ABSTRACT

Emilie S. Kane. SWAMP FOREST ROOT SYSTEMS: BIOMASS DISTRIBUTION, NUTRIENT CONTENT, AND ASPECTS OF GROWTH AND MORTALITY (Under the direction of Mark M. Brinson) Department of Biology, November 1981.

Lateral root biomass distribution and nutrient content were studied in an alluvial swamp forest and a headwater stream swamp forest in the Coastal Plain of North Carolina. Lateral root biomass to 40 cm depth was estimated to be 2345 $g \cdot m^{-2}$ in the alluvial swamp and 2702 $g \cdot m^{-2}$ in the headwater swamp, from excavations of 0.125 m^2 soil pits removed in 10 cm increments. Root biomass increased with depth in the alluvial swamp forest due to increasing contributions of large diameter roots while fine root (<2 mm diameter) biomass was distributed equally throughout the soil profile. This trend is in contrast to lateral root biomass distribution in the headwater swamp forest, where biomass was concentrated in the upper soil layers (to 20 cm) and decreased rapidly with greater depth.

Concentrations of N, P, K, Ca, Mg, Na and Fe were found to vary with root diameter and depth in both swamps, with N concentrations decreasing with increasing root diameter, probably reflecting the greater proportion of metabolically active tissue in finer roots. Total P concentrations were greater in roots of the alluvial swamp, possibly related to the abundance of P in floodwaters and sediments. Concentrations of K, Ca, Mg and Na varied with site, size class of roots, and depth, but failed to show consistent trends. Both root

biomass and stocks of N, P, K, Ca, Mg and Na were within the range of values for other forested ecosystems. However, Fe concentrations and stocks of Fe per unit area of swamp floor in both swamps were severalfold higher than for upland forests, suggesting precipitation of the Fe abundant in swamp waters and sediments on root surfaces, a possible consequence of cambial oxygen transport in flood-tolerant species.

Attempts were made to estimate mortality and production of roots. Counts of roots in cross sections of soil blocks, and correlation of root diameter with growth rings, suggest that about 85% of fine roots die within a one year interval. Observations of fine root growth in water tupelo (<u>Nyssa aquatica</u> L.) seedlings showed that opposing processes of growth and mortality were taking place simultaneously at different rates and that a net change in visible root length reflected only a fraction of the actual production of fine roots. Application of estimated fine root turnover rates to organic matter and nutrient stocks of roots per unit area of swamp floor suggests that fine root turnover contributes annually from two to nine times the quantities of organic matter and nutrients returned by aboveground litterfall to the soil. These results lend support to the theory of rapid fine root turnover and underscore the potential importance of roots in biogeochemical cycling.

SWAMP FOREST ROOT SYSTEMS:
BIOMASS DISTRIBUTION, NUTRIENT CONTENT, AND ASPECTS OF GROWTH AND MORTALITY

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Emilie S. Kane
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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Root uptake represents the major pathway by which the essential nutrient elements in the inorganic world are introduced into most higher forms of terrestrial life (Epstein 1977). Only recently has attention begun to focus on the role of roots in ecosystem processes. The importance of death and decomposition of fallen aboveground components such as leaves and branches in mineralization of nutrients and their return to the soil has long been recognized; interest in the contributions of roots to such processes is increasing. Recent evidence from a wide variety of ecosystems indicates that a large portion of root systems is replaced annually through normal processes of death and sloughing, especially of fine roots (Caldwell 1979). The potential importance of root contributions in returns of materials to the soil through sloughing and other processes such as exudation, leaching, and microbial activity justifies substantial investigation of the standing crop, nutrient content, and dynamics of the belowground system.

The ultimate aim of much recent work on roots has been to establish the magnitude of root production--the process of synthesis of new root material. Production is especially difficult to determine in underground parts because of their obscurity and inaccessibility. Thus many researchers have attempted to employ indirect methods of determining production whenever possible (Lieth 1968). One of the indirect methods used has been based on differences in measurements of standing crop over time, in which production has been equated with increments in biomass. Another method is based on the unverified assumption (Newbould 1968) that the ratio between aboveground and belowground biomass is equal to the ratio between aboveground and belowground production. Theoretically, if aboveground and belowground biomass and aboveground production are known, belowground production can be calculated.

The objective of this study on the root component of wetland forests was to obtain information on a poorly understood part of these important southeastern ecosytems. Although various studies have documented the quantity, distribution, and nutrient content of roots of upland forests, the unique physical and chemical characteristics of flooded soils necessitate separate investigations for wetland forests. The study consists of two parts. The first part involves measuring root biomass and its distribution and nutrient content in two swamp forests which represent general types of swamp forests in the Coastal Plain of North Carolina. This information provides a basis for comparison with other forested ecosystems. The second part of the study is a review of some of the methods which have been used in estimating root production generally and in forested ecosystems in particular, and an exploration of two approaches to deter--mining root production. The purpose of the second section is to evaluate the validity and feasibility of various approaches and to identify some of the components and processes of production in roots, as well as to provide an indication of the potential magnitude of the organic matter contribution of roots and their place in nutrient cycling.

Root Biomass Studies on Upland Forests

Studies of the rhizosphere of upland forests suggest that tree root penetration generally is limited to a comparatively shallow upper layer (<1 m) of soil (Hermann 1977). Concentration of biomass, particularly for fine roots, tends to be greatest close to the surface of the soil and to decrease with increasing depth (Kramer and Kozlowski 1960, Moir and Bachelard 1969, Harris et al. 1977, Montague and Day 1980). Environmental conditions such as depth of water table and soil compaction and texture have been shown to affect root penetration and distribution (White et al. 1971, Harris et al. 1977) and may override species differences in rooting morphology. Increased density of fine roots has been demonstrated in nutrient-rich strata of the soil horizon (Lyr and Hoffmann 1967). In upland forests, the concentration of absorbing roots observed close to the surface of the soil may reflect favorable aeration and nutrient conditions at this level. Oxygen-requiring root processes of growth, metabolism and uptake of materials are favored by aerated conditions while nutrient capture is enhanced by the proximity of fine absorbing roots to sites of element release in decomposing detritus.

Features of Wetland Substrates

Because of periodic submergence, sediment deposition, and persistent anaerobic conditions, the substrate of wetlands may differ physically and chemically from that of upland forests. Ponnamperuma (1972) notes that submergence of soils results in loss of molecular oxygen except for the presence of a thin oxidized layer at the soil-water interface when the overlying water is aerated. Consequent lowering of redox potentials affects not only the availability of oxygen to plant roots but the form of nutrients in the soil. In addition, the presence of an oxidized layer at the soil-water interface can act as a seal to prevent the exchange of nutrients, particularly phosphorus, with the water column above and thus inhibit nutrient release from the substrate.

The origins of alluvial soil and upland soils account for many of their observed differences. Soil formation in alluvial wetlands is largely a product of flood deposition of sediment carried by streams while typical upland soils result from processes of physical and chemical weathering of parent material. As deposition occurs in floodplains, the accumulation of organic matter in the soft sediments may be favored by lowered decomposition rates, resulting in lower bulk density and relative instability of the substrate of the wetland.

Belowground Studies of Wetlands

The unique chemical and physical nature of wetlands imposes a different set of stresses on plants than upland conditions, including anaerobiosis, excesses of potentially toxic substances (hydrogen sulfide and heavy metals), and substrate instability. Differences between upland and wetland ecosystems in root growth patterns, distribution, and nutrient content may be expected to occur.

Information about the belowground component of wetlands has for the most part been confined to marshes. Valiela et al. (1976) and de la Cruz and Hackney (1977) found that belowground biomass and production in salt marshes is at least as high or higher than aboveground and takes place mostly in the upper 20-25 cm of sediment. The few belowground studies of forested wetlands which have been conducted include those of Montague and Day (1980) in the Great Dismal Swamp and Lugo et al. (1978) and Burns (1978) in Florida cypress stands. Burns found that 90% of roots in the stand were present in the top 30 cm of soil, and that production of roots was significantly less in a site with artificially increased drainage. Montague and Day found that 80% of roots in a seasonally flooded maple-gum community and 76% of roots in an extensively flooded cypress community in the Dismal Swamp were located in the upper 30 cm of soil and that root biomass decreased with depth. They suggested that anaerobic conditions brought about by moderate to poor drainage in these two stands favored the development of shallow root systems, and hypothesized that the pattern of distribution of decreasing root biomass with depth may be typical of lateral root systems in general.

Methods of Determining Root Production in Forests

Determining production of roots is important to estimates of organic matter and nutrient turnover in roots and root contributions to soil and ecosystem budgets, yet has presented a fairly intractable problem. In their natural environment roots are mostly invisible and attempts to observe them or make them accessible may result in changes in the natural environment with consequent effects on root growth and behavior. Standing crop biomass at any one time is not necessarily the same as biomass present at other times of the year and gives no indication of dynamics of root growth. Even if periodic measurements show a nearly constant root biomass, this reveals only that processes of growth and mortality are approximately equal without any indication of their magnitude. Methods for estimating root production have included measurement of periodic changes in root biomass obtained from core samples of soil and roots, growth of roots into various kinds of substrates, and visual observations of root elongation in transparent chambers or containers.

By periodic core sampling in a yellow poplar (*Liriodendron tulipifera* L.) forest in Tennessee, Edwards and Harris (1977) found that biomass of <5 mm diameter roots exhibited large seasonal fluctuations, whereas biomass of roots >5 mm in diameter remained relatively constant over a year. By summing the differences between seasonal maxima and minima of <5 mm roots, Cox et al. (1977) estimated the production of this size class to be 750 $g \cdot m^{-2} \cdot yr^{-1}$. Harris et al. (1977), using similar core sampling methods, estimated that a managed pine plantation in Piedmont North Carolina annually turned over up to 900 $g \cdot m^{-2}$ of organic matter, mainly from <5 mm roots.

