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Morphological and anatomical relationships of loblolly pine fine roots

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Abstract Suberized or brown roots have been traditionally considered secondary or woody tissues. The validity of using morphological features such as color to infer root anatomy for southern pines is questionable and unproven. The objectives of this study were (i) to establish relationships between root color, diameter, and developmental stage (i.e., primary or secondary tissues) for loblolly pine, (ii) to determine the percentages of primary and secondary brown roots by diameter class, and (iii) to use these percentages to make first order estimates of the amount of brown root length and surface area that is in the primary and secondary developmental stages for sampled roots of a semi-mature loblolly pine stand. "Unsectioned" roots were collected by coring to a 25-cm depth 3 times a year and measuring roots for length and surface area by diameter class. "Sectioned" roots were sampled from a one-time core and from periodic grab samples. These roots were sectioned and characterized by their color, diameter and developmental stage. Diameters of sectioned roots (n=353) ranged from 0.21 to 8.24 mm. White and orange roots ranged from 0.23 to 2.50 mm, while brown roots spanned the range. White roots were developmentally primary, whereas orange/brown roots were either primary (from 0.21 to 2.50 mm), secondary (from 0.33 to 8.24 mm), or in transition (from 0.27 to 0.76). Total live root length of the sampled stands was estimated to be composed of 38% primary tissue, 58% secondary tissue, and 4% transition tissue. Lastly, neither root color nor diameter was a reliable predictor of developmental stage unless roots were white (primary), or orange/brown and >2.5 mm in diameter (secondary).

Key words Suberized · Non-woody roots · Woody roots · Brown roots

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Introduction

There is ample evidence to support the hypothesis that nutrient availability is the primary factor limiting productivity of southern pine stands on the lower coastal plain of USA (Neary et al. 1990). The use of mechanistic nutrient-uptake models and sensitivity analysis has further shown that the single most important factor determining uptake in these stands is the amount of absorbing root surface area (Van Rees et al. 1990; Kelly et al. 1992; Yanai 1994). Classification of these root surface areas into functional uptake units (e.g., primary and secondary tissues) has been frequently based on external morphological features such as root color (e.g., white roots=primary tissues) or diameter (Kramer and Bullock 1966; Chung and Kramer 1975; Sands et al. 1982). Deductive classifications such as these, however, provide little functional utility when considering water and nutrient uptake rates unless they are based on root anatomy which determines uptake characteristics.

Brown roots have been traditionally considered woody or secondary tissues (Blake and Hoogenboom 1988), and are often described as suberized (Addoms 1946; Kramer 1946; Van Rees and Comerford 1990). Suberization is an internal cellular process and may result from several conditions, including an injury or infection, or the presence of a hypodermis or periderm (Holloway and Wattendorf 1987). Moreover, the brown color commonly associated with suberized root tissues appears to be independent of the suberization process itself and also of secondary xylem development. It results from cellular death and the subsequent release and oxidation of phenolic compounds normally contained within the vacuole (Richards and Considine 1981; McKenzie and Peterson 1995).

Richards and Considine (1981) recognized the confusion created when terms such as brown, suberized, and woody are used to imprecisely or incorrectly describe root morphological and anatomical relationships. The reliability of using morphological characteristics of southern pine root systems to deduce anatomical attributes

(primary or secondary tissues) has not been proven. Consequently, relationships between root morphology and anatomy for species such as loblolly pine (*Pinus taeda* L.) remain ambiguous. This study addresses this problem through the following objectives: (i) to establish relationships between root color, diameter, and developmental stage (i.e., primary or secondary tissues) for loblolly pine, (ii) to determine the percentages of primary and secondary brown roots by diameter classs, and (iii) to use these percentages to make first order estimates of the amount of brown root length and surface area that is in the primary and secondary developmental stages for roots of a semi-mature loblolly pine stand growing in the surface soil of a Florida Spodosol. Terminology used in this paper follows the conventions of Sutton and Tinus (1983).

Materials and methods

Study site and experimental design

This field study was located 10 km north of Gainesville, Fl (29°30′N, 82°20′W). The experimental area was established in 1983, planted at a 2×4 m spacing, and consists of three replicates of a 2×2×2 factorial of species (slash vs loblolly pine), fertilization, and competition control arranged as a randomized split-plot (Swindel et al. 1988). The current investigation utilized a total of three of the plots from this study. They were the fertilized plots of loblolly pine, which received annual vegetation control (herbaceous and woody) since establishment (Colbert et al. 1990). Individual treatment plots were 0.08 ha in size and each contained a 0.03 ha measurement plot from which samples were collected.

