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Seasonal development of loblolly pine lateral roots in response to stand density and fertilization

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Abstract

In 1989, two levels each of stand density and fertilization treatments were factorially established in a 9-year-old loblolly pine plantation on a P-deficient Gulf Coastal Plain site in Rapides Parish, Louisiana, USA. In 199.5, a second thinning was conducted on the previously thinned plots and fertilizer was re-applied to the previously fertilized plots. The morphology of new long lateral roots was evaluated at 2-week intervals in five Plexiglas rhizotrons per plot of two replications. The overall objective of this study was to evaluate the seasonal initiation of six morphological categories of long lateral roots ($\geq$ 2.5 cm in length) in response to stand density and fertilization. Lateral root development exhibited a seasonal pattern with the initiation of branched lateral roots predominantly occurring in spring and summer. The initiation of non-branchedlateral roots occurred throughout the year regardless of season. Stand density did not affect lateral root morphological development. However, fertilization stimulated the initiation of branched lateral roots that were greater than 1 mm in diameter.

Introduction

Newly elongated roots that develop a vascular cambium and secondary vascular tissues persist in the soil and enlarge the infrastructure from which additional roots initiate (Coutts, 1983). With the proliferation of long lateral root branches and ectomycorrhizae, root system surface absorbing area increases (Eissenstat and Van Rees, 1994; Lynch, 1995). In resource-limiting environments, expansion of the root system infrastructure and surface absorbing area into unexplored soil insures the supply of water and mineral nutrients to forest trees (Eissenstat and Van Rees, 1994).

Forest management activities such as thinning and fertilization affect the growth of tree root systems (Haynes and Gower, 1995; Santantonio and Santantonio, 1987; Sword et al., 1996; Sword et al., in press). These silvicultural tools could be used to manipulate root system development and therefore, resource acquisition. The objectives of this study were to: (1) examine the seasonal initiation of lateral roots that differ in diameter and degree of branching, and (2) evaluate the response of seasonal lateral root development to stand density and fertilization in a 15-year-old loblolly pine (*Pinus taeda* L.) plantation. It was hypothesized that the morphological development of newly elongated lateral roots is seasonal, and is affected by silvicultural treatments that influence growth regulator and carbohydrate relations.

Materials and methods

The study is located on the Palustris Experimental Forest in Rapides Parish, Louisiana, USA, on a P-deficient Beauregard silt loam soil (fine-silty, silicous, thermic, Plinthaquic Paleudult) (Kerr et al., 1980). Three replications of stand density and fertilization treatments were factorially established in a uniformly-stocked 9-year-old loblolly pine plantation that was originally planted at a 1.83 x 1.83-m spacing. Levels of stand density treatment were either maintenance of the original stocking (2732 trees ha-‘), or removal of alternate

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rows and every other tree in residual rows in November 1988 (736 trees ha-‘). Levels of fertilization treatment were either no fertilization or broadcast application of 747 kg ha-’ diammonium phosphate (150 kg P + 135 kg N ha-‘) in April 1989. The fertilization rate was based on recommendations for loblolly pine grown on the nutrient-poor soil in this study (Kerr et al., 1980; Shoulders and Tiarks, 1983). Understory vegetation was minimized throughout the duration of this study by the application of herbicides as needed.

In December 1994, mean stand basal areas of the non-thinned and thinned plots were 42 and 25 m^2 ha-‘, respectively. In March 1995, a second thinning was conducted on the previously thinned plots so that 15.6 m^2 ha-’ of basal area remained. Plots were selectively thinned so that residual trees were evenly spaced and their crowns were released on at least one side. Foliar mineral nutrient concentrations in 1994 indicated that the trees would respond positively to fertilization with N, P and K (Gravatt, 1994; Shoulders and Tiarks, 1983). In March 1995, 444, 248 and 100 kg ha^{-1} of urea, triple super phosphate and potash (200 kg N + 50 kg P + 50 kg K ha-‘) were broadcast on the previously fertilized plots, respectively. Fertilization rates were based on fertilizer recommendations for loblolly pine (Shoulders and Tiarks, 1983).