Seasonal biomass changes do not include increases and decreases of fine roots which may take place within sampling intervals (Persson 1979). Nevertheless, the results of studies such as these suggest that turnover rates of roots vary with size class and that turnover of fine roots is high compared to that of coarse roots (Hermann 1977). In studies in an Amazon rain forest, Jordan and Escalante (1980) obtained values for fine root production which were similar for several types of ingrowth substrates (litter, screens placed on top of the soil and covered with litter, and pits excavated in the forest floor). In each case the total root biomass was measured after harvesting at the end of a sampling period of several months. Thus, like the summation of biomass differences from seasonal cores, these estimates of production do not include potential increases and decreases due to mortality, sloughing, and regrowth which may have taken place within this period. Persson (1979) used both periodic soil cores and ingrowth containers (net stockings filled with sand and peat to simulate soil horizons) in a Swedish Scots pine (<u>Pinus sylvestris</u>) forest and measured both living root biomass and dead root biomass (necromass) at biweekly and monthly intervals. Production in the soil cores was calculated as the sum of increments in living root biomass and combined biomass and necromass; in the ingrowth cores production was considered to be equivalent to the accumulated standing crop since observed mortality was very low. From these experiments Persson reported production values as high as two times the mean standing crop of fine roots and reported that the supply of organic matter from fine roots often exceeds that from aboveground litterfall. His method represents an attempt to include increases due to growth and decreases due to mortality in estimates of production.

Transparent containers and chambers have permitted observations of root elongation rates, spatial distribution and timing or periodicity of growth, and responses to environmental factors. Several investigators have observed root growth of seedlings or plants in boxes with transparent glass or plexiglass faces (Lyr and Hoffmann 1967, Merritt 1968, Wilcox 1968, Trent 1972, Shaver and Billings 1975). Others have watched root dynamics through windows of underground chambers constructed in stands of vegetation (Ovington and Murray 1968, Rogers and Head 1968, Arbez 1971). Ovington and Murray measured root growth in an English birch (*Betula verrucosa* and *B. pubescens*) forest by tracings and calculated an annual growth increment based on the area of the observation window. They were unable to estimate root mortality because of the difficulty of distinguishing dead roots from live ones, but hypothesized that over a longer period of time than the three years of observation, root mortality and production would balance each other as the system achieved steady state. Rogers and Head (1968) used time-lapse cinematography to document processes of darkening and sloughing of root cortex, thickening, consumer activity and exudation of fruit tree roots in the East Malling observatory chamber in England. In studies under artificial conditions such as these, there is always uncertainty of the effect of the observation process on the behavior being observed. In the absence of a better method for directly observing ongoing root dynamics, however, use of transparent faces gives an indication of the kinds of changes which are taking place, often simultaneously, in the root system if not the overall magnitude of the changes. Expressing root growth in terms of maximum and minimum rates of elongation does not give the whole picture, because at the same time that some roots are elongating, others are not growing and still others are dying and being sloughed. Thus, a figure of number of millimeters of elongation per day tells only what is possible for an individual root tip and cannot describe the dynamics of the root system as a whole.

Seasonal periodicity and duration of root growth are factors affecting annual production. Cox (1972) found maximum biomass accumulation in yellow poplar (*Liriodendron tulipifera* L.) seedling roots in early fall and substantial losses in winter; Edwards and Harris (1977) reported parallel root biomass maxima in early spring and early fall and minima in early summer and winter in a Tennessee yellow poplar forest. Cycles of root activity in the temperate zone are commonly observed to reach a peak in early spring, decrease somewhat in summer, attain a new peak in fall, then diminish to a low during the winter (Hermann 1977). Ovington and Murray (1968) found that root growth occurred only between April and December in an English birch forest, with active growth from May to August; they also noted that most individual root tips maintained active growth for less than three weeks but never for longer than eight weeks, and that root tips rarely showed growth for more than one year. Other authors have demonstrated periodic cycles of root growth in several species of *Pinus* (Merritt 1968, Wilcox 1968, Arbez 1971), incense cedar (*Libocedrus decurrens* Torr.) (Wilcox 1962), walnut (*Juglans regia*)

(Bode 1959), and maple (Acer saccharinum L.) (Richardson 1968). Lyr and Hoffmann (1967) reported a growth maximum in early summer for some deciduous trees (Populus, Quercus, Robinia) and a more uniform rate for conifers (Pinus, Picea, Larix, Pseudotsuga) with cessation of growth by the end of September in most of these species growing in root observation boxes in the greenhouse. Their observations also demonstrated diurnal cycles in root growth, with night growth exceeding day growth in several species. However, information on alternating cycles of root activity, either seasonal or diurnal, is lacking for most tree species. Root growth appears to be under the general control of internal or endogenous stimuli with external conditions such as light, moisture, temperature and nutrients playing an important role. Caldwell (1979) suggested that an internally-programmed ability to take advantage of changing microhabitats of water and nutrient conditions in the soil by allowing simultaneous death of fine roots in zones of depletion and "non-synchronous flushes" of growth in favorable regions may be energetically more advantageous to the plant than maintenance of a constant root biomass which is dense enough for adequate uptake.

Although evidence is still insufficient, support for several generalizations or working hypotheses has emerged from recent studies in belowground biomass and production:

1. Turnover of fine roots of trees can be quite rapid, taking place in only a few weeks to less than a year, depending on the diameter of the roots (Cox et al. 1977, Hermann 1977).

2. Because of the high turnover rates of fine absorbing roots compared to large roots, production of fine roots may account for the majority of total root production as well as belowground element turnover in forests (Cox et al. 1977, Edwards and Harris 1977, Persson 1978).

3. The root system, particularly fine roots, appears to constitute a major sink for carbon or photosynthate of the plant. Mortality of fine roots contributes at least as much, or more, organic matter and nutrients to the soil and, therefore, to ecosystem cycling as litterfall. Information about belowground biomass and production is thus as important as data on aboveground fluxes to a complete understanding of ecosystem cycling and function (Harris et al. 1973, Reichle et al. 1973, Cox et al. 1977, Caldwell 1979, Persson 1979).

4. Major cycles of root growth and replacement appear to occur periodically during the year, probably in response to both internal stimuli and environmental conditions (Lyr and Hoffman 1967, Ovington and Murray 1968, Hermann 1977). Estimates of annual root production may depend on knowledge of the timing and duration of the main periods of root growth.

5. Fine root mortality, sloughing and replacement may be an evolutionary adaptation allowing trees to take advantage of changing soil conditions in a manner more efficient energetically than maintenance of a constant biomass of absorbing roots (Caldwell 1979).

Other Approaches to Production

Based on the assumption that elongation in roots that are visible at the transparent face is proportional to elongation in the root system as a whole, Newbould (1968) suggested a method for obtaining an estimate of fine root production in seedlings or trees grown in root observation chambers. A measurement of visible root length at the transparent face of the box is made and elongation of roots is then recorded periodically with units of new elongation expressed per unit of original length. Conversions from length to weight are possible from the relationship between length and weight of fine roots. If weights of roots of individual diameter classes per square meter are available, a value for fine root production based on original standing crop biomass in a forested ecosystem can be obtained. Attempts to correct for physiological and anatomical differences in root growth between seedlings and mature trees and for ecological differences between greenhouse conditions and more competitive field conditions would be necessary; growing groups of seedlings under various sets of environmental conditions which could be expected to encompass the natural environment might help to solve some of these problems.

If the community being studied is at steady state, it is possible to obtain an estimate of production from an estimate of mortality. Mathews and Westlake (1969) applied demographic techniques derived from fisheries population studies to construct "Allen curves" (Chapman 1978) for various plant populations and noted that terminal biomass, that harvested at the end of the experimental period, was not a valid measure of production when plants were sown at high initial densities. Production, as measured by mortality at different stages and sloughed plant parts (litter), was two or more times as high as the maximum biomass attained (either the seasonal maximum biomass in annual plants or terminal biomass when seedlings were used).

A technique which has been used with aquatic invertebrate populations is organization of the number of individuals in each of several size/age classes into the form of a table and determination of mortality losses of individuals from one class to the next (Hynes and Coleman 1968, Waters and Hokenstrom 1980). From these losses, age-specific mortality rates are determined and can then be applied to the known average weight of individuals of that age. Summation of losses in terms of weight represents total mortality over a designated time period such as a year, which in turn represents biomass production over the same period. This value is probably closer to net production than to gross production, since respiration and possible growth increases and decreases of the animals are not taken into account.

Methods like these may be useful in determining root production in forest ecosystems. By examining the age structure of the standing crop or "population" of roots in which "age classes" might be defined by some means such as diameter or number of annual rings, percent mortality between classes could be calculated and applied to weight data. Some modifications of the methods used for invertebrates would be required.

SITE DESCRIPTIONS AND METHODS

Study Sites

The two swamp forests chosen for study, Tar Swamp and Creeping Swamp, have been described by Brinson et al. (1981). Both are located in the Coastal Plain of North Carolina (Figure 1). The Tar Swamp site is located in Pitt County on the north side of the Tar River, just east of secondary road 1565 (35^o 35' N, 77^o 10' W) and 15 km upstream from the head of the Pamlico River estuary. At this point the Tar River drains about 8000 km^2 of Piedmont and Coastal Plain North Carolina with an average annual discharge of 180 $m^3 \cdot s^{-1}$. The floor of this alluvial swamp is separated from the river by a natural levee and is covered by several cm of water almost continuously from November until late April, while trees are dormant. Local rains may cause accumulation of several cm of water in summer which disappears within a few days because of high rates of evapotranspiration. Overflow from the Tar River can result in flooding to as much as 1.3 m depth at any time of the year. The soil of Tar Swamp has low bulk density (0.35 $g \cdot cm^{-3}$) and high organic matter content (30-40% of dry wt).

