

## Seasonal patterns and vertical distributions of fine roots of alfalfa (*Medicago sativa* L.)

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### Abstract

Seasonal patterns and vertical distributions of alfalfa root systems were investigated with field experiments and a simulation model. We carried out root excavations on an established alfalfa stand at Davis, California, in 1982 and 1983. Thirty-six soil cores to a depth of 150 cm were taken seven times in 1982 and seventy-two soil cores to 30 cm were taken nine times in 1983 over the growth seasons. Live fine roots were recovered through six (in 1982) or seven (in 1983) procedures, including detailed hand sorting for removing debris. Our studies revealed that fine root mass was generally greatest in spring and fall and least during summer. Secondary minima were found within each harvest cycle. At all samplings, root mass declined exponentially with depth.

A simulation model was developed for studying dynamics of alfalfa fine roots. The model has two components: root growth and death. Actual growth rate of fine roots was determined by potential growth rate and dependent on soil temperature, water and carbohydrate supply. Root death was controlled by the maximum death rate and influenced by soil temperature and nonstructural carbohydrate in roots. Through differential changes in simulated growth and death rates, the model predicted well the temporal and vertical distributions of fine root mass. A high amount of fine root mass was maintained in spring by rapid growth and moderate death rates. Frequent harvests reduced root mass in summer. Root mass increased in fall again due to a prolonged high growth rate. Sensitivity analyses indicated vertical distributions varied strongly with carbohydrate supply and soil temperature.

*Keywords:* Carbohydrate supply; Management; Model; Root ecology; Root physiology; Root turnover; Soil environment

### 1. Introduction

Dynamics of root systems, which have important implications for water and nutrient uptake, are largely controlled by carbohydrate supply (Klepper, 1987) and substantially influenced by soil environments. Seasonal variation of alfalfa taproot growth, for example, is strongly correlated with carbohydrate supply from

shoots (Rapoport and Travis, 1984). Root growth slows or ceases when shoots are removed and this is commonly interpreted as resulting from limitations in carbohydrate supply (Brouwer, 1983). Although effects of soil environmental factors, including soil water potential, nutrients and temperature, on root growth have been extensively studied (Klepper et al., 1973; Fernandez and Caldwell, 1975; Jodari-Karimi et al., 1983; Stone et al., 1983), little information is available about environmental aspects of root death (Klepper, 1987). Correlative studies indicate that peaks of

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dead root mass generally coincide with decline of live root mass (Sims and Singh, 1978; Hansson and Andren, 1986).

Alfalfa root systems, the subject of this study, comprise a relatively permanent structure of cambial taproot and laterals from which noncambial fine roots arise (Weaver, 1922; Weaver et al., 1922). In an early study in Wisconsin (USA), Jones (1943) found that alfalfa root mass varies over the course of a season and is marked by a minimum during summer. Whilst this pattern may result from several factors, most field studies have focused on only one factor at a time. Bennett and Doss (1960), for example, demonstrated in Alabama (USA) that root mass becomes concentrated in upper soil layers as soil moisture increases. In contrast, Beckett and Huberty (1928) showed that root distribution in a deep loam at Davis, California, is not affected by frequency or amount of irrigation after a wet winter. The study by Smith (1962) in Wisconsin revealed that total nonstructural carbohydrate (TNC) in alfalfa taproots changes dramatically with different harvest schedules whereas Brown et al. (1990) found no effect of harvest schedule on root TNC in southeastern USA.

To help evaluate the relative roles of various environmental and physiological factors on dynamics of root systems, several integrative simulation models have been developed. Brouwer and de Wit (1969) simulated root growth through its dependence on carbohydrate supply and this approach continues in use by some workers (e.g., Ng and Loomis, 1984; Denison and Loomis, 1989). Simulation of vertical distribution of roots of annual crops has been done employing models with gradients of carbohydrate (Brugge and Thornley, 1985) but more commonly with allometric rules (e.g., in proportion to aboveground mass) and various soil physical properties, e.g. moisture content (Jones et al., 1991).

Our objectives in this study were to characterize temporal patterns and vertical distribution of fine root mass with field experiments and to explain them with a mechanistic model. Root excavations were carried out in 1982 and 1983 in an established stand of alfalfa. A new physiologically based root model consisting of fine root growth and death was developed and integrated with shoots and root-zone environments within the crop model ALFALFA (Denison and Loomis, 1989). Effects of various management practices and physiological

parameters on the seasonal patterns and vertical distributions were investigated with the model.

