

## Seasonal branch and fine root growth of juvenile loblolly pine five growing seasons after fertilization

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**Summary** In 1989, we established two replications of two fertilization treatments in a 10-year-old loblolly pine (*Pinus taeda* L.) plantation. Between March and September 1993, branch internode and needle fascicle expansion in the upper and lower third of crowns were measured weekly on three south-facing branches of each of four trees, and new root initiation and elongation were measured at 10-day intervals in three vertical rhizotrons per plot. In one replication, soil water content was measured daily.

Fertilization significantly increased the expansion of first flush internodes in the upper crown and first flush needle fascicles in the upper and lower crown. New root growth was stimulated by fertilization in the second half of the growing season. The timing of root growth responses to fertilization corresponded to branch phenologies in the upper and lower crown that were conducive to increased basipetal transport of photosynthate. We conclude, therefore, that new root growth was linked to source–sink activities in the crown.

Root initiation was greater in the upper than in the lower part of the soil profile; however, as the growing season progressed and water deficit increased, this relationship was reversed. The effect of soil depth on seasonal root growth was closely associated with water availability, suggesting that root initiation deep in the soil profile is critical for the continued production of new roots in environments subjected to short-term, but relatively severe, water deficits.

**Keywords:** branch phenology, rhizotrons, source–sink relations, water deficit.

### Introduction

Water and mineral nutrient absorption by tree root systems is closely associated with new root growth, which is controlled by environmental variables and the internal physiology of the tree (Torrey 1986, Klepper 1987, Eissenstat and Van Rees 1994). Both the light environment within a forest canopy and the quantity of foliage in tree crowns influence the amount of carbon dioxide fixed by the canopy (Stenberg et al. 1994, Teskey et al. 1994). Photosynthate production and the seasonal

source–sink relations within a tree regulate the amount of carbohydrate partitioned for root metabolism (Dickson 1991, Eissenstat and Van Rees 1994). Growing roots have a low sink strength for photosynthate relative to developing branches, which results in a complementary relationship between root and shoot growth (Drew and Ledig 1980, Reich et al. 1980, Dickson 1989, Dickson 1991).

Silvicultural treatments such as fertilization and thinning manipulate the availability of site resources to maximize stand productivity (Vose and Allen 1988, Cregg et al. 1990, Jack and Long 1991). These silvicultural tools also affect root activity through their influence on environmental and physiological variables such as light, mineral nutrient and water availabilities, and photosynthate production and partitioning (Santantonio and Santantonio 1987, Gower et al. 1992, Haynes and Gower 1995).

Water and mineral nutrient limitations occur frequently in southern pine forests, and anticipated changes in the climate of temperate forests may further reduce the availability of water and mineral nutrients for tree growth (Hansen et al. 1988, Peters 1990). Knowledge of root system responses to environmental change is needed to understand how changes in resource availabilities affect root function. With this information, management strategies that temper the negative effects or enhance the benefits of environmental change on root growth can be identified and implemented.

Our objectives were to: (1) evaluate the seasonal branch and root growth of juvenile plantation loblolly pine (*Pinus taeda* L.) in response to fertilization, and (2) compare the relationship between seasonal branch and root phenology in response to two fertilization treatments. We hypothesized that crown growth processes that affect photosynthate production and partitioning are related to seasonal changes in root growth.

### Materials and methods

The study site is a Beauregard silt loam (fine-silty, siliceous, thermic, Plinthaquic Paleudult) soil located on the Palustris Experimental Forest in Rapides Parish, LA (Kerr et al. 1980).

In 1981, 14-week-old container-grown loblolly pine were planted ( $1.83 \times 1.83$  m). Six treatment plots, consisting of 13 rows of 13 trees each (0.06 ha), were established. In November 1988, every other row of trees and every other tree in residual rows were mechanically removed (final density 721 trees  $\text{ha}^{-1}$ ). Two fertilization treatments were randomly assigned to treatment plots in a completely random design with three replications. Treatments were a nonfertilized control and a 747 kg  $\text{ha}^{-1}$  broadcast application of diammonium phosphate (150 kg P and 135 kg N  $\text{ha}^{-1}$ ), which was applied in April 1989. The fertilization rate was based on recommendations for loblolly pine grown on the inherently nutrient-poor soil at the study site (Kerr et al. 1980, Shoulders and Tiarks 1983).