The canopy of Tar Swamp is dominated by water tupelo (*Nyssa aquatica* L.) with some cypress (*Taxodium distichum* (L.) Richard). The understory consists of water ash (*Fraxinus caroliniana* Mill.) and red maple (*Acer rubrum* L.). Density is 2600 trees per ha. The age of the stand is about 35 yr.

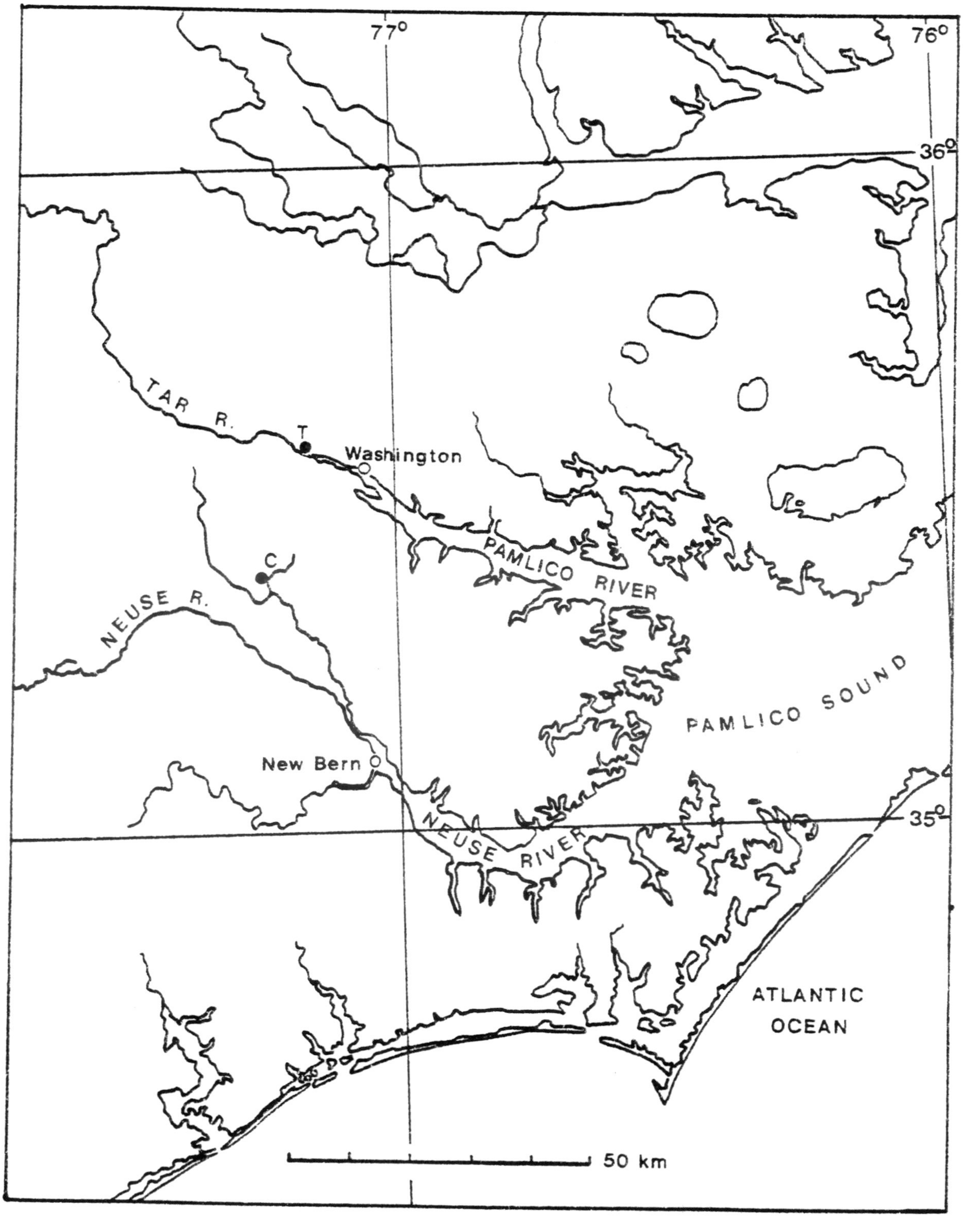


Figure 1. Regional map of eastern North Carolina Coastal Plain showing study sites. T, Tar Swamp; C, Creeping Swamp.

Logging for cypress took place about 35 yr ago and regrowth of cypress is scarce (Brinson 1977).

The Creeping Swamp study site is located in the floodplain of Creeping Swamp, a small headwater swamp stream, just upstream from the bridge on State Route 43 in Pitt County (35^o 25' N, 77^o 15' W). The stream drains 70 km^2 of the Coastal Plain with an average annual discharge of about 1.12 $m^3 \cdot s^{-1}$ (U.S. Geological Survey 1979). Flooding in this swamp is greatest in winter and early spring, to as much as 50 cm; the floodplain is dry much of the time from late June to December with intermittent temporary flooding after hard rains (Yarbro 1979). Organic matter content of soil varies with specific location within the floodplain; Mulholland (1979) reports 17% organic matter while other analyses are 31-33% (H. D. Bradshaw 1979, unpublished data). Bulk density at the sampling site is 0.52 $g \cdot cm^{-3}$. Impoundment by a weir constructed by the U.S. Geological Survey at the Route 43 bridge causes slightly greater water depths and a longer hydroperiod in the study site than in the remainder of the swamp.

Species present in the Creeping Swamp study area include *Nyssa sylvatica* var. *biflora*, *Acer rubrum* L., *Fraxinus caroliniana* Mill., *Nyssa aquatica* L., *Liquidambar styraciflua* L. and numerous shrubs and vines. This stand was partially logged about 40 yr ago (Yarbro 1979).

Biomass and Nutrient Determinations

In July and August 1979 four 0.125 m^2 quadrats were excavated to 40 cm below ground level at 10 m intervals along a transect in each swamp perpendicular to the stream channel. In Tar Swamp, quadrats were located from 65 to 105 m from the river's edge, and in Creeping Swamp they were located approximately 40 to 80 m from the stream channel, although here the channel is rather diffuse. Quadrats were located at least 0.5 m from any tree in order to obtain only lateral roots, that is roots not associated with the bole or stump of a tree. Excavations were made by sawing vertically through soil and roots along the edges of a 0.125 m^2 opening in a plywood template. Soil and roots were removed in 10 cm increments and each increment placed in a plastic bag. Soil was then cleaned from the roots by spraying with water. Washed roots were stored at 4°C until they were recleaned carefully of any remaining soil and debris under running tap water and sorted into size classes of 0-2, 2-5, 5-10, 10-20, 20-50, and 50-100 mm diameter at the cut root cross sectional surface. Roots were then oven-dried at about 85°C to constant weight. Although some loss of very fine roots and root hairs undoubtedly occurred in washing, this was judged to be less than 10% of the biomass of <5 mm diameter roots.

For nutrient analysis all roots of a given size class and depth in a swamp were combined and representative subsamples ground in a Wiley Mill. Representative subsamples of larger roots (10-100 mm) were obtained by cutting segments of roots from each quadrat approximately proportional to the weight of the roots supplied by that quadrat and mixing these together.

After grinding, roots were redried for 24 h. Total N was determined by the Kjeldahl method (Bremner 1965, Scheiner 1976). Determination of ash content and preparation for cation and phosphorus analysis was done by igniting samples in a muffle furnace at 500°C for 3 h. Ashed samples were acidified by the method described in Allen et al. (1974, p. 86), filtered, and diluted to 100 ml. They were stored at 4°C in polyethylene bottles, and analyzed for K, Ca, Mg, Na and Fe on a Perkin-Elmer Atomic Absorption Spectrophotometer. Analysis for total P was performed by the molybdate blue procedure (U.S. Environmental Protection Agency 1979). All analyses were carried out in duplicate. Two replicates of standard kale (*Brassica oleracea*) of known nutrient content provided by H. J. M. Bowen, University of Reading, England were also analyzed for reference. Means of results of replicate analyses are reported.