## 2. Methods

### 2.1. Measurement of fine roots

Fine root samples were obtained in 1982 and 1983 from experimental plots of alfalfa (*Medicago sativa* L., cv. 'Moapa 69') established in September 1980. The site was located at the University of California, Davis (121°45'W, 38°30'N; 20 m elevation) on Yolo silt loam (nonacid, thermic, Typic Xerothents; Andrews, 1972). Field activities of harvests and irrigations in 1982 and 1983 are listed in Table 1.

In 1982, a randomized, complete block design with nine blocks and four samples per block was laid out at the beginning of each harvest cycle. Soil cores (22 mm diam.) were removed in 30-cm segments to a depth of 1.5 m using Veihmeyer tubes. Cores were located between plants so as to avoid interference from large taproots. Fine root cleaning was initiated by mechanically agitating individual samples in nylon mesh (0.36-mm mesh) bags in a water tank. After removal from the bags and rinsing in clean water, large soil particles

Table 1  
Management activities of harvests and irrigations for the alfalfa crop in 1982 and 1983. Alfalfa stand was cut at a height of 7 cm and about 100 mm water was applied for each irrigation

| 1982         |            | 1983         |            |
|--------------|------------|--------------|------------|
| Date         | Activities | Date         | Activities |
| 5 May        | Harvest    | 20 April     | Harvest    |
| 13 May       | Irrigation | 4 May        | Irrigation |
| 10 June      | Harvest    | 24 May       | Harvest    |
| 16 June      | Irrigation | 31 May       | Irrigation |
| 23 June      | Irrigation | 10 June      | Irrigation |
| 7 July       | Harvest    | 22 June      | Harvest    |
| 13 July      | Irrigation | 2 July       | Irrigation |
| 23 July      | Irrigation | 11 July      | Irrigation |
| 4 August     | Harvest    | 20 July      | harvest    |
| 10 August    | Irrigation | 28 July      | Irrigation |
| 23 August    | Irrigation | 17 August    | Harvest    |
| 7 September  | Harvest    | 25 August    | Irrigation |
| 14 September | Irrigation | 6 September  | Irrigation |
| 24 September | Irrigation | 15 September | Harvest    |
| 14 October   | Harvest    | 23 September | Irrigation |
|              |            | 7 November   | Harvest    |

were allowed to settle out and floating debris was removed by suction. Roots and remaining secondary debris were collected on filter paper, dried at 70°C with forced draft, and weighed. After drying, obvious debris and roots exceeding 1 mm diameter were removed by hand.

Most of fine root mass was found in samples from the 0-30 stratum. Samples from this stratum, however, still contained significant amounts of debris whereas lower strata were essentially free of contamination. Further cleaning of the 1982 samples proved impractical and we therefore developed an adjustment factor during the 1983 study. Harvest and irrigation schedules in 1983 were similar to those in 1982 (Table 1). The nine samplings in 1983 focused on the 0-30 stratum. A randomized, complete block design with 12 blocks was used. Six cores (17.7 or 18.8 mm diam.) were taken from the 0-30 stratum in each block and combined. Initial cleaning was as in 1982, followed after drying by very detailed hand sorting to remove the additional debris. It was found that 'clean' fine roots accounted for only 33 to 50% of total mass for that stratum after initial cleaning as in 1982. A conservative factor (0.33) was used to adjust 0-30 cm mass data from 1982 for this report.

Attempts were made to distinguish between live and dead roots by visual examination of fresh root samples and with vital stains for samples in both years. The visual method was more successful but findings were inconclusive and total clean roots are reported here. Large changes in root mass were observed within harvest cycles and over the season, however, suggesting that dead roots decayed rapidly and thus were not a major component in cleaned roots. The specific root length (200 m g<sup>-1</sup> dry mass) used in the model was established in these studies.