Sample collection, processing, and measurement

Two types of root samples were collected via coring and these two types were classified as unsectioned or sectioned cores. The first type, "unsectioned" cores, was collected to quantify root length and root surface area by diameter class (for roots less than 4 mm in diameter). Roots from these cores are termed "unsectioned" roots. Measurement plots were sampled in September 1993 (Sample no. 1) and February (Sample no. 2) and June (Sample no. 3) 1994. Soil cores were extracted from the 0–15 cm (716.8 cm^3) and 15–25 cm (477.8 cm^3) depths within the bedded region of each measurement plot. A core sample was taken from each depth on each date, except in Sample no.1 when only the upper depth was sampled. Soil samples from the cores were placed in plastic bags and stored at 4°C until they were processed (within 48 h). Roots were removed from core samples by hand-washing the soil with deionized water through a series of sieves ranging from 2.0 to 0.25 mm. Washed roots were placed in deionized water and separated from the remaining debris into long and short roots. A long root is one of unlimited growth potential possessing the capacity for secondary growth, while a short root is developmentally primary and of limited growth potential.

Long roots from each unsectioned core were sorted by color (white or brown) and vitality (live, dead or unknown). The designation of dead was based on: color with black indicating a high probability of being dead; brittleness of the root, where a brittle root had a greater chance of being dead; and the appearance of a live stele, where a root with the stele missing (as seen under a dissecting microscope) was considered dead. The unknown category of long roots were all brown and comprised <1.6% of the total long root length of any individual core. All long roots (live, dead, unknown) were measured for length and diameter (both ends, using calipers). For each core, the length of live long roots was expressed as a percentage of total root length (live length/live + dead length; from 17 to 87%, μ=45.0%±21.0) and this percentage of live long roots was used to classify long roots of unknown vitality as live or dead by using the same percentage (e.g., 50% live roots × 10 cm unknown root length = 5 cm live root length). The surface area of each root was calculated as the product of root length and circumference using measured diameters. The length and surface area of each live long root was summed to give live long root length and surface area for each unsectioned core. Dead roots, both long and short, and white roots (<1.2% of the total long root length of any unsectioned core sample) were not included in root length and surface area estimates. White roots were not included simply because their numbers were so small that they had virtually no effect on the totals.

Short roots attached to long roots were excised under a dissecting microscope and classified as live or dead based on color and flexibility as described above. Unattached short roots were separated into the same categories and counted as well. Mean short root length (0.16 cm±0.12) and diameter (0.04 cm±0.03) were estimated from Samples no.1 and no.2 core samples (n=15 to 50 short roots/core) using image analysis software (JAVA 1990). Total short root length for each core is the product of short root quantity and mean short root length. Total short root surface area is the product of short root length and short root circumference (0.13 cm, using mean short root diameter).

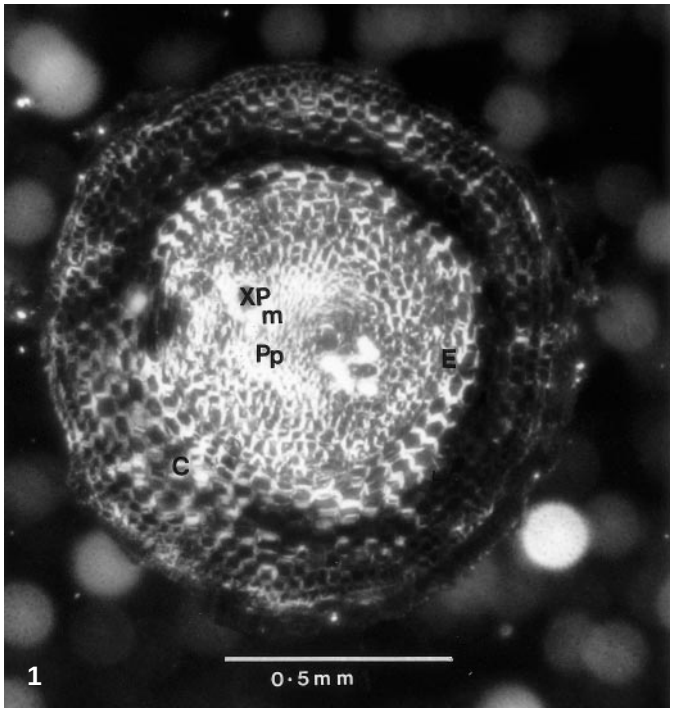
The second type of core, the "sectioned core", was collected in two ways. First, an additional soil core was extracted from the 15–25 cm depth of one plot in October 1994 for characterization of developmental stage (primary vs secondary) of all roots. Short and long roots from this core were separated using the aforementioned washing procedures, and then placed in a 2% formaldehyde/3% glutaraldehyde fixative solution for preservation. Long root length was measured to the nearest millimetre prior to sectioning. Long root surface area was estimated as before, except that diameters were measured to the nearest 0.01 mm after sectioning using image analysis software (JAVA 1990). Vitality of sectioned long roots was determined under a compound microscope as previously described. The length and surface area of each live long root was summed to give live long root length and surface area for the sectioned core.