Dynamics of Root Production and Mortality

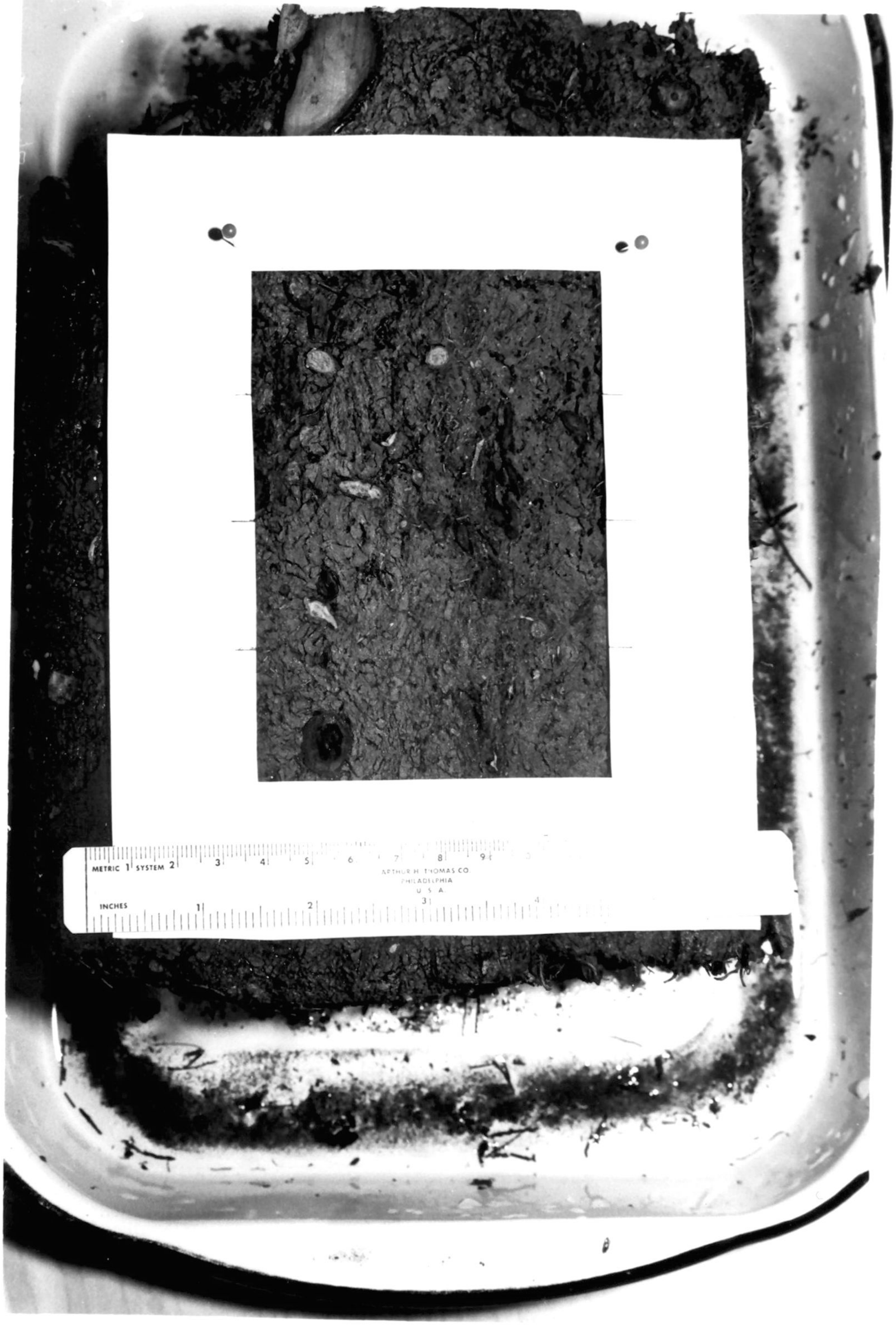
Two approaches were utilized in investigations of root mortality and production dynamics: age structure analysis of roots in soil blocks collected from the field and observations of fine root growth rates in greenhouse-grown seedlings.

Age structure analysis used in studies of aquatic invertebrate populations to obtain estimates of production by summation of mortality losses (converted to a weight basis) between size/age classes (Hynes and Coleman 1968, Hamilton 1969, Benke 1979) has been termed the "size-frequency method" (Waters and Hokenstrom 1980). In this part of the present study, the potential and limitations for using age structure analysis with the "population" of roots in soil blocks are considered. The possibility of determining root age, which is necessary for this method, from a regression of root diameter and number of growth rings is assessed.

Eleven soil blocks were excavated from the upper 20 cm of soil in Tar Swamp during October 1980 in an area close to the transect used for biomass sampling. Sampling points were located at least 1 m from any tree or shrub and at least 5 m apart. The blocks, 20-25 cm on a side and 15-20 cm deep, were removed by sawing through soil and roots on all sides with a pruning saw and lifting them out with a spade. The rough blocks were transported as intact as possible to the laboratory where they were frozen.

The frozen blocks were then sliced through vertically either manually with a bow saw or with a heavy duty bandsaw. The bandsaw was found to give a cleaner cut with far less labor but greater expense since this needed to be done in a commercial establishment. A stream of tap water was allowed to run over the frozen cut surface which removed a thin layer of soil and revealed cut root ends more clearly (Figure 2). An 8 x 12 cm rectangular template was placed horizontally on the cut surface to enclose an area between 2 and 15 cm below the upper surface of the soil. The number of root ends within this rectangle was counted for the 0-0.5, 0.5-1.0, and 1.0-2.0 mm diameter classes and for each successive 1 mm diameter class to the largest root diameter present. Because of the labor involved

Figure 2. Photograph of cross section of soil block from Tar Swamp showing cut root ends.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in collecting and transporting as well as space limitations for freezing, some soil blocks were sliced in two places, making the cuts at least 15 cm apart. Counts of all roots in all samples were combined by size class into the form of a life table (Krebs 1972, pp. 154-163).

For correlating root diameter and age, a large number of fresh roots was collected from the Tar Swamp site, cleaned under running water, and stored in plastic bags at 4^{0}C until they could be examined. Thin sections were cut from these with a razor blade, stained with phloroglucin in alcohol and HCl, and examined under a stereobinocular dissecting microscope for growth rings. Diameter was measured with calipers and growth rings were counted in 80 root sections, from which a linear regression was calculated. In addition, roots of greenhouse-grown water tupelo seedlings were sectioned and examined for growth rings at seven and sixteen months of age.

Another approach to estimating root production arose from the necessity for resolving further the production of roots of <1 mm diameter, since most of these do not have growth rings. Since high rates of fine root turnover have been reported in several studies (Cox et al. 1977, Hermann 1977, Persson 1979), a potentially large fraction of production would be missed by a technique which is dependent on growth rings for age determination.

For obtaining information about the dynamics of fine roots, direct observation of fine root growth in water tupelo (Nyssa aquatica L.) seedlings was attempted. Water tupelo is the dominant species of mature tree present in the forest canopy of Tar Swamp. Other species, notably water ash (*Fraxinus caroliniana* Mill.) and red maple (*Acer rubrum* L.) are more abundant than water tupelo as understory trees but represent an insignificant proportion of the mature vegetation of Tar Swamp. It was expected that observations of root growth in water tupelo would give an indication of actual root growth in the swamp. In addition, water tupelo is fairly easy to germinate and grow from fruits collected in the field; working with just one species would eliminate some sources of variation among plants.

On March 6, 1981 eight one-year-old seedlings grown in the greenhouse from water tupelo fruits collected from the Tar Swamp study area in February 1980 were planted individually in root observation boxes in root-free, sieved soil obtained from Tar Swamp. Four plants designated for the "Flooded" treatment were approximately matched in height with four plants designated for the "Unflooded" treatment. Boxes were constructed according to a design modified from Trent (1972) used for study of tundra plant roots. Two right triangles of pine, 20 cm at the base and 30 cm high, formed the sides of the boxes (Figure 3). Sheets of 2.5 mm thick acrylic were fastened to the wood sides with wood screws to form two 20 cm wide transparent faces on each box. An attempt was made to make the four boxes for the "Flooded" treatment watertight by sealing the edges with household latex caulking compound.

The sides of the boxes were completely covered with two layers of heavy black garden plastic fastened with black electrical tape.

Figure 3. Photograph of seedling root observation box.

The four boxes in each treatment group were set in each of two plastic rectangular baskets which were also covered with the black plastic. Plants were kept under ambient conditions in the greenhouse and watered with 1.25 l of distilled water at least three times a week until it was judged that they were acclimated to the containers and soil. On March 18 the four "Flooded" plants were transferred in their containers to a watertight stone tub and the watering regime was changed so that the water level in the tub was kept at a constant level approximately 15 cm below the surface of the soil. There was no change in the conditions of the "Unflooded" plants.

By April 15 a sufficient number of roots had appeared at the transparent faces of several of the boxes to begin marking growth. Several root tips per plant were marked with permanent marking pen on Thermofax acetate sheets placed over the uncovered acrylic face of the root box. The location of root tips on subsequent dates was recorded by successive numbers next to marks over the root tips. Distance between marks in mm and the number of days elapsed were noted and a growth rate determined for each root tip. If no growth occurred on a given date, "no change" was recorded. Periodically, new root tips which appeared were marked for observation. Each time markings were made the acetate sheet was lined up by matching lines drawn on the acrylic face.

Because it was felt that not enough growth information was being obtained by this method of marking selected root tips, a method of "mapping" all visible roots was begun on May 15. On this date all roots visible at one face of each box for two Flooded and two Unflooded plants (designated 1F and 4F, 1U and 2U, respectively) were traced on an acetate sheet in order to follow changes in the entire visible root system. Every five days thereafter for 35 days, a new color of permanent marker was used to trace additional visible root segments onto the original sheet. Five-day increments in length divided by the original length could be used as a measure of production of new roots, using Newbould's (1968) assumption that visible root increments would be proportional to total root increments. At 35 days (June 19) the entire visible root system of each of the four plants under observation was again traced onto a separate acetate sheet.

Measurement of root length was attempted with a rolling wheel map measure (Alvin Map Measure) used to measure length of roads and streams on maps. This method was compared for convenience and accuracy with the method of superimposing the root tracings on transparent acetate sheets over a 0.25 cm grid of lines and counting the number of intersections of roots with lines on the grid (Newman 1966, Tennant 1975). The second method was tested by counting grid-line intersections using irregular segments of thin black wire of known length (photocopied on the grid paper) and half circles of known circumference superimposed on the grid. The grid system was found to be more accurate and consistent in its results and left less chance for human error, as well as being easier to use, and was therefore selected.