### 2.2. The root model

The root model, developed within ALFALFA (Denison and Loomis, 1989), includes principal routines for simulation of growth and death. Fine root growth in each of 10 soil layers depends on potential root growth rate, based on the existing structural mass of fine roots ( $R$ ), maximum relative growth rate ( $G_m$ ), and fraction of fine root mass capable of growing ( $F_g$ ). Potential growth for each hour then is reduced by soil constraints ( $S$ ) and the current most-limiting factor among non-

structural carbohydrate concentration in roots ( $C$ ), soil temperature ( $T$ ), and soil water content ( $W$ , Fig. 1). The actual growth rate ( $G$ ) of fine roots within a 1-h interval is then estimated by:

$$G = RG_m F_g S \min(E_{C,g}, E_{T,g}, E_{W,g}) \quad (1)$$

where  $E_{C,g}$ ,  $E_{T,g}$ , and  $E_{W,g}$  are effects on root growth of nonstructural carbohydrate in fine roots, soil temperature, and relative available soil water content, respectively. The algorithm  $\min(\text{argument})$  selects the minimum value among alternatives.

Fraction of fine root mass capable of growing ( $F_g$ ) is related phenomenologically to root-length density (cm root cm<sup>-3</sup> soil, Fig. 2A). When root-length density is small and little of the soil has been explored, the number of root tips per unit root mass is relative high, leading to a large value of  $F_g$ . As roots grow,  $F_g$  is reduced to account for a smaller fraction of root tips in the total root mass (depletion of soil nutrients may also be involved in this effect).

Relative available soil water content is taken as the difference between actual water content and water content at wilting point, divided by the difference between field capacity and wilting point. The relationship between root growth and soil water content (Fig. 2B)

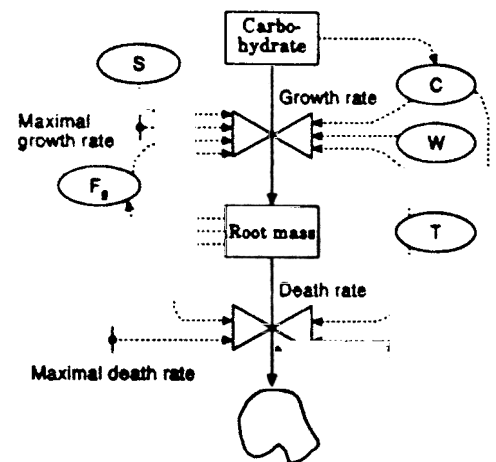


Fig. 1. A state-variable diagram illustrating growth and death rates of alfalfa fine root as influenced by physiological and environmental variables. Growth rate is determined by the maximal growth rate ( $G_m$ ), existing root mass ( $R$ ), fraction of root mass capable for growing ( $F_g$ ), and soil constraints ( $S$ ). Root growth is also influenced by soil water content ( $W$ ), temperature ( $T$ ), and carbohydrate ( $C$ ). Death rate is controlled by the maximal death rate ( $D_m$ ) and existing root mass and affected by soil temperature and carbohydrate supply.

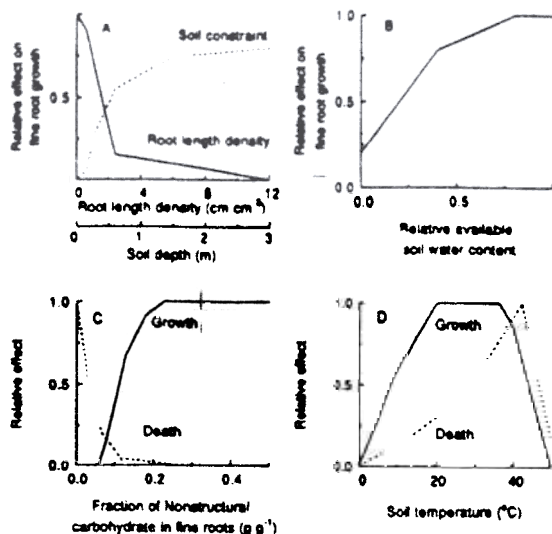


Fig. 2. (A) Relative effects on fine root growth of root length density (solid line) and soil constraint (dash line), the latter being a function of soil depth; (B) relative effect of soil water content on fine root growth; (C) relative effects of fraction of nonstructural carbohydrate in fine roots on fine root growth (solid line) and death (dash line); and (D) relative effects of soil temperature on fine root growth (solid line) and death (dash line).

follows a generalized concept from Kramer (1983). A threshold level of carbohydrate for fine root growth is set at 0.08 ( $\text{g carbohydrate g}^{-1}$  dry mass). Growth then increases linearly to its maximum rate at carbohydrate levels beyond 0.25 (Fig. 2C). Effect of soil temperature on root growth is characterized by the function given by Fick et al. (1988; Fig. 2D).