Total short root length (live + dead) for the sectioned core was estimated using the line intersect method introduced by Newman (1966) and modified by Harris and Campbell (1989). The modified version is part of a computer program (*BranChing*, Berntson 1994) for analyzing digitized images of plant root systems. Digitized images of short roots from the sectioned core were produced by photocopying the short roots, and scanning the photocopies with a flatbed scanner. Scanned images were processed by *BranChing* (Berntson 1994). Live short root length was estimated as the product of scanned short root length and the mean percentage of live short roots (μ=17%±16.4) determined (live short roots/total short roots) from unsectioned core samples. Short root surface area was estimated as the product of live short root length and mean short root circumference (0.13 cm, using mean short root diameter).

Additional live long roots were collected individually for sectioning on 11 March, 27 June, and 15 September 1995 from the top 15 cm of soil from two of the sample plots. A total of 134 roots were collected. These roots were excavated by hand, wrapped in wet paper towels, and transported to the laboratory on ice. After washing with deionized water to remove any remaining soil, roots were placed on moist paper towels and stored in the refrigerator in plastic bags, or immediately cut into small pieces and placed in the aforementioned fixative for preservation. These roots were measured, sectioned, and characterized in the same manner as long roots from the sectioned core, and are termed "sectioned roots" as well. Sectioned roots, collected individually and from the sectioned core (October 1994 sample), were combined for data analyses except where noted.

Root sectioning

Thin sections of long roots were cut on a freezing stage or rotary microtome and permanently mounted for subsequent evaluation of



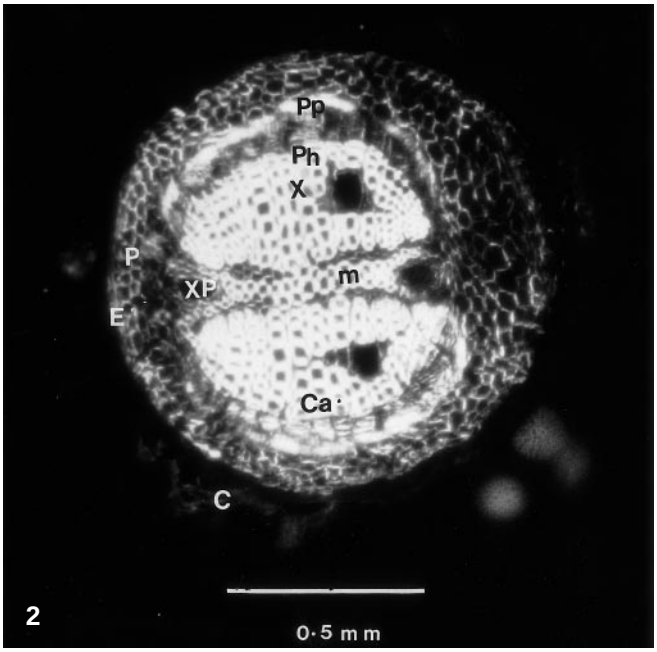


Fig. 1 Cross-section of long, brown root of loblolly pine (1.25 mm diameter) in primary stage of development (×40). (*C*, cortex; *E*, endodermis; *Pp*, protophloem; *m*, metaxylem; *XP*, xylem poles)

Fig. 2 Cross-section of long, brown root of loblolly pine (1.17 mm diameter) in secondary stage of development (×40). (*C*, cortex; *E*, endodermis; *P*, pericycle; *Pp*, protophloem; Ph, phloem; *Ca*, cambium; *X*, xylem; *m*, metaxylem; *XP*, xylem poles)