Two replications were chosen as blocks for the intensive measurement of long lateral root development. Vertical Plexiglas rhizotrons (0.3 x 35.4 x 76 cm) were established at five interior locations per plot (Sword et al., in press). At 2-week intervals between April and December 1995, new long lateral root growth was traced with a permanent marker onto heavy-duty acetate sheets attached to the left and right side of rhizotrons. Two weeks after initiation, four to eight independently appearing new roots ($\geq$2.5 cm in length) at 0–15 and 15-30 cm depths on each acetate sheet were placed in one of either six morphological, or two non-morphological categories. Categories were: (1) $\leq$ 1 mm in diameter, no lateral root branches, (2) >1 mm in diameter, no lateral root branches, (3) $\leq$1 mm in diameter with long lateral root branches, (4) > 1 mm in diameter with long lateral root branches, (5) $\leq$ 1 mm in diameter with short plus long lateral root branches, (6) $\leq$1 mm in diameter with short lateral root branches, (7) appearing dormant or senescent, and (8) obscured from view. Non-mycorrhizal short roots and ectomycorrhizae were classified as short lateral roots.

The fractions of new lateral roots placed in categories 1 through 6 were transformed to arcsin of the square root values. Transformed data were subjected to analyses of variance using a randomized complete block, split-plot in space and time design with two blocks. Whole plots were soil depth and subplots were measurement intervals and levels of stand density and fertilization. Data were subjected to analyses of variance by measurement interval to explain significant main and interaction effects. Main and interaction effects were considered significant at $P \leq 0.05$ unless otherwise noted.

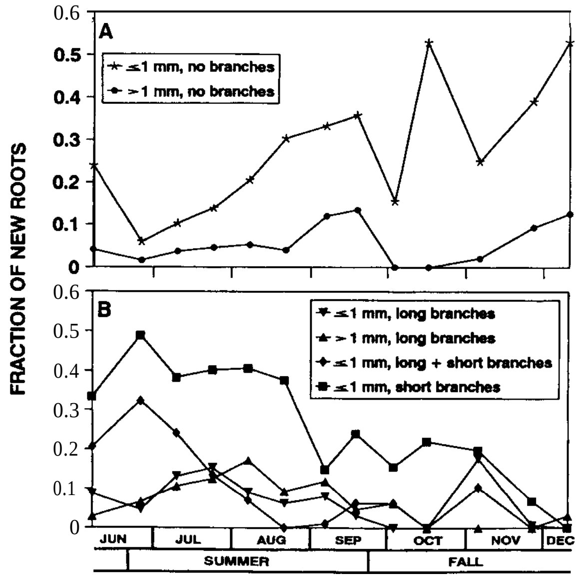

Figure 1. Fraction of new loblolly pine long lateral roots observed in rhizotrons in each of six morphological categories between June and December 1995 at age 15 [(A) non-branched long lateral roots; (B) branched long lateral roots].

Results

The fraction of new roots that developed into long lateral roots that were either $\leq$ 1 mm, or > Imm in diameter and not branched was not significantly affected by measurement interval, stand density or fertilization. The fraction of new roots that developed into long lateral roots that were branched and either $\leq$1 mm, or > 1 mm in diameter was significantly affected by measurement interval (Table 1). Analyses of variance by measurement interval indicated that the proportion of newly elongated roots that were $\leq$1 mm in diameter with short root branches was greater in June through August than in September through mid-December (Figure 1). Roots that were $\leq$1 mm in diameter with long lateral root branches responded similarly with an additional

Table I. Probability of a greater F-value for the main and interaction treatment effects in the analyses of variance of the transformed fraction of new roots ($\geq$2.5 cm in length) in rhizotrons that developed into each of four morphological categories of branched long lateral roots during April through December 1995 in a 15-year-old loblolly pine stand