Measurement plots consisting of the interior four rows of three trees each were established within the treatment plots. Herbicides were applied as needed to minimize the understory vegetation. Two replications were chosen as blocks for intensive measurement of branch and root phenology. Blocks were identified based on the effect of topography on soil drainage, with one block more readily drained than the other. Scaffolding was installed to support wood walkways in the upper and lower one-third of the canopy.

At the start of our study in March 1993, fertilization continued to increase tree height and diameter, and stand basal area (Haywood 1994). At this time, crown closure had not been achieved, but photosynthetic photon flux densities in the lower crown of the fertilized and non-fertilized plots were 70 and 14% less, respectively, than those in the upper crown (Gravatt, unpublished results).

In early March 1993, three south-facing branches in the upper and lower one-third of the crowns of each of four trees in each measurement plot were randomly selected from those that were accessible from the walkways. At approximately weekly intervals through September 1993, branch internode expansion was measured. Similarly, three needle fascicles on each expanding internode were randomly chosen, and their lengths measured at weekly intervals.

New root initiation and elongation were measured in Plexiglas rhizotrons at three locations on measurement plots where branch phenology was monitored. Locations were randomly chosen from those that had a uniform microtopography and stocking. At each location, a Plexiglas sheet ( $0.3 \times 35.4 \times 76$  cm) was attached to a vertical plane of the soil with sheet metal screws. Between root observations, rhizotrons were insulated with styrofoam.

At 10-day intervals, new long lateral roots ( $\geq 0.5$  cm in length and elongating independently of a visible parent root), visible on each side ( $21.6 \times 30$  cm) of the rhizotrons, were traced onto heavy-duty, transparent acetate sheets with a permanent marker. Observations were recorded cumulatively. After each measurement interval, the acetate sheets were photocopied, a computer image file of each photocopy was created with a desktop scanner, and the lengths of the lines in the image files were quantified with GSROOT software (PP Systems Inc., Bradford, MA). The roots that initiated during each measurement interval at 0 to 5, 5 to 15 and 15 to 30 cm depths of the rhizotrons were counted.

Precipitation was recorded in an open field 25 m from the experimental plots with an electronic weather station (Omni-data International, Inc., Logan, UT). At 6-h intervals, soil water content was measured at 5, 15 and 30 cm through ports in the center of one rhizotron per plot of one replication with a time domain reflectometer (Soil Moisture Equipment Corp., Santa Barbara, CA).

Branch and root phenological data were subjected to analyses of variance. Branch internode and needle fascicle expansion of the first flush were analyzed with a split plot in space and time design with two blocks. Whole plots were crown levels and subplots were fertilization treatments and measurement intervals. Root initiation was similarly analyzed with soil depths as whole plots, and fertilization treatment and measurement intervals as subplots. Internode and needle fascicle expansion of the second flush in the upper crown and cumulative root elongation were analyzed with a split plot in time design with two blocks. Whole plots were fertilization treatments and subplots were measurement intervals. Results were evaluated by analysis of variance by measurement interval to elucidate significant main and interaction effects. Main and interaction effects were considered significant at  $P < 0.05$  and significantly different treatment means were compared with the Least Significant Difference test at  $P < 0.05$ , unless otherwise noted.

## Results

First flush internode length was significantly greater in the upper crown than in the lower crown (Table 1). Fertilization significantly increased first flush internode length in the upper crown, but not in the lower crown ( $P = 0.0593$ ) (Figure 1). The length of first flush needle fascicles was not significantly affected by crown level but it was significantly affected by an interaction between time and fertilization. Fertilization consistently increased the lengths of needle fascicles in both the upper and lower crown after the fourth measurement interval ( $P < 0.10$ ) (Figure 2). Although not significant, fertilization consistently increased branch internode and needle fascicle lengths of the second flush in the upper crown (Figure 3).

All sample trees exhibited first flush internode expansion in the upper and lower crowns. By mid-September, a second flush had occurred in the upper crown of all trees in both treatments, but only 38 and 25% of the nonfertilized and fertilized trees, respectively, exhibited a second flush in the lower crown. A third flush was observed in the upper crown of 89 and 75% of the nonfertilized and fertilized trees, respectively. In the non-fertilized treatment, 38% of the trees exhibited a third flush in the lower crown, and 13% had a fourth flush in the upper crown. No similar third and fourth flush events were observed in fertilized trees.

