0.97$ for NT; bar = S.E.

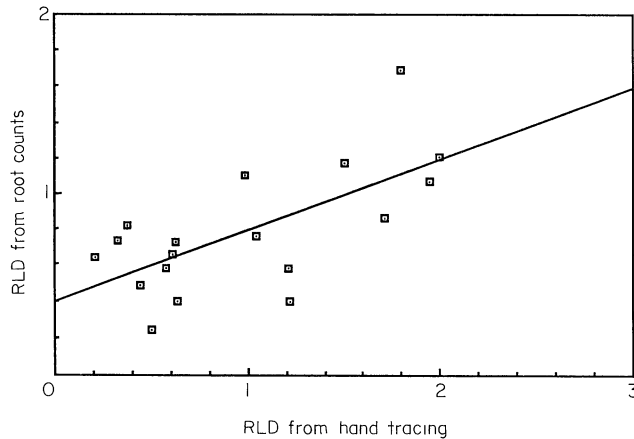


FIG. 8. Linear correlation between root-length density (RLD) (cm cm^{-3}) measured by root counts of minirhizotrons and that measured by hand-tracing of minirhizotron tapes ($r = 0.66$, $P < 0.01$).

correlation with the root-length densities produced from live root counts of the minirhizotrons (Fig. 8).

Total root production during the whole growing season in the 0–28.2 cm soil layer of CT and NT was estimated, based on the data presented in Table 1. These estimates were based upon the assumptions that the ratio of the live root biomass from soil core method to the live root-length density from hand-tracing of the minirhizotrons was constant

TABLE 1. Root production in no-tillage (NT) and conventional tillage (CT) agroecosystems in 0–28.2 cm soil layer

Source	CT (\pm S.E.)	NT (\pm S.E.)	Significance
Root mass from soil core (7 Sep 1986) (g m^{-2})			
Live	67.5 (9.34)	67.5 (3.40)	N.S.
Root length from minirhizotrons (7 Sep 1986) (cm tube^{-1})†			
Live	27.8 (7.15)	20.1 (2.91)	N.S.
Ratio [Line (1)/line (2)]			
Live	2.43	3.36	
Root length from minirhizotrons (10 Oct 1986) (cm tube^{-1})‡			
Live	27.6 (4.21)	21.3 (5.73)	N.S.
Dead	64.8 (1.76)	44.1 (2.86)	**
Total	92.4 (6.55)	65.4 (7.22)	*
Estimated production (10 Oct 1986) (g m^{-2})			
Live	67.5 (9.34)	67.5 (3.40)	N.S.
Dead	157 (4.27)	148 (9.60)	N.S.
Total	224 (15.9)	220 (24.2)	N.S.

* $P < 0.1$; ** $P < 0.05$; N.S., not significant.

† Root length (cm) in a 1.5-cm wide, 30-cm deep transect along each minirhizotron tube.

‡ Calculated by multiplying data lines 4, 5 and 6 by line 3, respectively.

TABLE 2. Above-ground biomass in no-tillage (NT) and conventional tillage (CT) agroecosystems (g m^{-2})

Source	CT (\pm S.E.)		NT (\pm S.E.)
Sorghum	134 (85.6)	**	477 (58.1)
Weeds	312 (32.6)	N.S.	236 (52.7)
Total	445 (67.8)	*	713 (102)

Differences significant at * $P < 0.1$; ** $P < 0.05$; N.S., not significant.

through the growing season, and that the ratio for dead roots was the same as for the live roots. The numbers on line 3 in Table 1 were calculated by dividing line 1 by line 2 and the numbers on lines 7, 8 and 9 were calculated by multiplying lines 4, 5 and 6 by line 3, respectively. The estimated total root production in the 0–28.2 cm soil layer was 220 g m^{-2} for NT and 224 g m^{-2} for CT, and was not significantly different.

The above-ground biomass production of crop and weeds in CT and NT is shown in Table 2. Both sorghum and total above-ground biomass for NT were significantly higher ($P < 0.05$ for sorghum, $P < 0.1$ for total) than for CT.