The empirical parameter of soil constraints ( $S$ ) represents root growth restrictions imposed by soil factors not explicitly simulated in the model. Levels of nutrients, oxygen, and carbon dioxide and soil texture are assumed to become less favorable for root growth conditions with increasing depth, i.e. more soil constraint, (Fig. 2A).

Fine root death rate ( $D$ ) depends on nonstructural carbohydrate fraction in fine roots (Marshall and Waring, 1985) and soil temperature (Fig. 1):

$$D = RD_m E_{C,d} E_{T,d} \quad (2)$$

where  $D_m$  is the maximum relative death rate of fine roots, and  $E_{C,d}$  and  $E_{T,d}$  are effects of nonstructural carbohydrate (Fig. 2C) and soil temperature, respectively, on the death rate (Fig. 2D).

### 2.3. Simulation

The root model was linked to the crop model ALFALFA 1.5 that provides hourly values of nonstructural carbohydrate in roots, soil temperature, and volumetric water contents for 10 soil layers within a 3-m soil profile (Denison and Loomis, 1989; Luo, 1991). In the model, soil temperature is predicted from the energy balance at the soil surface and soil heat transfer (Luo et al., 1992). Volumetric water content in each soil layer is estimated after water uptake by roots, evaporation, infiltration and drainage are calculated (Denison and Loomis, 1989). Dynamic carbohydrate supply from shoots to roots is determined using a stratified-canopy photosynthesis model (Duncan et al., 1967) and a partitioning model with three pools of nonstructural carbohydrate (Luo, 1991).

Successive thicknesses chosen for the 10 soil layers, commencing from the uppermost, were 10, 10, 10, 30, 30, 30, 30, 60, and 60 cm and initial soil water contents were 17, 17, 17, 80, 80, 80, 80, 80, 160, and 160  $\text{kg m}^{-2}$  layer $^{-1}$ , respectively. Volumetric soil water content was 0.27 at field capacity and 0.10 at wilting point. Total soil porosity was 0.50 ( $v/v$ ). Initial values of crop variables corresponded to those observed in spring. Plant population was 200 plants  $\text{m}^{-2}$ . Beginning at the surface, initial root mass in each layer was 0.23, 0.20, 0.19, 0.37, 0.22, 0.19, 0.16, 0.08, 0.053, and 0.03  $\text{g plant}^{-1}$  layer $^{-1}$ . Specific length of fine roots was 200  $\text{m g}^{-1}$ . Initial nonstructural carbohydrate in the carbon pool of fine roots was 0.24  $\text{g plant}^{-1}$ . Glucose consumption for root growth was 1.28  $\text{g g}^{-1}$  dry root mass. Maximum specific growth and death rates of fine roots were 0.035  $\text{g g}^{-1} \text{h}^{-1}$  and 0.0012  $\text{g g}^{-1} \text{h}^{-1}$ , respectively.

All simulations were based on field activities listed in Table 1 and weather data in 1982 and 1983. To be comparable with experimental data, simulated root mass to a depth of 1.5 m was presented in this paper.

To facilitate comparison of measured and simulated values of fine root mass, we used a ln–ln equation (Gerwitz and Page, 1974) to describe root vertical distributions. That is

$$\ln Y = a + b \ln X \quad (3)$$

where  $Y$  is fine root mass in each layer ( $\text{g m}^{-2}$  layer $^{-1}$ ),  $X$  is midpoint of the layer (m), and  $a$  and  $b$  are empirical parameters. The value of  $b$  becomes more negative

when root mass is concentrated towards the soil surface layers and approaches zero when root mass is distributed evenly through the profile.