New root initiation was significantly influenced by soil depth and season (Table 2). Analyses of variance by measurement interval indicated that root initiation at 0–5 cm was significantly greater than that at 5–15 and 15–30 cm in spring and early summer, but was significantly less than that at 15–30 cm in late summer (Figure 4).

Table 1. Analyses of variance of branch internode and needle fascicle lengths of the first flush during March through September 1993.

| Source                                 | Branch internode length |             |         | Needle fascicle length |             |         |
|--|-------------------------|-------------|---------|------------------------|-------------|---------|
|  | df                      | Mean square | $P > F$ | df                     | Mean square | $P > F$ |
| Block (R)                              | 1                       | 553.95      | 0.1243  | 1                      | 83.94       | 0.3131  |
| Crown level (C)                        | 1                       | 13926.97    | 0.0251  | 1                      | 93.39       | 0.2992  |
| R × C (Error a)                        | 1                       | 21.65       |         | 1                      | 24.09       |         |
| Fertilization (F)                      | 1                       | 504.38      | 0.1052  | 1                      | 140.47      | 0.1221  |
| F × C                                  | 1                       | 966.20      | 0.0593  | 1                      | 1.25        | 0.8296  |
| F × R + F × R × C<br>(Error b)         | 2                       | 62.80       |         | 2                      | 20.90       |         |
| Time (T)                               | 24                      | 15.46       | 0.0001  | 24                     | 183.07      | 0.0001  |
| T × R (Error c)                        | 24                      | 0.14        |         | 24                     | 0.73        |         |
| T × C                                  | 24                      | 4.88        | 0.0001  | 24                     | 0.92        | 0.4594  |
| T × C × R (Error d)                    | 24                      | 0.89        |         | 24                     | 0.88        |         |
| T × F                                  | 24                      | 0.85        | 0.0001  | 24                     | 1.25        | 0.0013  |
| T × F × C                              | 24                      | 0.99        | 0.0001  | 24                     | 0.07        | 1.0000  |
| T × F × R + T × F × R × C<br>(Error e) | 48                      | 0.15        |         | 48                     | 0.45        |         |

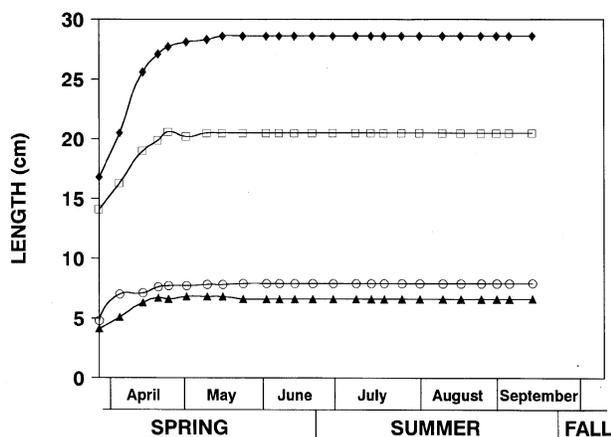


Figure 1. Mean branch internode lengths of the first flush in the upper and lower crown five growing seasons after fertilization (○ lower crown, non-fertilized; ▲ lower crown, fertilized; □ upper crown, non-fertilized; ◆ upper crown, fertilized).

There was a significant interaction between fertilization and soil depth on root initiation ( $P = 0.0658$ ) (Table 2). Significant interactions between fertilization and soil depth were not detected when analyses of variance were conducted by measurement interval. However, throughout the growing season, root initiation at all soil depths appeared to be stimulated by fertilization, except in spring, when root initiation was greater at the 15–30 cm depth in the nonfertilized plots than in the fertilized plots. Although not significant, cumulative root elongation in the fertilized plots was consistently decreased in spring, and increased in fall compared with that in the nonfertilized plots (Figure 5).