A linear regression was calculated for the number of intersections between grid lines and known lengths of half-circles and irregular lines formed by thin wire, shown by the following equation:

$$y = 0.187x + 0.181$$

(where y = length in cm and x = number of intersections;

$r = 0.999$).

This equation, which was used to predict values of y (length in cm) from values of x (intersections), tended to overestimate by about 7% at low values of x (8), to predict within 1% at values of x between 32 and 50, and to underestimate by about 1.3% at higher values of x (78). Thus longer root lengths would tend to be slightly underestimated, and ratios of five-day increments to total root length would tend to be overestimated by this method. These aberrations were judged to be minor, since ratios between numbers of intersections could be used without conversion to length in most calculations of growth rates, production, and mortality, and since other methods involving direct measurement would have introduced greater error.

On July 2 and 6, approximately two weeks after the last root tracings were made, shoots and roots of all plants were harvested separately and cleaned of soil. Plant parts were refrigerated in sealed plastic bags until they could be examined under the dissecting microscope. For examination of growth rings, thin sections of roots and shoots were cut with a razor blade and treated with a few drops of phloroglucin in alcohol and HCl to stain xylem tissue.

Six subsamples of <1 mm diameter roots were cut from several plants in each treatment and placed in a single layer in a Ziplock bag. Tracings of these roots were made on acetate sheets and the grid method used to estimate total length. Dry weight of the subsamples was obtained on an analytical balance (Mettler Model H10Tw) after oven drying to constant weight at 80°C. From these subsamples (three each from flooded and unflooded plants, respectively) an estimate of dry weight per unit length of <1 mm roots was made in order to convert length measurements made in root tracings to biomass.

All roots, including cross sections and fine root subsamples, and shoots of each plant were then separately oven dried at 80°C to constant weight to obtain root/shoot ratios of flooded vs. unflooded plants.

RESULTS

Biomass Distribution of Lateral Roots

Biomass of lateral roots to 40 cm depth was similar in the two swamps with 2345 $g \cdot m^{-2}$ in the Tar Swamp site and 2702 $g \cdot m^{-2}$ in the Creeping Swamp site. However, vertical distribution of root biomass showed markedly different trends for each site (Figure 4). In Tar Swamp, biomass was lowest in the top 10 cm and increased with depth, while in Creeping Swamp biomass was relatively high in the first 10 cm, peaked at 10-20 cm depth, and decreased rapidly with increasing depth. In Tar Swamp about 12% of root biomass was found at 0-10 cm, increasing steadily to 36% at 30-40 cm (Table 1). In Creeping Swamp, 34% of biomass was found at 0-10 cm, increasing slightly to 38% at 10-20 cm, and then decreasing to about 6% at 30-40 cm. Observations indicated that roots were present in Tar Swamp below the sampling limit of 40 cm. Total root biomass in Tar Swamp may thus be underestimated. In contrast, 40 cm appeared to be the maximum depth to which roots extended in Creeping Swamp.

Vertical distribution of different sizes of roots was also distinctly different between the alluvial and headwater swamps. In Tar Swamp, the biomass of fine roots (<2 mm diam) was distributed fairly evenly through all depths while larger roots contributed an increasing proportion to biomass with increasing depth (Table 2). In Creeping Swamp, biomass of the finest roots (<2 mm diam) was greatest at the top level, forming a mat densely interlaced with

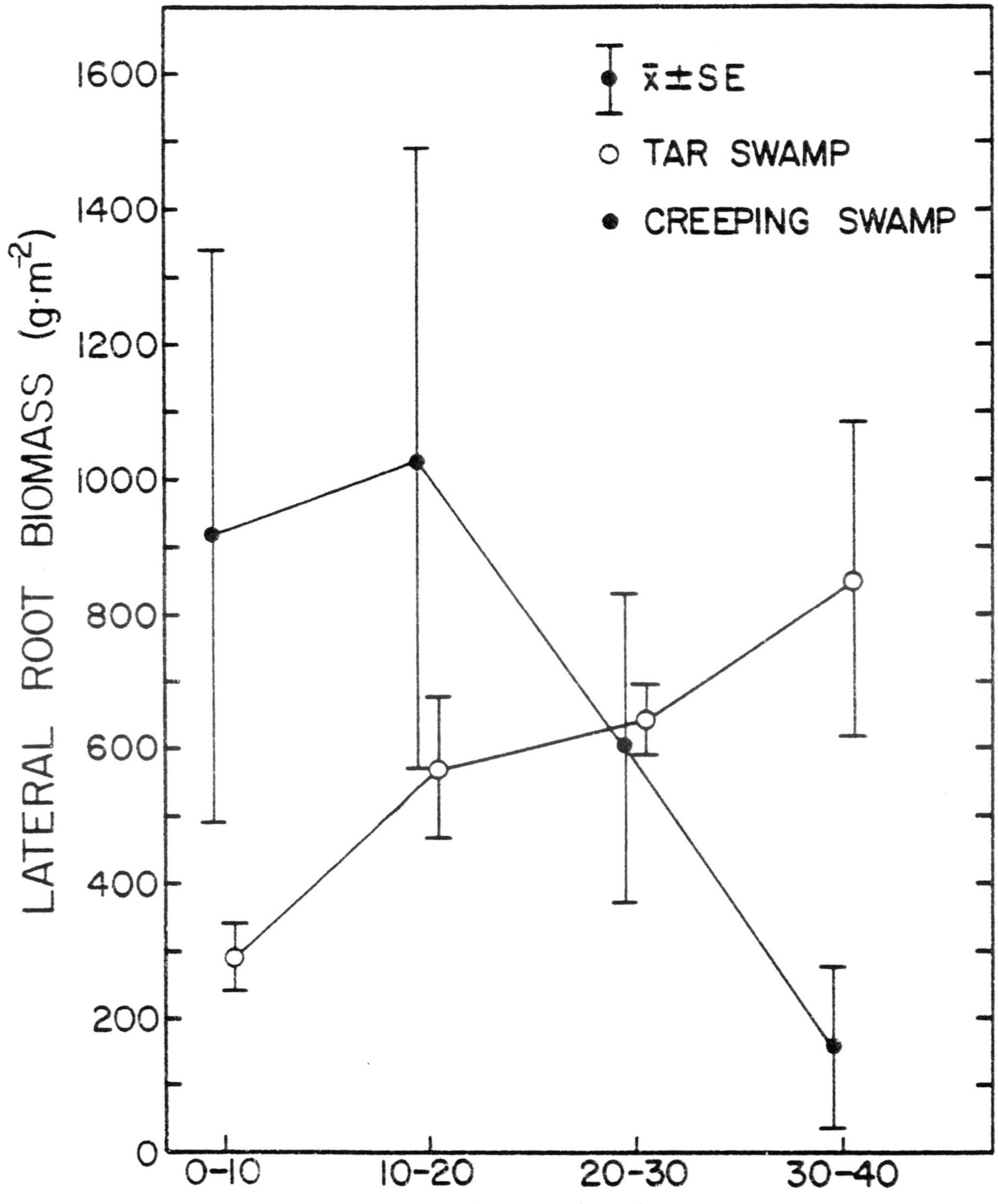

Figure 4. Trends of lateral root biomass with depth in two swamps.

Table 1. Lateral root biomass in two swamps.

		Tar Swamp		Creeping Swamp	
Depth interval (cm)	Diameter class (mm)	Biomass ($g \cdot m^{-2}$)	Percent of total biomass	Biomass ($g \cdot m^{-2}$)	Percent of total biomass
0-10	<2	137.9		365.2	
	2-5	86.3		97.3	
	5-10	39.2		70.8	
	10-20	---		140.4	
	20-50	30.1		246.0	
	50-100	---		---	
	Sum	293.5	12.5	919.7	34.0
10-20	<2	162.4		190.8	
	2-5	124.6		62.2	
	5-10	139.5		90.1	
	10-20	69.4		71.1	
	20-50	70.2		230.9	
	50-100	---		383.7	
	Sum	566.1	24.1	1028.8	38.1
20-30	<2	138.5		136.9	
	2-5	128.0		33.0	
	5-10	178.1		46.1	
	10-20	129.0		102.6	
	20-50	63.4		109.2	
	50-100	---		172.5	
	Sum	637.0	27.2	600.3	22.2
30-40	<2	142.6		62.0	
	2-5	132.2		19.8	
	5-10	173.9		32.5	
	10-20	181.3		15.6	
	20-50	169.7		23.5	
	50-100	48.8		--	
	Sum	848.5	36.2	153.4	5.7
Total		2345.1	100.0	2702.2	100.0

Table 2. Percentage of lateral root biomass of each size class at each depth in two swamps.

		Diameter (mm)					
Site	Depth (cm)	<2	2-5	5-10	10-20	20-50	50-100
Tar Swamp	0-10	23.7	18.3	7.4	0	9.0	0
	10-20	27.9	26.4	26.3	18.3	21.1	0
	20-30	23.8	27.2	33.6	34.0	19.0	0
	30-40	24.5	28.0	32.8	47.8	50.9	100.0
	TOTAL	100	100	100	100	100	100
Creeping Swamp	0-10	48.4	45.8	29.5	42.6	40.4	0
	10-20	25.3	29.3	37.6	21.6	37.9	69.0
	20-30	18.1	15.5	19.3	31.1	17.9	31.0
	30-40	8.2	9.3	13.6	4.7	3.8	0
	TOTAL	100	100	100	100	100	100

litter at and just under the surface. Larger roots contributed increasingly to biomass at the middle levels, but at the deepest level, total biomass of all size classes was very low.