### 3. Results

#### 3.1. Seasonal pattern: Field measurements and model predictions

In 1982, fine root mass to a depth of 1.5 m was maximum in late spring ( $307 \text{ g m}^{-2}$  on 15 June), decreased to a minimum of  $187 \text{ g m}^{-2}$  in mid-July, recovered in mid-September, and then declined at the end of the September–October harvest cycle (Fig. 3A). Fine root mass to a depth of 0.3 m in 1983 was also highest in late spring ( $148 \text{ g m}^{-2}$  on 22 June) and decreased to a minimum of about  $90 \text{ g m}^{-2}$  in mid-July followed by fluctuation of root mass between 90 and  $130 \text{ g m}^{-2}$  (Fig. 3B). Within each harvest cycle, fine root mass declined first, followed by recovery towards the end of the cycle. A statistical analysis indicated that root mass on 15 June and 8 September was

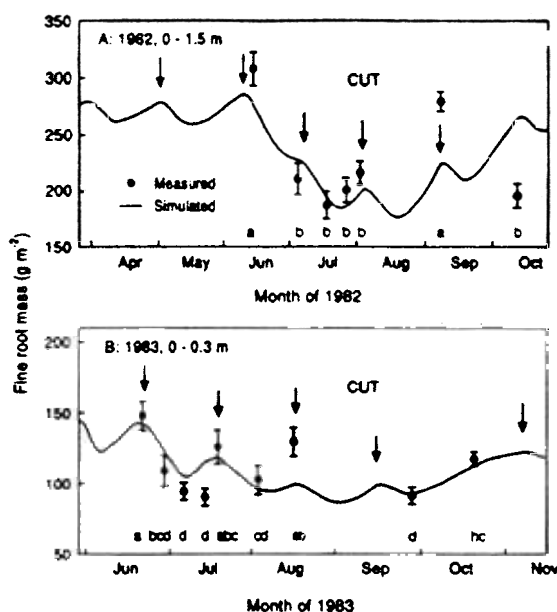


Fig. 3. (A) Measured (solid circles, mean  $\pm$  s.e.,  $n = 9$ ) and predicted (solid lines) total mass of alfalfa fine roots in the 0–1.5 m soil profile in 1982; and (B) measured ( $n = 12$ ) and predicted fine root mass in the 0–0.3 m soil profile in 1983. Letters in the lower part of the figures indicate statistical significance. Measured root mass with different letters significantly differ from each other.

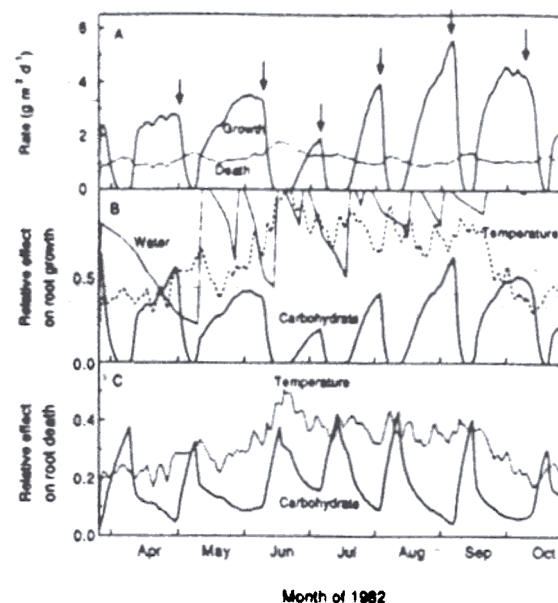


Fig. 4. (A) Dynamics of predicted growth (solid line) and death (dot line) rates of fine roots in the 0–1.5 m soil profile in 1982; (B) dynamics of predicted daily mean relative effects of carbohydrate (solid line), relative available soil water content (dot line), and soil temperature (dash line) on fine root growth at depth of 0.25 m; and (C) dynamics of predicted daily mean relative effects of carbohydrate (solid line) and soil temperature (dot line) on root death at depth of 0.25 m.

significantly different from that on other sampling dates in 1982 (Fig. 3A). Root mass did not significantly differ among sampling dates within the intensively sampled cycle in July 1982 but did so within the June–July cycle in 1983. A turnover of nearly 25% of the fine roots is evident from death and regrowth during the June–July harvest cycle of 1983 (Fig. 3B).

Our root model reasonably simulated seasonal variations of root mass in both 1982 and 1983 (Fig. 3). Simulated root mass to a depth of 1.5 m in 1982 oscillated around  $275 \text{ g m}^{-2}$  in spring, decreased to about  $180 \text{ g m}^{-2}$  in summer and increased in fall again (Fig. 3A). Simulated root mass in the surface 0.3-m layer in 1983 had a similar pattern as in 1982 (Fig. 3B).