There was a positive relationship between soil water content and soil depth (Figure 6). Mean daily soil water content was

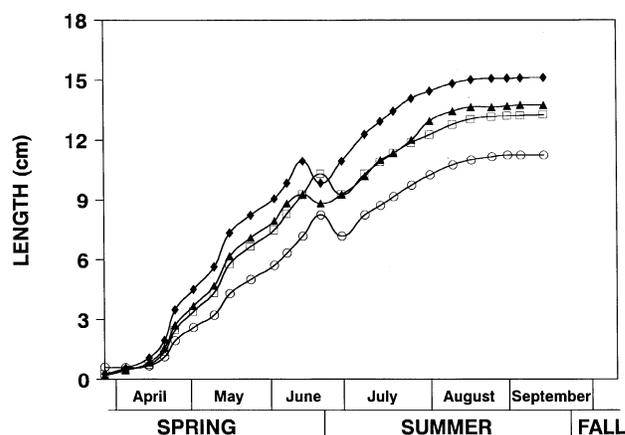


Figure 2. Mean needle fascicle lengths of the first flush in the upper and lower crown five growing seasons after fertilization (○ lower crown, non-fertilized; ▲ lower crown, fertilized; □ upper crown, non-fertilized; ◆ upper crown, fertilized).

reduced during periods of low precipitation and high water use by the trees.

## Discussion

Foliage ceases to import carbohydrate and begins exporting photosynthate at approximately 50% expansion (Watson and Casper 1984, Dickson 1989, Dickson 1991). By mid-June, expansion of first flush internodes in the upper and lower crown was complete, and needle fascicles in both the upper and lower crown had achieved greater than 75% of their final length. At this time, the export of photosynthate from needle fascicles of the first flush potentially increased the amount of carbon partitioned to the root system. However, in species

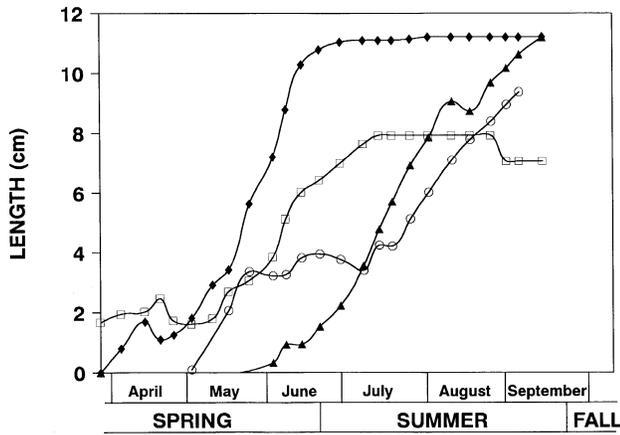


Figure 3. Mean branch internode and needle fascicle lengths of the second flush in the upper crown five growing seasons after fertilization ( $\square$  branch internode, non-fertilized;  $\blacklozenge$  branch internode, fertilized;  $\circ$  needle fascicles, non-fertilized;  $\blacktriangle$  needle fascicles, fertilized).

Table 2. Analysis of variance of root initiation  $\text{dm}^{-2} \text{ day}^{-1}$  at depths of 0–5, 5–15 and 15–30 cm during April through September 1993.

| Source   | df | Mean square | $P > F$ |
|--|----|-------------|---------|
| Block (R)  | 1  | 0.0033      | 0.1019  |
| Soil depth (D)   | 2  | 0.0181      | 0.0213  |
| R $\times$ D (Error a)   | 2  | 0.0004      |         |
| Fertilization (F)  | 1  | 0.0012      | 0.2690  |
| F $\times$ D   | 2  | 0.0049      | 0.0658  |
| F $\times$ R + F $\times$ D $\times$ R (Error b)                       | 3  | 0.0006      |         |
| Time (T)   | 18 | 0.0124      | 0.0001  |
| T $\times$ R (Error c)   | 18 | 0.0013      |         |
| T $\times$ D   | 36 | 0.0027      | 0.0038  |
| T $\times$ D $\times$ R (Error d)                                      | 36 | 0.0011      |         |
| T $\times$ F   | 18 | 0.0015      | 0.2788  |
| T $\times$ F $\times$ D  | 36 | 0.0009      | 0.7852  |
| T $\times$ F $\times$ R + T $\times$ F $\times$ D $\times$ R (Error e) | 54 | 0.0012      |         |

characterized by multiple growth flushes, such as loblolly pine (Dougherty et al. 1994), photosynthate exported from terminal shoots is partitioned acropetally for the growth of subsequent shoots produced in the current growing season (Rangnecker et al. 1969, Dickson 1986, Dickson 1991). Although self-sufficiency of the first flush allows the basipetal partitioning of photosynthate produced by the previous year's foliage (Dickson 1989), the limited photosynthetic capacity of this tissue relative to new mature foliage (Chung and Barnes 1980) suggests that this photosynthate is not a significant source of energy for root growth.