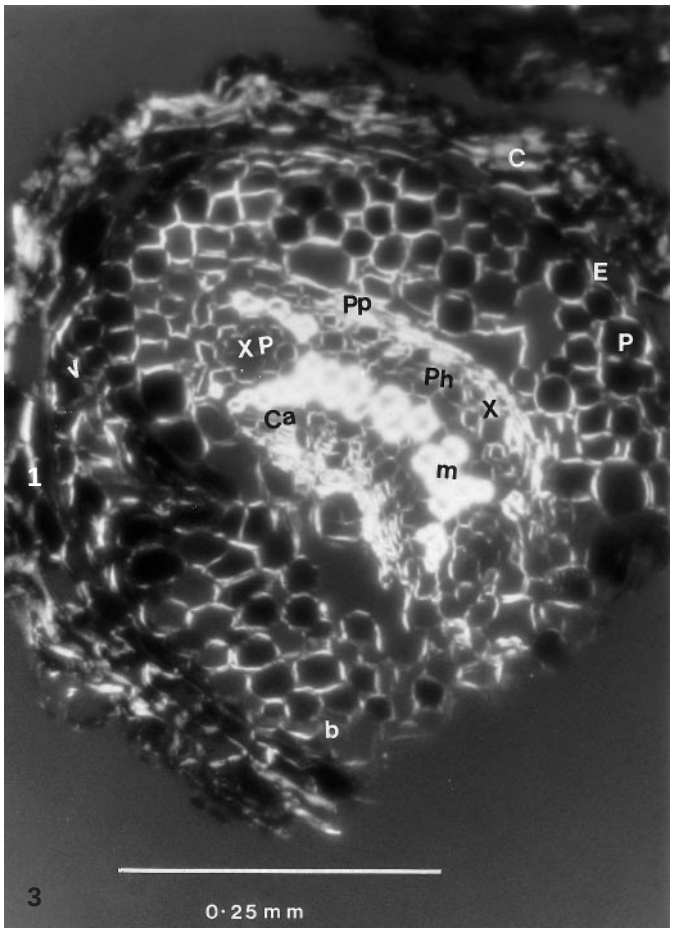


Fig. 3 Cross-section of long, brown root of loblolly pine (0.59 mm diameter) in transition between primary and secondary growth stages (×100). (*C*, cortex; *E*, endodermis; *P*, pericycle; *Pp*, protophloem; *Ph*, phloem; *Ca*, cambium; *X*, xylem; *m*, metaxylem; *XP*, xylem poles)

developmental stage. Roots cut on the rotary microtome were dehydrated in an ethanol, tertiary butyl alcohol series and embedded in paraffin (Johansen 1940). Sectioned roots were characterized based on their color (white, orange, or brown), diameter, developmental stage (primary, secondary, or transition), and cortex (intact, sloughing, or collapsed or crushed) and periderm (complete or incomplete) conditions. Root developmental stage was determined under brightfield or polarized light. Roots were considered primary (non-woody) if no vascular cambium or secondary xylem elements were present external to the centrally located metaxylem (Fig. 1). Roots with secondary xylem elements located external to the metaxylem were classified as secondary (woody) (Fig. 2). Roots with a visible vascular cambium but no secondary xylem development were considered to be in transition between primary and secondary growth stages (Fig. 3).

Data analysis

The similarity of the diameter distributions between the sectioned and unsectioned roots was assessed by plotting the percentages of live long roots by diameter class and visually comparing the sectioned roots (segregated by sampling date and depth) and the unsectioned roots.

The developmental stage and color of the sectioned roots was used to established their relationship to root diameter. These relationships were quantified using frequency (number of white, orange, and brown roots by diameter class) and percent (percentages of primary, secondary, and transition orange/brown roots by diameter class) diameter distributions (SAS 1985). Estimates of live long-root length and surface area were made by categorizing root developmental stage by diameter class. All roots from all the coring dates and depths were combined in order to have a population on which a frequency diagram could be drawn. The objective of

this study was to test if a root of a certain diameter or color had a distinct relationship to its developmental stage; not to determine if this relationship is a function of season. It was thought that this former objective was more important than the latter in that a definable relationship would add a great deal of interpretive ability to root observations in the field.