A comparison of the size class distribution of the total root biomass also revealed differences between the two swamps. In Tar Swamp the finest roots (<2 mm diameter) made up 25% of the total lateral root biomass, and contribution to total lateral root biomass decreased steadily with progressively larger size classes of roots (Table 3). In Creeping Swamp changes among size classes were more complex, with lower percentages of total biomass occurring in intermediate size classes (2-5, 5-10, and 10-20 mm) than in the smallest (<2 mm) and larger (20-50 and 50-100 mm) size classes. However, the percentage of biomass in the smallest size class was similar for both swamps.

Nutrient Concentrations in Roots

Results of nutrient analyses suggest that site, diameter and depth below ground are related to nutrient concentrations. N concentrations were within a similar range in the two swamps (0.2-1.0% of root dry wt), showing a general tendency to decrease with increasing root diameter at all depths in each swamp (Figure 5). In Tar Swamp, total N concentrations in the finest roots (<2 mm) were greatest (close to 1%) at the shallowest level and decreased by about half (to about 0.5%) at the deepest level; in large roots (20-50 mm) N concentrations were lower and varied inconsistently with depth.

Table 3. Size class distribution of lateral root biomass in two swamps.

	Tar Swamp		Creeping Swamp	
Size class (mm)	$g \cdot m^{-2}$	% of total	$g \cdot m^{-2}$	% of total
<2	581.4	25	754.9	28
2-5	471.1	20	212.3	8
5-10	530.7	23	239.5	9
10-20	379.7	16	329.7	12
20-50	333.4	14	609.6	22
50-100	48.8	2	556.2	21
Total	2345.1	100	2702.2	100

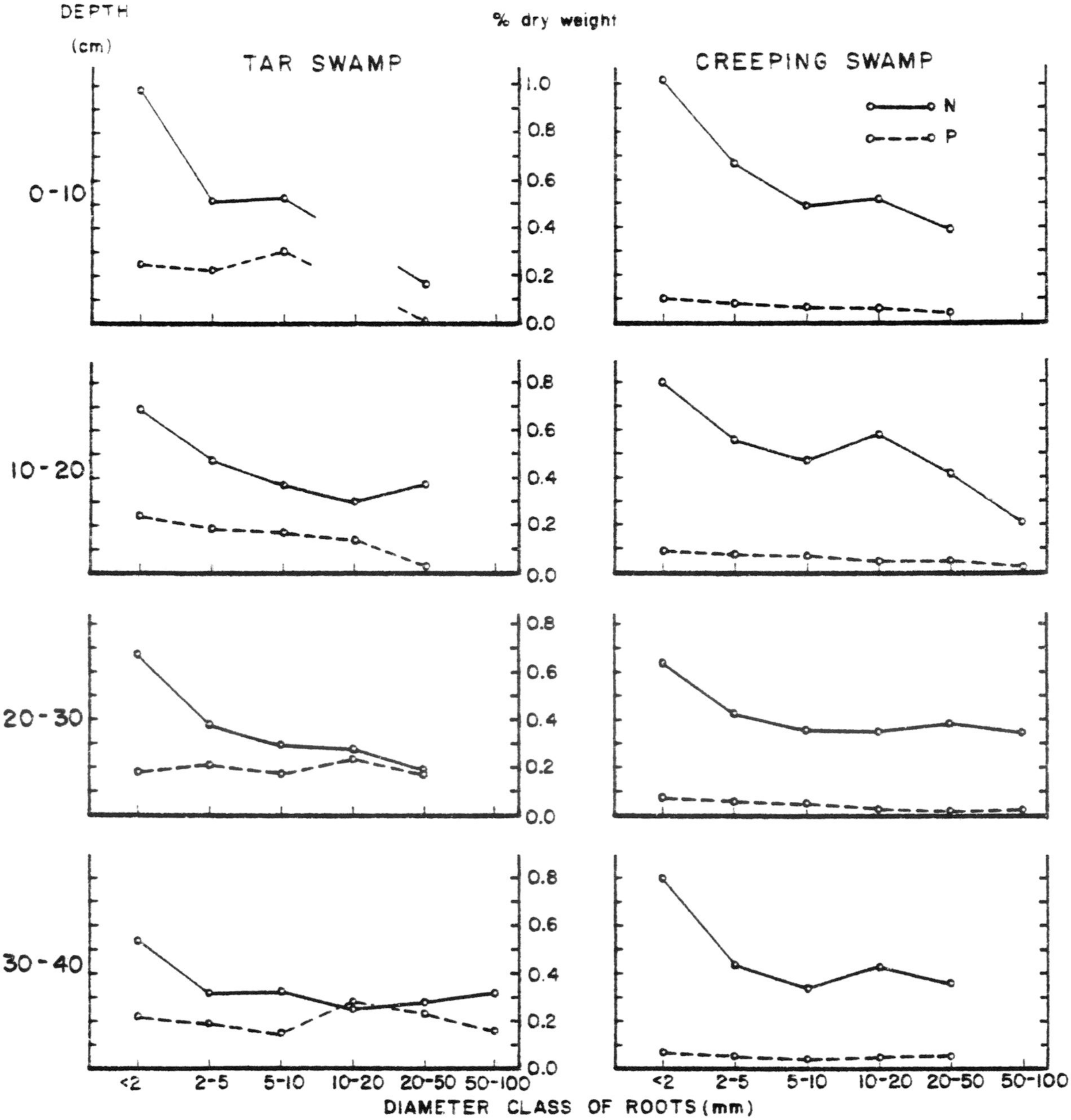

Figure 5. Concentrations of nitrogen and phosphorus in lateral roots.

N concentrations of the finest roots of Creeping Swamp decreased with depth to 20-30 cm, then increased at 30-40 cm. Large-root N concentrations in Creeping Swamp showed little change with depth. Diameter of roots could be expected to affect N concentration, since fine roots are likely to contain the most growing and metabolically active tissue in which N is an important component.

Total P concentrations were generally somewhat higher in Tar Swamp (44-3052 $\mu g \cdot g$ dry wt^{-1}) than in Creeping Swamp roots (218-2004 $\mu g \cdot g$ dry wt^{-1}) and varied inconsistently with size and depth, except that within the <2 mm size class, P concentrations in Tar Swamp showed little change with depth and P levels in large roots (20-50 mm) tended to increase with depth (Figure 5). In Creeping Swamp, P concentrations were less variable and tended to decrease very gradually with increasing size of root at the same depth.

In Tar Swamp, concentrations of K, Ca, Mg, and Na followed trends somewhat similar to each other (Figure 6). At the two shallowest levels, these elements tended to be present in highest concentrations in the finest roots and to decrease in concentration as root diameter increased, while at the two deeper levels, these elements showed a more variable pattern; in particular, K was in highest concentration in >10 mm roots. High concentrations of K, Ca, Mg and Na in fine roots (<2 mm) of the shallowest depth tended to decrease and level off with greater depth, while in large roots (20-50 mm) the opposite trend was found (Figure 6).

In Creeping Swamp, Ca concentrations were somewhat higher generally and much more variable. Unexplained high peaks in Ca occurred

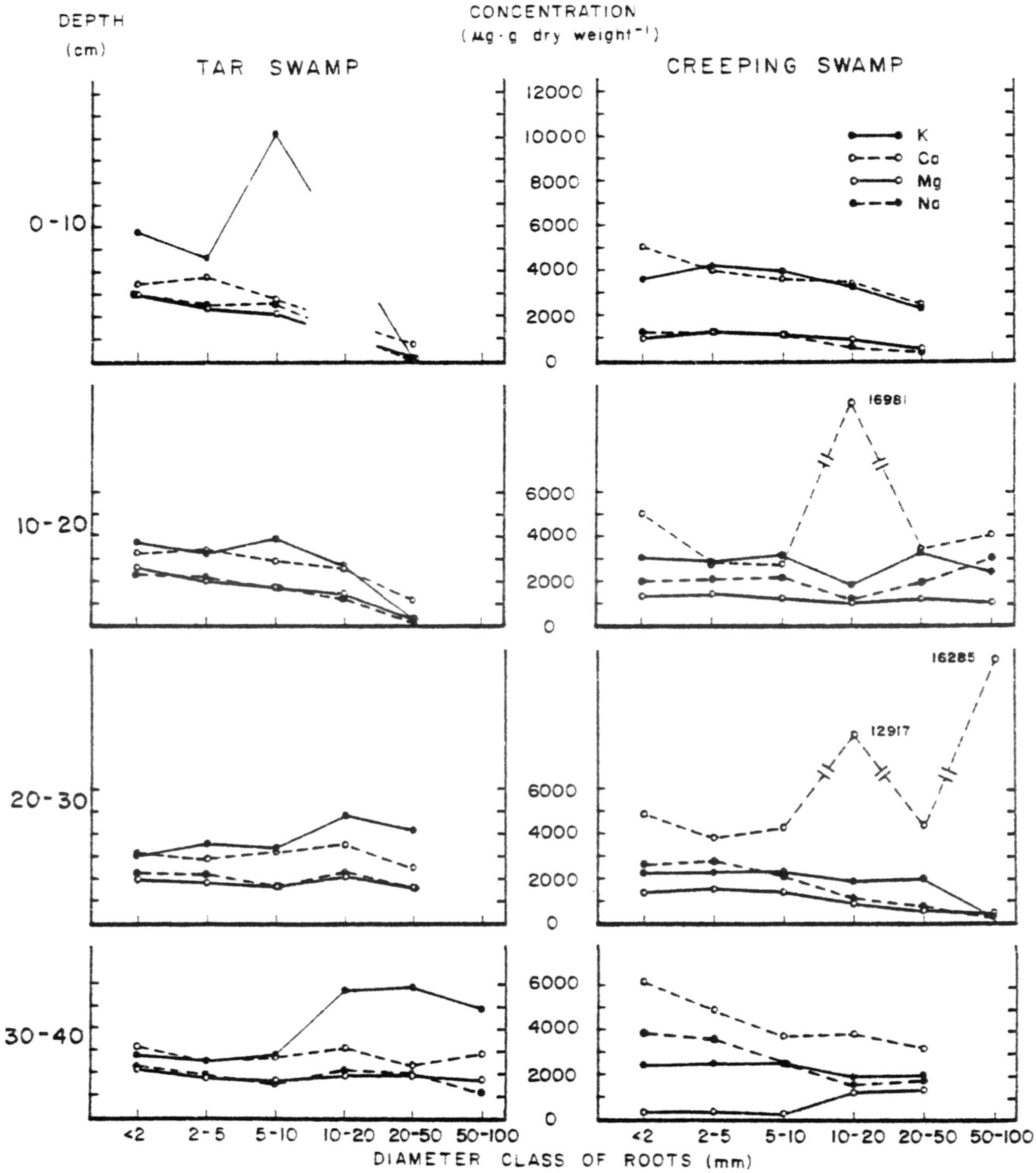

Figure 6. Concentrations of potassium, calcium, magnesium, and sodium in lateral roots.