Fertilization greatly increased first flush internode and needle fascicle expansion in the upper crown. Thus, in response to

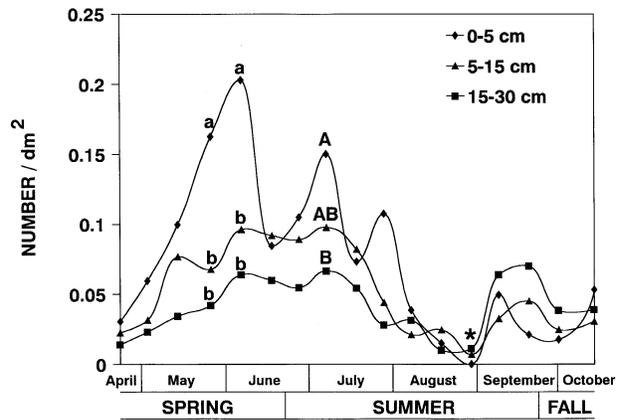


Figure 4. Mean number of roots  $\text{dm}^{-2}$  initiated at 0–5, 5–15 and 15–30 cm in rhizotrons during April through September 1993. Within measurement intervals, means associated with the same letter are not significantly different by the LSD test at  $P < 0.05$  (lower case), and  $P < 0.10$  (upper case). The asterisk between August and September data denotes: 0–5 cm (b), 5–15 cm (ab) and 15–30 cm (a).

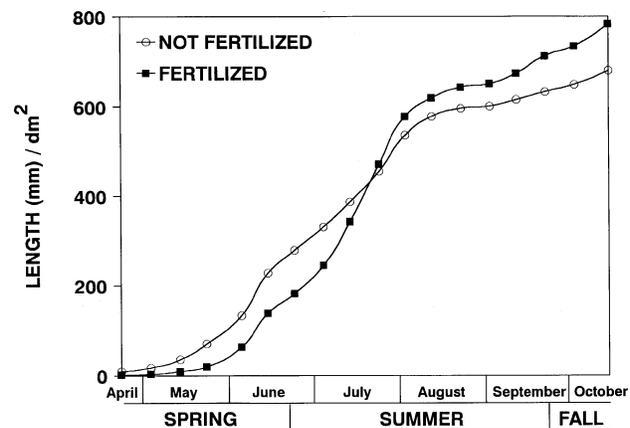


Figure 5. Root length (mm)  $\text{dm}^{-2}$  that accumulated in rhizotrons at 0–30 cm in response to fertilization during April through September 1993.

fertilization, the amount of photosynthate exported for the growth of the second flush may have been increased. Although not significant, we found that, at the end of the growing season, second flush internodes and needle fascicles in the upper crown of fertilized trees were 59 and 13% longer, respectively, than those of nonfertilized trees.

Fertilization also increased needle fascicle expansion in the lower crown. Thus, by mid-June when needle fascicles were 75% expanded, fertilization had caused a 26% increase in first flush needle fascicle expansion in the lower crown. At this time, a second flush had not occurred in the lower crown of the fertilized trees but had begun in the lower crown of 13% of the nonfertilized trees. During active growth, a larger proportion of the carbon fixed by branches in the lower crown is translocated basipetally compared with that fixed by branches in the upper crown (Watson and Casper 1984, Dickson 1986). We