Results

Root morphology and anatomy

The diameter distribution for sectioned live long roots was similar to distributions for unsectioned live long roots (Fig. 4). The majority of sectioned (64%) and unsectioned (from 39 to 47%) roots were found in the diameter range from 0.4 to 0.6 mm. Sectioned long roots (n=353) ranged in diameter from 0.21 to 8.24 mm, with 90% <2.0 mm in diameter, and 99% <4.0 mm in diameter. For this reason roots under 4.0 mm in diameter are the focus of this study. Sectioned white (n=18) and orange (n=18) colored roots ranged in diameter from 0.23 to 2.50 mm, while brown (n=317) roots spanned the entire diameter range (Fig. 5).

As expected, all white loblolly pine roots were anatomically primary. By contrast, the anatomy of orange and brown colored roots could be either primary, secondary, or transitional between the two. More importantly, though, was the fact that the diameter distributions for primary (from 0.21 to 2.50 mm) and secondary (from 0.33 to 8.24 mm) orange/brown roots were not mutually exclusive; they were coincident over 27% of their combined diameter range (Fig. 6). Sectioned roots categorized as transitional ranged in diameter from 0.27 to 0.76 mm and were all brown as opposed to orange.

Percent diameter distributions for orange and brown colored roots <2.0 mm in diameter indicated that about 30% of these roots were anatomically primary, 62% were secondary, and the remaining 8% were in transition. These percentages changed little when the diameter

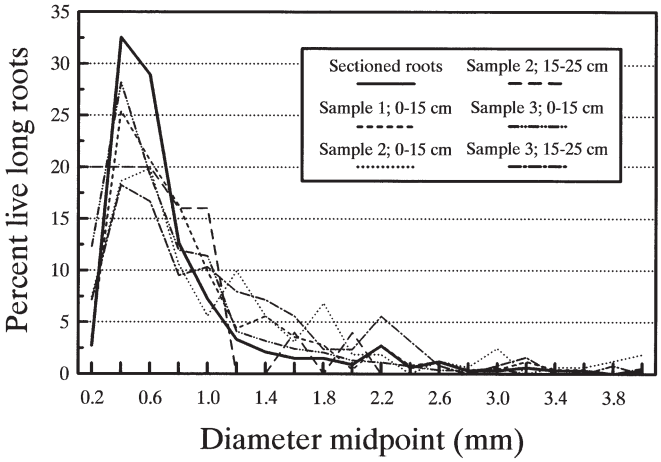


Fig. 4 Percent diameter distributions for live, long roots (orange/brown) of loblolly pine for each date and depth sampled. Sectioned roots include the October 1994 core sample and those collected individually

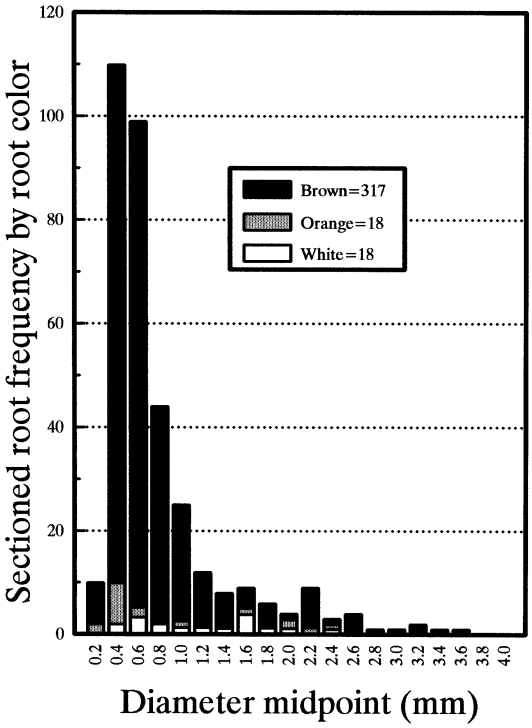


Fig. 5 Frequency diameter distribution by root color for sectioned, live, long roots of loblolly pine. Sectioned roots include the October 1994 core sample and those collected individually