Temporal variation in root mass resulted from differential changes in root growth and death rates (Fig. 4A). Within each harvest cycle, simulated rate of fine root growth declined to zero and death rate increased after harvest, leading to a decrease of fine root mass. The opposite changes in root growth and death rates led to increased root mass in the late period of a cycle.

Cumulative root growth in the first and last two harvest cycles in 1982 was higher than cumulative root death, leading to increased root mass in spring and fall, respectively. In the middle two harvest cycles in summer, however, root growth was much smaller than death, leading to declined root mass.

The differential changes in root growth and death rates resulted from the dynamics of carbohydrate supply, soil temperature, and water content (Figs. 4B and 4C). The three factors interactively limited root growth in the early spring and late fall in 1982. In summer, carbohydrate became the most limiting factor for root growth because frequent removal of foliage and fast aboveground growth reduced carbohydrate availability in roots. Influences of carbohydrate and temperature on root death were confounded by root mass (Fig. 3A). Low relative death rate coincided with high mass in spring and fall whereas the opposite combination occurred in the summer. Thus, the seasonal pattern of absolute death rate appeared less fluctuating (Fig. 4B). Nevertheless, mean death rate averaged over the three harvest cycles in summer was nearly 20% higher than that averaged over the two cycles in spring.

### 3.2. Vertical distribution: Field measurements and model predictions

Measured fine root mass decreased exponentially with depth on all seven sampling dates in 1982 (Fig. 5) and was well described with Eq. 3 (Table 2). The  $b$  values were least negative on 28 July and most negative on 8 September (Table 2). That indicated that fine roots were most evenly distributed through the profile on 28 July and mostly concentrated in the surface layers on 8 September (Figs. 5D versus 5F). A statistical analysis was performed on measured root mass over the growth season separately for each depth stratum. Significant differences were found in all cases except for the 60–90 cm and 120–150 cm strata.

The measured root distributions were predicted well with the root model except on 8 September. On that date, the model underpredicted total fine root mass and predictions of root mass in the 0–30 and 30–60 cm layers were substantially smaller than the measurements (Fig. 5F). The reverse occurred for all but the 30–60 layer on 13 October when the model overestimated total fine root mass (Fig. 5G).

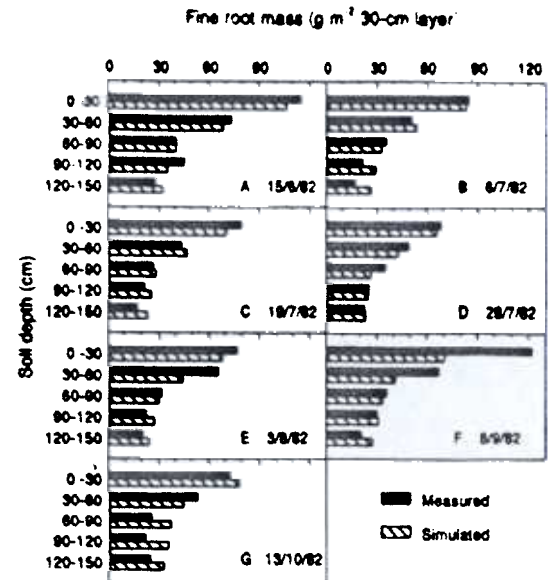


Fig. 5. Measured (solid bars, mean  $\pm$  se,  $n = 9$ ) and predicted (striped bars) fine root mass in 30-cm strata on 15 June, 6, 19, and 28 July, 3 August, 8 September, and 13 October 1982.

### 3.3. Effects of harvest and irrigation schedules on model predictions

The behavior of the model system was explored in two series of simulations. In one series, the six harvests were changed to either four or eight. With four harvests, fine root mass to a depth of 1.5 m reached a seasonal peak of  $300 \text{ g m}^{-2}$  in May and a low of  $160 \text{ g m}^{-2}$  in September (Fig. 6A). The longer growth period led to increased root mass in the first harvest cycle but not in the others. The model stems did not initiate new leaves