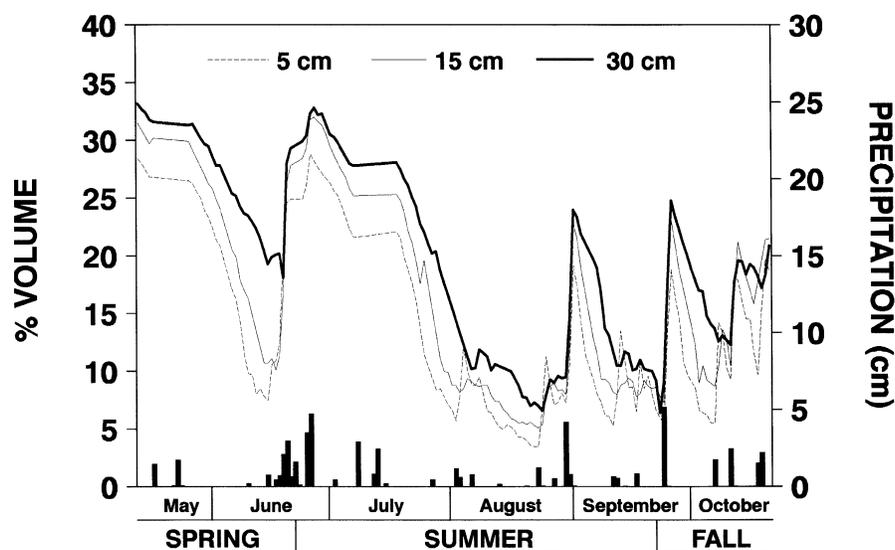


Figure 6. Precipitation (cm) and mean daily soil water content (% volume) at 5, 15 and 30 cm at one location in one control plot (no fertilization).

hypothesize that, on the fertilized plots, a greater amount of photosynthesizing tissue and a lack of acropetal photosynthate transport in the lower crown increased the amount of carbohydrate partitioned to the root system, and stimulated root growth during the second half of the growing season.

The growth of the nonfertilized loblolly pine was limited by site fertility (Haywood 1994). Foliar mineral nutrient concentrations on plots that were not fertilized indicated that tree height and diameter would respond positively to nitrogen and phosphorus fertilization (Shoulders and Tiarks 1983, Gravatt 1994). A stronger third flush occurred in the upper crown of nonfertilized trees compared with fertilized trees. A third flush in the lower crown and a fourth flush in the upper crown were observed on nonfertilized trees, but not on fertilized trees. Although not detected in our root growth data, this episodic pattern of growth is indicative of a feedback loop between above- and belowground growth processes that is triggered to reduce resource limitations (Geiger and Servaites 1991).

If temperatures are not limiting, root growth begins before branch internode expansion using current photosynthate and sugars that are mobilized from stored starch (Dickson 1989). In our study, with the exception of lateral root elongation in spring, root and branch growth were generally stimulated by fertilization. Although mineral nutrient limitations were evident, high rates of photosynthesis were consistently observed in the nonfertilized trees throughout the growing season (Gravatt 1994). With correspondingly lower rates of root and branch growth, more photosynthate may have been partitioned to starch in the nonfertilized trees than in the fertilized trees. A subsequent increase in the availability and mobilization of starch for root metabolism at the beginning of the growing season provides one explanation for the greater spring root growth that we observed in nonfertilized trees compared with fertilized trees.

Root growth differed by soil depth as the growing season progressed. In spring and early summer, root initiation at 0–5 cm was greater than at 5–15 and 15–30 cm. However, in

late summer, root initiation at 15–30 cm was greater than that at 0–5 cm. The change in the relationship between root growth and soil depth during the growing season was related to seasonal trends in soil water content. For example, a 59% decrease in soil water content that occurred in late spring was associated with a 58% reduction in root initiation in the 0–5 cm soil layer, whereas root initiation in the 5–15 and 15–30 cm soil depths was unaffected.

In midsummer, a severe 8-week period of water deficit caused a 94% reduction in root initiation at all soil depths studied. Although water availability was greatly reduced at all measured depths during the drought, soil water content was slightly higher at 30 cm than at 5 or 15 cm. Root initiation resumed with the occurrence of precipitation in early September resulting in a positive relationship between soil depth and root initiation. We suggest that increased water availability deep in the soil profile reduced drought-induced root mortality and that roots present in the deep portion of the soil profile were the primary source of parent roots from which new roots were initiated in late summer and fall.

We conclude that new root growth of young loblolly pine is closely linked to branch phenology and growth and, therefore, to sink activity in the crown. Although fertilization increased foliage production, it reduced the initiation of multiple flushes, especially in the lower crown. Together, these factors may have increased the basipetal transport of photosynthate after maturation of the first flush of needle fascicles, and thereby stimulated root growth. Early in the growing season, root growth was greater in the upper portion than in the lower portion of the soil profile, but this relationship was reversed at the end of the growing season. Similarity between the patterns of soil water content and root growth indicate that water deficit severely inhibited root activity. Thus, as water became more limiting and was attained only at increased soil depth, root initiation deeper in the soil profile became critical for the continued production of new roots.

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