DISCUSSION

The pattern of root dynamics in these systems is comparable to that described theoretically by Huck, Hoogenboom & Peterson (1987) as a 'normal' pattern for most annual agricultural crops. Root growth dominates the early half of the season and root death dominates the latter half of the season, with a growth–death overlap period in the middle. Measurements of total root production in a system with this kind of dynamic pattern can be seriously underestimated if only root biomass from the soil core method is used (Huck, Hoogenboom & Peterson 1987; Singh *et al.* 1984). About 40% of the total root production cannot be accounted for if only the peak values of live roots are used (Fig. 1). This may suggest that below-ground production estimates based solely on live root sampling are substantially underestimated. One critical assumption is that the root dynamics observed from the soil–tube interface are representative of the bulk soil. The validity of this assumption has been discussed by Atkinson (1985) and Huck & Taylor (1982) in regard to rhizotrons. Vos & Groenwold (1987) have demonstrated that minirhizotron observations can be related quantitatively to soil core analyses.

The under-estimation of root density by the minirhizotron technique at the upper surface soil layer has been reported repeatedly (Bragg, Govi & Cannell 1983; Upchurch & Ritchie 1983; van Noordwijk, de Jager & Floris 1985; Levan, Ycas & Hummel 1987). The under-estimation of root density at the surface soil layer by the minirhizotron method may be due to light leaks through the soil–tube interface (Levan, Ycas & Hummel 1987), root damage during late installation (Bragg, Govi & Cannell 1983), and gaps existing between the soil and the minirhizotron wall (van Noordwijk, de Jager & Floris 1985). However, this problem can be partially solved by using light-shielding precautions (Levan, Ycas & Hummel 1987) and proper installation procedures (Box & Johnson 1987). The under-estimation of root density in the surface soil layer by the minirhizotron method was probably one of the factors which caused the lack of correlation between soil core data and minirhizotron data in the 0–28.2 cm layer mentioned above. These under-estimates of root densities in the surface soil layer by the minirhizotron method are probably more severe in NT than in CT, because more roots concentrate in the surface layer in NT (Fig. 7).

Tillage practices affect root distribution along the soil profile. First, roots in NT tend to concentrate in the upper surface layer (0–5 cm) (Fig. 7), as has been reported (Barber 1971; Anderson 1987; Newell & Wilhelm 1987). This phenomenon may be due to the more favourable physical, chemical and biological conditions for root growth in the surface soil of NT than in CT. Previous work done by Groffman *et al.* (1986) showed higher organic carbon content, higher organic nitrogen content, and lower bulk density of NT surface soil than CT. Doran (1980) and Linn & Doran (1984) have found higher microbial population and water content in NT surface soil compared to CT surface soil. Second, higher root density occurred in CT than in NT in the middle layer (5–60 cm), because soil conditions become relatively more favourable for root growth in this layer in CT than in NT (Groffman *et al.* 1986, 1987; Doran 1980; Linn & Doran 1984; Radcliffe *et al.* 1988). Third, the no-tillage treatment tended to have more roots in the deep soil layers below the depth of 60 cm (Fig. 6). A similar result was found by Hargrove *et al.* (1988). They surmised that this resulted from considerably more water stored under the no-tillage treatment, which had a higher water infiltration rate than conventional tillage treatment. Their suggestion is especially likely for our situation as this experiment was carried out in a severe drought year for Athens, Georgia. There was very little rainfall during the period

between late spring and early summer. However, there might be other factors which cause better rooting in NT deep layers. Earthworm activities may play an important role (roots may grow through earthworm burrows) as earthworm populations are much higher in NT than in CT (House & Parmelee 1985). Old root channels can also cause deeper rooting in NT. Zero tillage preserves old root channels so that roots in NT can follow them into deeper soil zones. The deeper rooting in NT may be one of the factors which leads to the higher above-ground biomass production of NT (Table 2).