Table 2

Description of vertical profiles of measured fine root mass on seven sampling dates in 1982 with a ln–ln equation (Eq. 3, see the text). Parameter  $b$  defines shapes of vertical distribution,  $a$  is an empirical coefficient, and  $r^2$  is the determinant coefficient

| Date        | $a$  | $b$   | $r^2$ |
|-------------|------|-------|-------|
| 15 June     | 6.46 | –0.61 | 0.92  |
| 6 July      | 6.51 | –0.72 | 0.95  |
| 19 July     | 6.33 | –0.71 | 0.99  |
| 28 July     | 5.76 | –0.53 | 0.94  |
| 3 August    | 6.30 | –0.66 | 0.87  |
| 8 September | 7.04 | –0.79 | 0.97  |
| 13 October  | 5.96 | –0.59 | 0.88  |



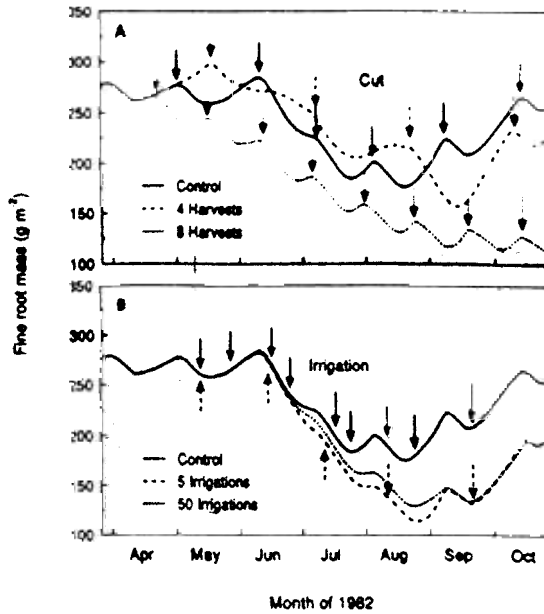


Fig. 6. Predicted fine root mass in the 0-1.5 m soil profile in 1982 as affected by harvest and irrigation schedules with length of season and amount of irrigation water fixed as in the control simulation. (A) In one simulation experiment, the six harvests were changed to either four or eight with 9 irrigations. Arrows indicate harvest dates. (B) In the other simulation experiment, the nine irrigations, each of 100 mm, were either combined to five irrigations of 180 mm each or spread to fifty with 18 mm each and harvests remained to be six. Arrows indicate irrigation dates for the control and experiment with 5 irrigations. Simulated irrigations were applied every three days during the summer and every four days in spring and fall for the experiment with 50 irrigations (irrigation dates not indicated with arrows).

after flowering. The latter occurred nearly 40 d after harvest in spring and only 25-30 d in summer and fall. Therefore, as old leaves died, photosynthesis declined and root growth did not get the benefit from the longer harvest period in summer and fall. With eight harvests, fine root mass declined after each harvest and recovery was poor (Fig. 6A).

In a second series, the nine irrigations, each of 100 mm, were either combined to five irrigations of 180 mm each or spread to fifty with 18 mm each. Changes in irrigation frequency hardly affected fine root dynamics in the early harvest cycles but did influence root mass in summer (Fig. 6B). Both five and fifty irrigations led to a moderate loss of water through either drainage or surface evaporation. Water supply to root growth in deep soil layers was restricted, leading to reduced total root mass.

### 3.4. Sensitivity analyses

Sensitivity analyses (Table 3) for the 1982 season were conducted with variations in  $G_m$  (the maximum relative growth rate of fine roots),  $D_m$  (the maximum relative death rate of fine roots),  $P$  (photosynthetic rate),  $S$  (soil constraints),  $T$  (soil temperature), and  $W_i$  (amount of irrigation water). Each parameter was altered by  $\pm 20\%$  from original values. Effects on total fine root mass and its vertical distribution (parameters  $a$  and  $b$  of Eq. 3) were investigated on both 15 June and 28 July. Sensitivity index is expressed as  $100 \times (E - C) / C / 20$ , where  $E$  and  $C$  are the values of the tested variable in the sensitivity simulation and in control simulation, respectively. The index represents a percent change in tested variable for a 1% change of the testing parameter.