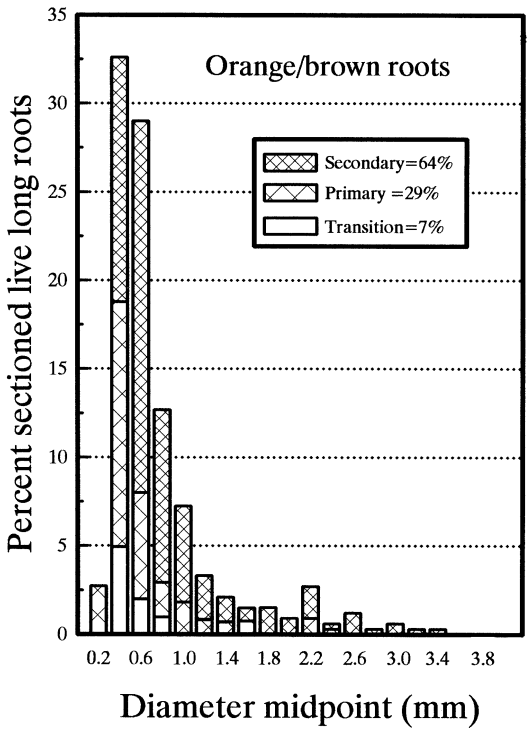


Fig. 6 Percent diameter distribution by root developmental stage (primary, secondary, and transition) for sectioned, live, long roots (orange/brown) of loblolly pine. Sectioned roots include the October 1994 core sample and those collected individually

range was extended to include orange and brown colored roots <4.0 mm in diameter (i.e., 1°=29%, 2°=64%, transition=7%; Fig. 6).

Initiation of secondary xylem growth was not always associated with periderm formation; 53% (*n*=114) of sectioned roots with secondary xylem development (*n*=215) had no visible periderm. The majority of secondary roots without a periderm (61%, *n*=69) still retained a cortex in some form, while the remainder had shed the cortex leaving only the vascular cylinder and surrounding pericycle. Development of the first formed periderm was observed in roots as small as 0.42 mm in diameter.

Root length and surface area by developmental stage

The sectioned core contained a total live root length of approximately 614 cm, which had 53% long brown roots (no white roots were present) and 47% short roots (Table 1). About 12% of the long brown roots were in the primary stage of growth, 8% were in transition to secondary growth, and the remaining 80% exhibited some degree of secondary xylem development. Total live root length of the sectioned core included 53%primary root tissue, 43% secondary root tissue, and 4% transition tissue. A majority (88%) of the primary root length was composed of short roots, with the remainder being primary brown roots. Collectively, primary root tissues contributed more to total core root length than did secondary root tissues (53 vs 43%), due mainly to the large number of short roots. The reverse was true for total core root surface area – secondary tissues contributed more than primary tissues (59 vs 37%) – and reflects the influence of the greater diameter of long versus short roots.

Estimated percent root length and surface area by root type and developmental stage for the unsectioned core samples are shown in Table 2. Mean values (combining all dates and depths) indicate that 23% of the long, root length in these samples was developmentally primary long roots, 58% was secondary, and 4% was in transition. The length of short roots accounts for the remaining 15%. Differences in tissue type percentages between the sectioned (Table 1) and unsectioned core samples primarily reflect the greater number of short roots found in the sectioned core. It is not known why this difference occurred. Short roots from the sectioned core accounted for 47% of the total live root length and 88% of the primary root length, while for the unsectioned cores they comprised 15% of the total live root length and 39% of the primary root length.

Table 1 Live root length and surface area by root type (short and long) and root developmental stage (primary, secondary, transition) for orange/brown roots less than 4 mm in diameter. These roots are from the sectioned core taken in October 1994. (*%Total* represents the percent contribution of each tissue type (primary, secondary, transition) to total core root length and surface area, *NA* not applicable, and *Core total*, total core root length and surface area)

Developmental Stage	Root length		Root surface area		% Total	
	Short (cm)	Long (cm)	Short (cm^2)	Long (cm^2)	Length	Surface Area
Primary	287	40	37	6	53	37
Secondary	NA	261	NA	68	43	59
Transition	NA	26	NA	4	4	3
Total	287	327	37	78	NA	NA
Core total	614		115			

Discussion

The main objective of this study was to evaluate the ability to identify the developmental stage of a root less than 4 mm in diameter based on its morphology (diameter or color). This, combined with a better understanding of root nutrient uptake function based on developmental stage, should improve the predictive ability of current nutrient uptake models by allowing us to more accurately define effective root length or surface area.