Higher root turnover in NT during the early half of the growing season tends to support the hypothesis that fine root turnover rates are higher in resource-rich soil environments (Caldwell 1979; Chapin 1980; Nadelhoffer, Aber & Melillo 1985). The NT surface soil is relatively more resource-rich than CT surface soil as already discussed above. It is also possible that differential biotic regulation of root turnover, such as soil faunal predation on roots, exists in these different tillage systems. Parmelee & Alston (1986) noted that plant parasitic nematode populations were higher throughout the summer growing season in NT than in CT.

At present, minirhizotrons are mostly used to produce root counts, which are then converted into other types of measurements. Root production and turnover can be studied *in situ* if the minirhizotron technique is combined with other methods, such as the soil coring method and hand-tracing of video tapes from minirhizotrons. But the hand-tracing we employed is tedious and labour-intensive.

The development of the modern minirhizotron system has taken place over a relatively short period of time. It has the potential to make root observation nearly as routine as the study of the above-ground portion of the field-grown plants (Brown & Upchurch 1987). Smucker *et al.* (1987) are developing a computer-based technique to analyse the recorded video data from minirhizotrons. We expect the minirhizotron technique will be further improved, calibrated, and automated to be employed in many related below-ground studies.

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REFERENCES

- Anderson, E. L. (1987). Corn root growth and distribution as influenced by tillage and nitrogen fertilization. *Agronomy Journal*, **79**, 544–549.
- Atkinson, D. (1985). Spatial and temporal aspects of root distribution as indicated by the use of root observation laboratory. *Ecological Interactions in Soil* (Ed. by A. H. Fitter, D. Atkinson, D. J. Read & M. B. Usher), pp. 43–65. Special Publication No. 4 of the British Ecological Society. Blackwell Scientific Publications, Oxford.
- Barber, S. A. (1971). Effect of tillage practice on corn (*Zea mays* L.) root distribution and morphology. *Agronomy Journal*, **63**, 724–726.
- Bland, W. L. & Dugas, W. A. (1988). Root length density from minirhizotron observations. *Agronomy Journal*, **80**, 271–275.
- Böhm, W. (1974). Mini-rhizotrons for root observations under field conditions. *Z. Acker- Und Pflanzenbau*, **140**, 282–287.