Source	df	Morphological category			
		(3) $\leq$ 1 mm, long laterals	(4) $>$1 mm, long laterals	(5) $\leq$ 1 mm, long+short laterals	(6) $\leq$ 1 mm, short laterals
Block (R)	1	0.7853	0.6672	0.1581	0.7670
Soil Depth (D)	1	0.8117	0.2082	0.0522	0.5 158
Stand density (S)	1	0.1556	0.6244	0.0881	0.9512
Fertilization (F)	1	0.2440	0.0558	0.1752	0.9756
S×F	1	0.8233	0.8372	0.1169	0.9294
S×D	1	0.8269	0.6470	0.6258	0.6692
F×D	1	0.8071	0.2904	0.3564	0.3579
S×F×D	1	0.7442	0.8710	0.1052	0.2756
Measurement interval (T)	12	0.0008	0.0046	0.0030	0.0017
T×D	12	0.8792	0.6295	0.3647	0.378 1
S×T	12	0.8509	0.4260	0.4260	0.4804
F×T	12	0.1287	05922	0.5922	0.06 13
S×F×T	12	0.9648	0.7386	0.7386	0.7089
S×D×T	12	0.6512	0.8228	0.8228	0.1896
F×D×T	12	0.4686	0.7833	0.7833	0.4508
S×F×D×T	12	0.4043	0.1336	0.1336	0.7340

increase in early November. A greater proportion of new roots developed into long lateral roots that were $\leq$ 1 mm in diameter with short plus long lateral root branches in June through July than in August through mid-December. The fraction of new roots that were $>$ l mm in diameter with long lateral root branches was greater in July through mid-August than in June or between mid-August and mid-December.

The fraction of new roots that developed into long lateral roots that were either $\leq$1 mm, or $>$1 mm in diameter and branched was not significantly affected by stand density (Table 1). However, fertilization significantly increased the fraction of newly elongated roots that developed into long lateral roots that were $>$ 1 mm in diameter with long lateral root branches (P = 0.0558) (Figure 2). The initiation of branched roots that were $\leq$1 mm in diameter was not significantly affected by fertilization.

The fraction of roots that developed into long lateral roots with short plus long lateral root branches was significantly greater (105%) at the O-15 cm depth than at the 15-30 cm depth (P = 0.0522) (Table 1). The initiation of other lateral root morphological categories was not significantly affected by soil depth.

Discussion

The results of this study indicate that loblolly pine lateral root morphological development is characterized by a seasonal pattern with the formation of branched long lateral roots predominately occurring when loblolly pine produces multiple branch flushes (Dougherty et al., 1994). Since the formation and elongation of lateral root primordia is controlled, in part, by growth regulator and carbohydrate relations that are governed by shoot development (Charlton, 1996; Coutts, 1987), branch phenology and growth may strongly affect loblolly pine lateral root branching.

Silvicultural treatments such as thinning and fertilization manipulate crown structure and leaf area (Brix, 1981; Teskey et al., 1994; Vose and Allen, 1988) and