Variation in  $G_m$  influenced total root mass on 28 July but had little effect on 15 June. Root mass and coefficients  $a$  and  $b$  were moderately sensitive to  $D_m$  on both days. The root system was distributed more evenly with depth when  $D_m$  decreased. Changes in photosynthesis had by far the greatest effects. Reduction of  $P$  by 1% reduced fine root mass by 1.4 and 2.2% on 15 June and 28 July, respectively, and generated much more even distributions of roots. Increasing  $P$  led to opposite results. Lowering  $T$  by 1% increased fine root mass by

Table 3

Sensitivity (% change) of total fine root mass and distribution parameters  $a$  and  $b$  on 15 June and 28 July 1982 to  $\pm 1\%$  change in parameters  $G_m$  (the maximum growth rate of fine roots),  $D_m$  (the maximum death rate of fine roots),  $P$  (photosynthesis rate),  $S$  (soil constraint),  $T$  (soil temperature), and  $W_i$  (amount of irrigation)

| Parameter | % Change | 15 June |       |       | 28 July |       |       |
|-----------|----------|---------|-------|-------|---------|-------|-------|
|           |          | Mass    | $a$   | $b$   | Mass    | $a$   | $b$   |
| $G_m$     | -1       | -0.03   | -0.03 | 0.09  | -0.52   | -0.12 | 0.00  |
|           | +1       | -0.07   | 0.03  | 0.00  | 0.20    | 0.12  | -0.19 |
| $D_m$     | -1       | 0.22    | 0.07  | -0.09 | 0.25    | 0.17  | -0.39 |
|           | +1       | -0.20   | -0.21 | 0.17  | -0.38   | -0.19 | 0.29  |
| $P$       | -1       | -1.43   | -0.36 | -0.38 | -2.17   | -0.55 | -0.31 |
|           | +1       | 0.84    | 0.22  | 0.31  | 1.98    | 0.43  | 0.49  |
| $S$       | -1       | -0.04   | -0.07 | -0.16 | -0.29   | -0.13 | -0.19 |
|           | +1       | -0.03   | 0.04  | 0.08  | 0.17    | 0.08  | 0.10  |
| $T$       | -1       | 0.53    | 0.23  | 0.41  | 1.76    | 0.49  | 0.65  |
|           | +1       | -0.71   | -0.25 | -0.37 | -1.45   | -0.48 | -0.51 |
| $W_i$     | -1       | -0.03   | -0.01 | 0.00  | -0.18   | -0.02 | 0.02  |
|           | +1       | 0.00    | 0.00  | 0.00  | -0.00   | -0.00 | -0.00 |

0.5% and 1.8% on 15 June and 28 July, respectively, and caused roots to be concentrated towards the surface. In contrast, higher  $T$  decreased fine root mass by 0.7% and 1.5% and caused more even distribution. Changes in soil constraint  $S$  and irrigation had only small effects on fine root mass and distribution.

#### 4. Discussion

This study provides the first systematic measurements of fine root mass of the alfalfa crop within harvest cycles over the growing seasons in 1982 and 1983. Despite uncertainties with the last two data points in the 1982 growth season, combined data from the two-year study revealed a general seasonal pattern, that root mass peaks in spring and fall separated by a period with less mass. In addition, our study also suggested a general dynamic pattern of fine root mass within each harvest cycle, root mass declining after foliage harvest and recovering in the late part of the cycle.

The root dynamic patterns over growth seasons and within cycles were achieved in the simulations and explained by differential changes in root growth and death rates under the influence of temperature and supplies of water and carbohydrate. The model predicted rapid growth in spring and fall and slow growth in summer, and a reverse pattern of root death. The patterns of root growth and death are consistent with that observed for cambial activity of alfalfa roots at Davis (Rapoport and Travis, 1984). Although the model embodies functional balance mechanisms based on water status, soil moisture had little influence on root dynamics within the range tested here whereas photosynthate supply to roots substantially influenced root systems.

With annual crops, vertical distributions of fine roots have been simulated using diffusion processes (Brugge and Thornley, 1985) and dependence on age (Jones et al., 1991). In those models, time-sequential colonization into different soil layers is an important factor shaping distribution. In this study, the dynamics of root mass in each soil layer depended mainly on the balance between growth and death. The model presented here satisfactorily predicted the distribution of fine roots even as their mass varied dramatically over the seasons. It appears that the main features of growth and death rates of stratified root systems of well-watered alfalfa

crops can be simulated reasonably from limitations imposed by carbohydrate supply and temperature.

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