- Box, J. E., Jr & Johnson, J. W. (1987). Minirhizotron rooting comparisons of three wheat cultivars. *Minirhizotron Observation Tubes: Methods and Applications for Measuring Rhizosphere Dynamics* (Ed. by H. M. Taylor), pp. 123–130. American Society of Agronomy Special Publication No. 50. Madison, Wisconsin.
- Bragg, P. J., Govi, G. & Cannell, R. Q. (1983). A comparison of methods, including angled and vertical minirhizotrons, for studying root growth and distribution in a spring oat crop. *Plant and Soil*, **73**, 435–440.
- Brown, D. A. & Upchurch, D. R. (1987). Minirhizotrons: a summary of methods and instruments in current use. *Minirhizotron Observation Tubes: Methods and Applications for Measuring Rhizosphere Dynamics* (Ed. by H. M. Taylor), pp. 15–30. American Society of Agronomy Special Publication No. 50. Madison, Wisconsin.
- Caldwell, M. M. (1979). Root structure, the considerable cost of belowground function. *Topics in Plant Population Biology* (Ed. by O. T. Solbrig, S. Jain, G. B. Johnson & P. H. Raven), pp. 408–427. Columbia University Press, New York.
- Chapin, F. S. III. (1980). The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics*, **11**, 223–260.
- Coleman, D. C. (1985). Through a ped darkly: an ecological assessment of root–soil–microbial–faunal interactions. *Ecological Interactions in Soil* (Ed. by A. H. Fitter, D. Atkinson, D. J. Read & M. B. Usher), pp. 1–21. British Ecological Society Special Publication No. 4. Blackwell Scientific Publications, Oxford.
- Doran, J. W. (1980). Soil microbial and biological changes associated with reduced tillage. *Soil Science Society of America Journal*, **44**, 765–771.
- Eissenstat, D. M. & Caldwell, M. M. (1988). Seasonal timing of root growth in favorable microsites. *Ecology*, **69**, 870–873.
- Fogel, R. (1985). Roots as primary producers in below-ground ecosystems. *Ecological Interactions in Soil* (Ed. by A. H. Fitter, D. Atkinson, D. J. Read & M. B. Usher), pp. 23–35. British Ecological Society Special Publication No. 4. Blackwell Scientific Publications, Oxford.
- Gregory, P. J. (1979). A periscope method for observing root growth and distribution in field soil. *Journal of Experimental Botany*, **30**, 205–214.
- Groffman, P. M. (1985). Nitrification and denitrification in conventional and no-tillage soils. *Soil Science Society of America Journal*, **49**, 329–334.
- Groffman, P. M., Hendrix, P. F., Scott, D. E. & Crossley, D. C., Jr. (1986). Nitrogen cycling as affected by interactions of components in a Georgia Piedmont agroecosystem. *Ecology*, **67**, 80–87.
- Groffman, P. M., Hendrix, P. F. & Crossley, D. C., Jr. (1987). Nitrogen dynamics in conventional and no-tillage agroecosystems with inorganic fertilizer or legume nitrogen input. *Plant and Soil*, **97**, 315–332.
- Hansson, A. C. & Andren, O. (1987). Root dynamics in barley, lucerne and meadow fescue investigated with a mini-rhizotron technique. *Plant and Soil*, **103**, 33–38.
- Hargrove, W. L., Box, J. E. Jr., Radcliffe, D. E., Johnson, J. W. & Rothrock, C. S. (1988). Influence of long-term no-tillage on crop rooting in an Ultisol. *Conservation Farming: Focus on a Better Future* (Ed. by J. E. Hairson & K. H. Remy), pp. 22–25. Proceedings of 1988 Southern Conservation Tillage Conference. Tupelo, Mississippi.
- House, G. J. & Parmelee, R. W. (1985). Comparison of soil arthropods and earthworms from conventional and no-tillage agroecosystems. *Soil and Tillage Research*, **5**, 351–361.
- Huck, M. G., Hoogenboom, G. & Peterson, C. M. (1987). Soybean root senescence under drought stress. *Minirhizotron Observation Tubes: Methods and Applications for Measuring Rhizosphere Dynamics* (Ed. by H. M. Taylor), pp. 109–121. American Society of Agronomy Special Publication Number 50. American Society of Agronomy, Madison, Wisconsin.
- Huck, M. G. & Taylor, H. M. (1982). The rhizotron as a tool for root research. *Advances in Agronomy*, **35**, 1–35.
- Levan, M. A., Ycas, J. W. & Hummel, J. W. (1987). Light effects on near-surface soybean rooting observed with minirhizotrons. *Minirhizotron Observation Tubes: Methods and Applications for Measuring Rhizosphere Dynamics* (Ed. by H. M. Taylor), pp. 89–98. American Society of Agronomy Special Publication No. 50. American Society of Agronomy, Madison, Wisconsin.
- Linn, D. M. & Doran, J. W. (1984). Aerobic and anaerobic microbial population in no-till and plowed soils. *Soil Science Society of America Journal*, **48**, 794–799.
- McMichael, B. L. & Taylor, H. M. (1987). Applications and limitations of rhizotrons and minirhizotrons. *Minirhizotron Observation Tubes: Methods and Applications for Measuring Rhizosphere Dynamics* (Ed. by H. M. Taylor), pp. 1–13. American Society of Agronomy Special Publication No. 50. American Society of Agronomy, Madison, Wisconsin.
- Milchunas, D. G., Lauenroth, W. K., Singh, J. S., Cole, C. V. & Hunt, H. W. (1985). Root turnover and production by ¹⁴C dilution: implications of carbon partitioning in plants. *Plant and Soil*, **88**, 353–365.
- Nadelhoffer, K. J., Aber, J. D. & Melillo, J. M. (1985). Fine roots, net production, and soil nitrogen availability: a new hypothesis. *Ecology*, **66**, 1377–1390.
- Newell, R. L. & Wilhelm, W. W. (1987). Conservation tillage and irrigation effects on corn root development. *Agronomy Journal*, **79**, 160–165.
- Parmelee, R. W. & Alston, D. G. (1986). Nematode trophic structure in conventional and no-tillage agroecosystems. *Journal of Nematology*, **18**, 403–407.