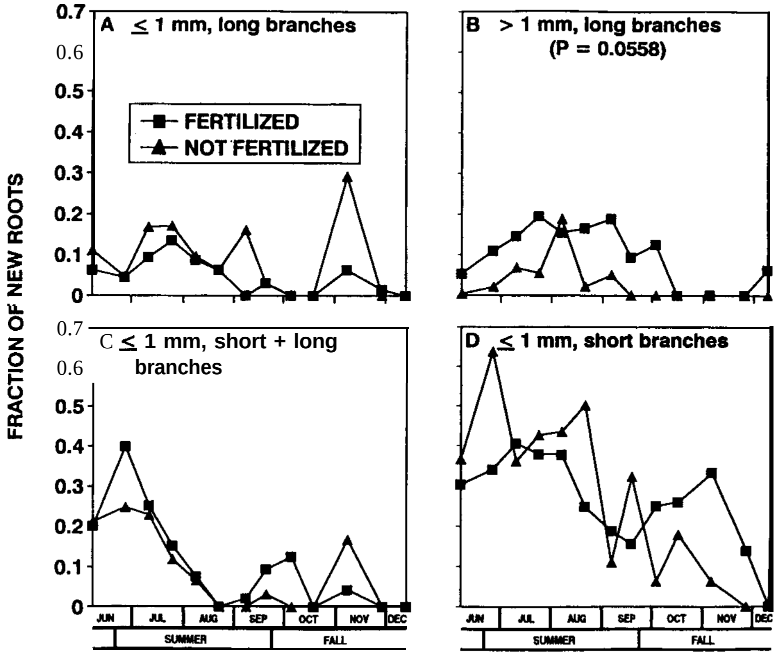

Figure 2. Fraction of new, branched loblolly pine long lateral roots observed in rhizotrons between June and December 1995, in response to no fertilization, or broadcast application of N and P at age 9, and N, P and K at age 15 [(A) ≤ 1 mm in diameter with long lateral root branches; (B) > 1 mm in diameter with long lateral root branches; (C) ≤ 1 mm in diameter with short plus long lateral root branches; (D) ≤ 1 mm in diameter with short lateral root branches].

therefore, growth regulator and carbohydrate relations. In the present study, fertilization resulted in an increase in the proportion of newly elongated lateral roots that were branched and > 1 mm in diameter. However, the initiation of branched roots that were ≤ 1 mm in diameter was not affected by fertilization. A similar effect of fertilization on the proportion of fine roots within specific diameter classes was reported by Gower et al. (1992). Fertilization of 50-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) was associated with a decrease in fine root net primary productivity, but an increase in the proportion of root biomass composed of roots that were > 2 ≤5 mm in diameter when compared to roots that were ≤2 mm in diameter. In the present study and that of Gower, foliage production was stimulated in response to fertilization (Gower et al., 1992; Sword et al., 1996). Increasesin thediameter of lateral roots may have been caused by a fertilizer-induced increase in leaf area, carbon fixation and root carbohydrate availability.

It has been hypothesized that after forest fertilization, fewer fine roots are required for mineral nutrient acquisition (Eissenstat and Van Rees, 1994; Gower et al., 1992; Haynes and Gower, 1995). With an increase in resource availability, a shift in carbon allocation away from fine root production and toward above-ground growth occurs (Eissenstat and Van Rees, 1994; Gower et al., 1992; Haynes and Gower, 1995; Keyes and Grier, 1981; Vogt et al., 1983). In the present study, a greater proportion of branched lateral roots that were > 1 mm in diameter was initiated in response to fertilization when compared to the proportion of branched lateral roots that were ≤ 1 mm in diameter. Since root morphology affects root function (Eissenstat and Van Rees, 1994), the purpose of new branched roots for either the expansion of root system infrastructure or surface absorbing area may have changed in response to fertilization. In the future, characterization of morphology among fine root diameter classes could be useful to the study of resource acquisition and carbon allocation responses to forest fertilization.

The longevity of fine roots is extended as their diameter increases. This phenomenon was demonstrated by Schoettle and Fahey (1994) who compared the fine root longevities reported among eight studies and found that fine root longevity increased with the maximum diameter used to define fine root categories. In the present study, fertilization resulted in an increase in the initiation of large, rather than small diameter branched lateral roots. Furthermore, in 1993, fertilization was associated with an increase in the persistence of lateral roots that grew in rhizotrons during an 8-week period of water deficit (Sword et al., in press). Perhaps the persistence of these roots was attributed to their larger initial diameter and resistance to desiccation in the moisture-limiting environment.

In addition to the diameter of branched, new lateral roots, loblolly pine shoot and fascicle expansion, lateral root elongation and stand productivity were greater in response to fertilization on this site (Haywood, 1994; Sword et al., 1996; Sword et al., in press). In resource-limiting environments such as the P-deficient site in this study, an increase in the production of large diameter, branched new roots, their tendency to persist as part of the root system infrastructure, and increase resource uptake may be an important mechanism by which fertilization stimulates whole tree growth and stand productivity.

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