in 10-20 mm roots of the 10-20 and 20-30 cm depths as well as in 50-100 mm roots at 20-30 cm depth. Repeated analyses resulted in similar high values. Concentrations of K, Ca, Na, and Mg tended to decrease with increasing root diameter at the shallowest depth, but this trend was not clear at deeper levels.

Fe concentrations in roots of both swamps were high and showed a trend of decreasing concentration with increasing root diameter at all depths (Figure 7). In Tar Swamp, Fe levels in finest roots were commonly ten times those of the largest roots, and this ratio was even higher in Creeping Swamp. Fe concentrations also tended to increase with depth in Tar Swamp. In Creeping Swamp, Fe concentrations increased with depth in roots of the smaller size classes. Fe concentrations of the finest roots in Creeping Swamp at depths lower than 10 cm were about 2-5 times higher than those of Tar Swamp.

Nutrient capital or standing stocks of elements contained in each size class of roots were calculated by multiplying nutrient concentrations by dry weight m^{-2} of roots of each size class at each depth (Tables 4 and 5). Tar Swamp had less N but more P and more K per m^2 in roots than Creeping Swamp. The amount of N contained in roots remained about the same at all depths in Tar Swamp, while it decreased with depth in Creeping Swamp. Both swamps held the greatest proportion of N in the finest roots (<2 mm diam). The stock of P and K held in roots increased with depth in Tar Swamp and decreased in Creeping Swamp. Both swamps had the greatest proportion of P in finest roots, but K was more evenly distributed among size classes of

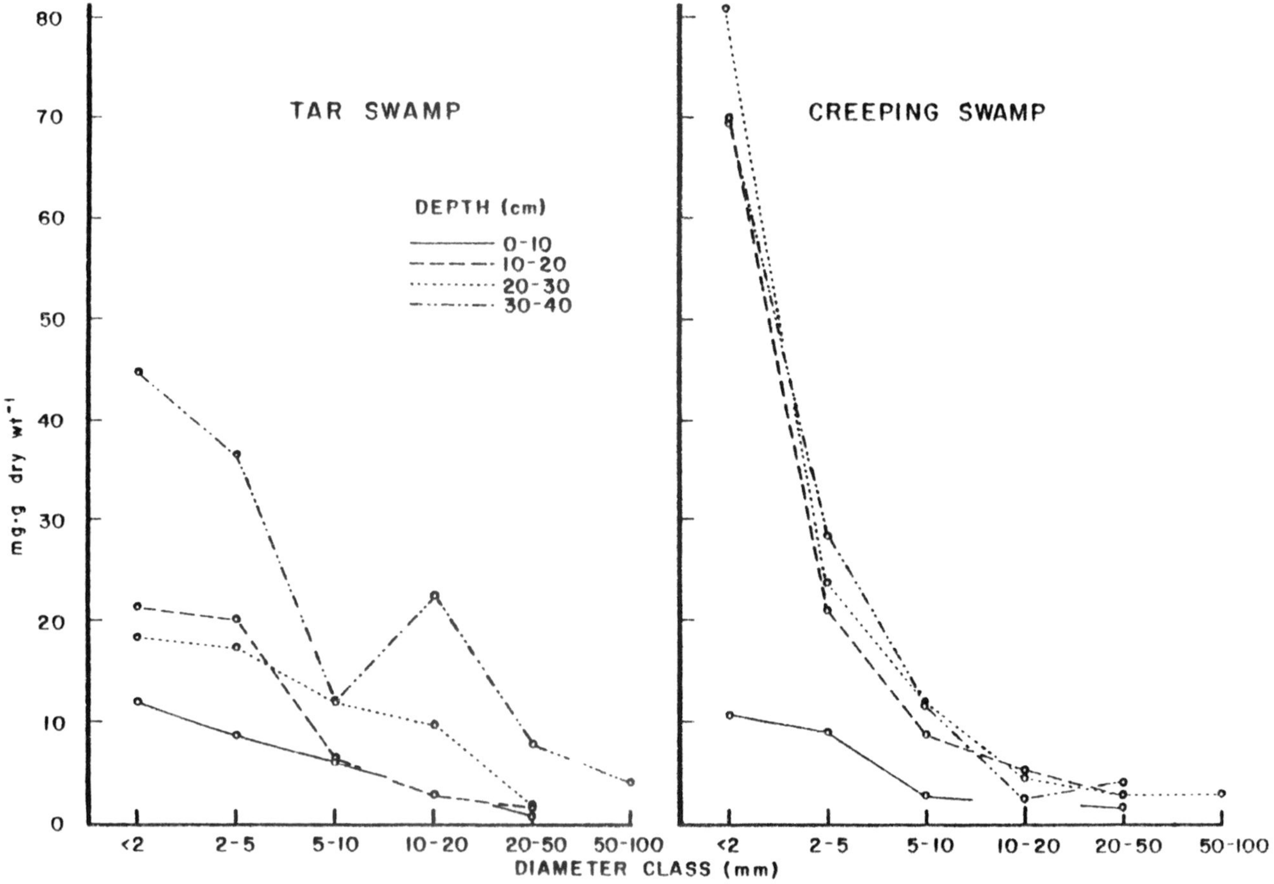

Figure 7. Concentrations of iron in lateral roots.

Table 4. Root nutrient and organic matter stocks ($g \cdot m^{-2}$) in Tar Swamp by size class and depth.

Depth interval and diameter class of roots	Organic matter	N	P	K	Na	Ca	Mg	Fe
0-10 cm depth								
<2 mm	127.5	1.35	0.34	0.79	0.41	0.47	0.41	1.67
2-5	82.1	0.44	0.19	0.40	0.22	0.33	0.21	0.76
5-10	37.0	0.21	0.12	0.40	0.11	0.11	0.08	0.25
10-20	--	--	--	--	--	--	--	--
20-50	29.9	0.05	0.00	0.00	0.00	0.02	0.00	0.02
50-100	--	--	--	--	--	--	--	--
Sum	276.5	2.05	0.65	1.59	0.74	0.93	0.70	2.70
10-20 cm depth								
<2 mm	149.2	1.12	0.39	0.61	0.38	0.53	0.42	3.48
2-5	117.9	0.59	0.23	0.40	0.26	0.43	0.25	2.53
5-10	133.4	0.52	0.24	0.55	0.22	0.36	0.22	0.92
10-20	66.8	0.21	0.08	0.19	0.09	0.18	0.10	0.21
20-50	69.4	0.26	0.02	0.02	0.01	0.08	0.02	0.10
50-100	--	--	--	--	--	--	--	--
Sum	536.7	2.70	0.96	1.77	0.96	1.58	1.01	7.24
20-30 cm depth								
<2 mm	129.6	0.93	0.25	0.42	0.31	0.44	0.27	2.56
2-5	121.2	0.49	0.27	0.46	0.28	0.37	0.24	2.23
5-10	169.2	0.52	0.30	0.60	0.29	0.57	0.29	2.15
10-20	122.5	0.36	0.31	0.62	0.29	0.46	0.27	1.26
20-50	60.2	0.12	0.11	0.26	0.09	0.16	0.10	0.10
50-100	--	--	--	--	--	--	--	--
Sum	602.7	2.42	1.24	2.36	1.26	2.00	1.17	8.30
30-40 cm depth								
<2 mm	126.6	0.77	0.31	0.40	0.32	0.46	0.31	6.39
2-5	122.7	0.42	0.25	0.34	0.26	0.33	0.24	4.85
5-10	164.5	0.57	0.26	0.49	0.27	0.47	0.29	2.13
10-20	167.5	0.45	0.51	1.05	0.38	0.57	0.35	4.10
20-50	162.9	0.47	0.40	1.00	0.34	0.41	0.32	1.34
50-100	46.3	0.16	0.08	0.24	0.06	0.14	0.08	0.21
Sum	790.5	2.84	1.81	3.52	1.63	2.38	1.59	19.02
Total for all roots	2206.4	10.01	4.66	9.24	4.59	6.89	4.47	37.26

Table 5. Root nutrient and organic matter stocks ($g \cdot m^{-2}$) in Creeping Swamp by size class and depth.