This study clearly showed that no useful qualitative relationship exists between root color and diameter for loblolly pine roots <2.5 mm in diameter. White, orange, and brown colored roots occurred simultaneously in most diameter classes <2.5 mm, while all roots >2.5 mm

Table 2 Estimated live root length and surface area by root type (short and long) and root developmental stage (primary, secondary, transition) for each date and depth sampled. Estimates were made by applying the proportions of primary, secondary and transition developmental stage from sectioned root data (from both the October '94 core and the individually collected roots) to the root type categories in the unsectioned core data. (Depth: 1=0-15 cm, 2=15–25 cm; Depth 2 was not sampled in September 1991)

Date	Depth[a]	Root length				Root surface area			
		Primary		Secondary	Transition	Primary		Secondary	Transition
		Short (cm)	Long (cm)	(cm)	(cm)	Short (cm^2)	Long (cm^2)	(cm^2)	(cm^2)
September 1991	1	232	285	771	53	26	81	294	9
February 1992	1	91	168	514	30	11	41	230	5
	2	18	41	64	6	2	7	17	1
June 1992	1	273	459	1080	88	32	108	383	14
	2	54	115	277	13	6	42	128	2

were brown. The possibility of finding white roots with diameters greater than 2.5 mm cannot, however, be eliminated; white roots emerging from the tips of brown roots were often observed to have diameters exceeding those of the parent root. Root color was a reliable predictor of root developmental stage only for white roots (primary) and for orange/ brown with a diameter >2.5 mm (secondary). The developmental stage of the vast majority of long roots could not be predicted based on color. Richards and Considine (1981) found that the brown color of primary grapevine roots was associated with either a suberized hypodermis, or the breakdown of cortical cells on an otherwise healthy white root. The latter has been observed for roots of *Malus* (Head 1967) and *Prunus* (Bhar et al. 1970) as well. The color of primary roots of loblolly pine also appears to be related to the vitality of the cortical tissues; 84% of the primary brown roots had a cortex that was crushed or collapsed, or was in the process of shedding, while 78% of white roots had an intact cortex. These observations lend support to the presumption that, upon epidermal or cortical cell death, the release and oxidation of phenols normally enclosed within the cell vacuole results in a brown coloration of the root surface (Richards and Considine 1981). McKenzie and Peterson (1994) also found that, while suberin was associated with white and brown roots, tannin was only associated with brown roots whose cortex had collapsed.

While it is not possible to measure the primary and secondary root length and surface area of this study's unsectioned roots based on their morphology, one can use the proportion of roots in different developmental stages within diameter classes (based on the sectioned roots) to estimate these values. However, these estimates, as presented in Table 2 require consideration of the limitations of the data used to derive them. It can be argued that the characterization of the developmental stage of only a small number of roots relative to the total number sampled limits the usefulness of the estimates, and this is a valid concern. We believe, however, that the close correspondence between percent diameter distributions for sectioned and unsectioned roots indicates that the sectioned roots accurately reflect root system composition for this site at the current stage of stand development.

Although the specific role and effectiveness of woody tree roots in water and nutrient uptake is still uncertain, it is apparent from this and other cited studies that secondary root tissues constitute a majority (from 62 to 80%; Table 2) of the surface area of long roots, at least for loblolly pine. The importance of woody roots in nutrient uptake, as reviewed by Comerford et al. (1994), is poorly documented. However, evidence suggests that they do have a function in uptake and that while their rates of uptake are probably lower than white roots, they could represent a significant amount of uptake simply based on their amount. These statements are not meant to underestimate the role of short roots and extramatrical hyphae of mycorrhizae, but only to express the potential importance of woody roots. The significance of these results for woody tree species is that secondary root tissues, due to their abundance, likely play a significant role in water or nutrient uptake, or both.

The results of this study have several implications. First, the common assumption that all brown loblolly pine roots are developmentally secondary (woody) is incorrect, and is likely false for other pine species as well. Research efforts attempting to quantify the non-woody and woody portions of a root system using root color or diameter as discriminators of the two, should consider the fact that some percentage of the smaller diameter brown roots will be developmentally primary. Likewise, future water and nutrient uptake studies should not rely on root color alone to accurately identify primary and secondary tissues. More reliable anatomical methods should be used instead. Second, modeling efforts which have estimated rates of water and nutrient uptake for woody roots may need to be reexamined. Depending on the methods used to identify and separate woody and non-woody roots, calculated rates of uptake may not exclusively represent the woody portion of the root system. Lastly, investigators should avoid the use of ambiguous terminology when relating the surface morphology of roots to their developmental stage. Use of the word suberized to denote root developmental stage is confusing and incorrect, and should be avoided. The terms primary and secondary are preferable.

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