- Pearson, R. W. (1974).** Significance of rooting patterns to crop production and some problems of root research. *The Plant Root and Its Environment* (Ed. by E. W. Carson), pp. 247–270. University Press of Virginia, Charlottesville, Virginia.
- Radcliffe, D. E., Tollner, E. W., Hargrove, W. L., Clark, R. L. & Golabi, M. H. (1988).** Effect of tillage practice on infiltration and soil strength of a typic Hapludult soil after ten years. *Soil Science Society of America Journal*, **52**, 798–804.
- Rush, C. M., Upchurch, D. R. & Gerik, T. J. (1984).** *In situ* observations of *Phytophthora omnivorum* with a borescope mini-rhizotron system. *Phytopathology*, **74**, 104–105.
- Sanders, J. L. & Brown, D. A. (1978).** A new fiber optic technique for measuring root growth of soybean under field conditions. *Agronomy Journal*, **70**, 1073–1076.
- Singh, J. S. & Coleman, D. C. (1973).** A technique for evaluating functional root biomass in grassland ecosystems. *Canadian Journal of Botany*, **51**, 1867–1870.
- Singh, J. S. & Coleman, D. C. (1974).** Distribution of photo-assimilated ¹⁴Carbon in the root system of a shortgrass prairie. *Journal of Ecology*, **62**, 359–365.
- Singh, J. S. & Coleman, D. C. (1977).** Evaluation of functional root biomass and translocation of photoassimilated ¹⁴C in a shortgrass prairie ecosystem. *A Synthesis of Plant-associated Processes. Range Science Department Science Series* (Ed. by J. K. Marshall), No. 26, pp. 123–131. Colorado State University, Fort Collins, Colorado.
- Singh, J. S., Lauenroth, W. K., Hunt, H. W. & Swift, D. M. (1984).** Bias and random errors in estimators of net root production: a simulation approach. *Ecology*, **65**, 1760–1764.
- Smucker, A. J. M., Ferguson, J. C., DeBruyn, W. P., Belford, R. K. & Ritchie, J. T. (1987).** Image analysis of video-recorded plant root systems. *Minirhizotron Observation Tubes: Methods and Applications for Measuring Rhizosphere Dynamics* (Ed. by H. M. Taylor), pp. 67–80. American Society of Agronomy Special Publication No. 50. American Society of Agronomy, Madison, Wisconsin.
- Upchurch, D. R. & Ritchie, J. T. (1983).** Root observations using a video recording system in mini-rhizotrons. *Agronomy Journal*, **73**, 1009–1015.
- van Noordwijk, M., de Jager, A. & Floris, J. (1985).** A new dimension to observations in minirhizotrons: a stereoscopic view on root photographs. *Plant and Soil*, **86**, 447–453.
- Vogt, K. A., Grier, C. C., Gower, S. T., Sprugel, D. G. & Vogt, D. J. (1986).** Overestimation of net root production: a real or imaginary problem? *Ecology*, **67**, 577–579.
- Vos, J. & Groenwold, J. (1987).** The relation between root growth along observation tubes and in bulk soil. *Minirhizotron Observation Tubes: Methods and Applications for Measuring Rhizosphere Dynamics* (Ed. by H. M. Taylor), pp. 39–49. American Society of Agronomy Special Publication No. 50. American Society of Agronomy, Madison, Wisconsin.
- Warembourg, F. R. & Paul, E. A. (1977).** Seasonal transfers of assimilated ¹⁴C in grassland: plant production and turnover, soil and plant respiration. *Soil Biology and Biochemistry*, **9**, 295–301.

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