Depth interval and diameter class of roots	Organic matter	N	P	K	Na	Ca	Mg	Fe
0-10 cm depth								
<2 mm	341.5	3.72	0.37	1.33	0.49	1.86	0.36	3.94
2-5	92.9	0.65	0.08	0.41	0.12	0.39	0.12	0.90
5-10	68.5	0.35	0.05	0.28	0.09	0.26	0.08	0.20
10-20	136.7	0.73	0.08	0.47	0.09	0.48	0.13	0.32
20-50	242.1	0.96	0.10	0.55	0.11	0.61	0.12	0.42
50-100	--	--	--	--	--	--	--	--
Sum	881.7	6.41	0.68	3.04	0.90	3.60	0.81	5.78
10-20 cm depth								
<2 mm	159.3	1.53	0.17	0.58	0.38	0.97	0.26	13.38
2-5	58.6	0.35	0.05	0.18	0.13	0.18	0.09	1.31
5-10	86.2	0.42	0.06	0.29	0.20	0.25	0.11	0.80
10-20	66.4	0.41	0.03	0.13	0.08	1.21	0.07	0.39
20-50	223.5	0.97	0.12	0.76	0.45	0.80	0.28	0.68
50-100	363.7	0.81	0.09	0.95	1.16	1.58	0.41	0.88
Sum	957.7	4.49	0.52	2.89	2.40	4.99	1.22	17.44
20-30 cm depth								
<2 mm	105.5	0.88	0.10	0.31	0.36	0.67	0.19	11.02
2-5	30.9	0.15	0.02	0.07	0.09	0.13	0.05	0.79
5-10	43.8	0.17	0.02	0.11	0.10	0.20	0.06	0.56
10-20	97.3	0.36	0.03	0.20	0.12	1.32	0.09	0.47
20-50	105.4	0.43	0.02	0.22	0.09	0.48	0.06	0.31
50-100	162.8	0.60	0.04	0.05	0.05	2.81	0.08	0.53
Sum	545.7	2.59	0.23	0.96	0.81	5.61	0.53	13.68
30-40 cm depth								
<2 mm	51.8	0.50	0.05	0.15	0.24	0.38	0.02	4.31
2-5	18.2	0.09	0.01	0.05	0.07	0.10	0.01	0.56
5-10	30.7	0.11	0.01	0.08	0.08	0.12	0.01	0.38
10-20	15.0	0.07	0.01	0.03	0.02	0.06	0.02	0.04
20-50	22.5	0.08	0.01	0.05	0.04	0.08	0.03	0.10
50-100	--	--	--	--	--	--	--	--
Sum	138.2	0.85	0.09	0.36	0.45	0.74	0.09	5.39
Total for all roots	2523.3	14.34	1.52	7.25	4.56	14.94	2.65	42.29

roots in Tar Swamp and tended to be concentrated in the finest root fraction in Creeping Swamp.

Stocks of Mg and Fe in roots were larger at greater depths in Tar Swamp; in Creeping Swamp Mg and Fe pools were largest at the 10-20 cm depth and decreased with increasing depth. The two swamps held about the same total amount of Na and Fe in roots, but Creeping Swamp roots held more than twice as much Ca as Tar Swamp while Tar Swamp roots contained more Mg than Creeping Swamp.

Root Dynamics

Growth Ring Analyses

Sections of roots of a seven-month-old greenhouse-grown water tupelo seedling examined in September 1980 showed one growth ring visible in the upper part of the main root, 5.5 mm in diameter. Lower parts of this same root and lateral roots of this seedling had no growth rings. Sections of eight 16-month old seedlings examined after two springs of growth in July 1981 showed the presence of two growth rings in most of the larger-diameter parts of the main roots (7.7-11.3 mm diameter). Nine out of 14 roots 7.7-11.3 mm in diameter had two growth rings; five had one ring. Nine roots between 4.1 and 7.3 mm in diameter in these seedlings were examined and all had at least one ring; two out of nine had two rings or more. Only two sections (2.4 and 2.7 mm diameter) out of a total of 24 root sections >1 mm in diameter examined in the 16-month old seedlings had no growth rings.

Lateral roots collected at random from Tar Swamp in fall 1980, stained with phloroglucin in alcohol and HCl, and examined under the dissecting microscope showed a fairly strong relationship between diameter and number of growth rings (N = 80 sections examined; r = 0.8418) (Figure 8). A linear regression calculated for this relationship is

$$y = 1.1105\ x + 1.4078$$

(where y = number of rings; x = diameter in mm).

The regression showed best fit for roots between 3.5 and 8 mm diameter

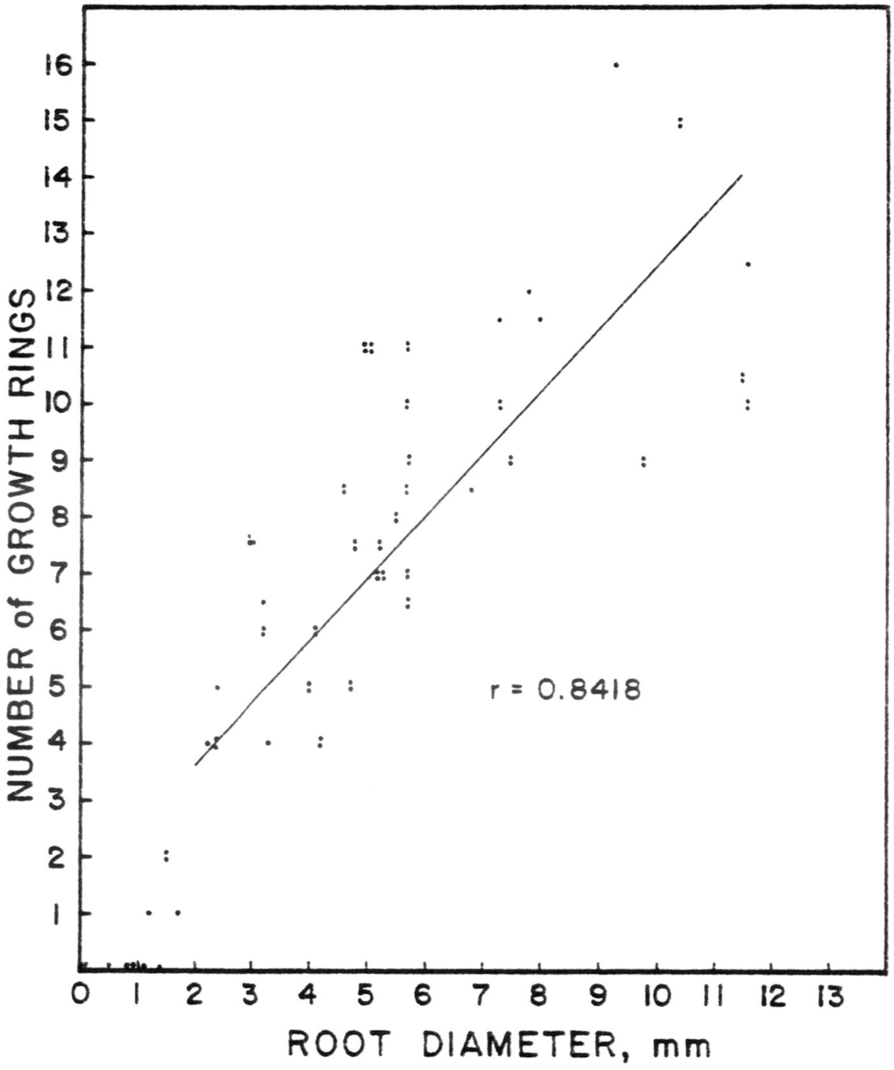

Figure 8. Root diameter and number of growth rings in lateral roots collected from Tar Swamp.

and poorest fit between 0.1 and 2 mm diameter and above 8 mm diameter. The equation was judged not to be a good predictor of the number of growth rings at root diameters in these ranges. Observations of ten roots below 1.5 mm diameter revealed that nine had no growth rings, whereas the regression predicted that a root of 1 mm diameter should have 2.5 rings and a root of 0.5 mm diameter should have 2.0 rings. No roots above 11.6 mm diameter were examined for growth rings; extrapolation of the regression line for roots of greater than 11.6 mm would be invalid.

Main roots of 16-month-old seedlings might be as much as 11.3 mm in diameter and yet possess only two growth rings. The seedling roots examined showed a maximum of two distinct and complete rings, although sometimes three or four indistinct or partial rings might be present. Thus seedling roots with one or two rings might be much larger in diameter than lateral roots with the same number of rings which were collected from Tar Swamp, where seedlings were almost completely absent.

These findings indicate that generally only one growth ring was formed annually in at least the greenhouse-grown plants. Experiences of other investigators have shown that more than one annual ring may be formed in various species of trees depending on environmental conditions (Kozlowski 1971, Vol. I, p. 234), and there is evidence of as many as three rings per year in some stems of water tupelo, although other stems showed annual rings (D. D. Hook 1980, personal communication). Thus the assumption of one ring = one growing season in water tupelo must be made with caution. Even if an estimate of age based on the regression of diameter and number of growth rings can be made for roots of 3.5-8 mm diameter, this correlation would not hold true for lateral roots of much less thickness and, therefore, the age of these finer roots cannot be safely estimated by their diameter.

Root Age Structure

Information about population parameters can be collected and organized in several ways. One method, used in invertebrate studies, is to identify and enumerate the individuals belonging to each of several age classes (cohorts) and to follow the progress of each cohort over a period of time in order to collect information on growth and mortality. In the case of roots, destructive sampling procedures preclude following a "cohort" of roots through time; therefore, a second method, that of determining age structure from samples taken all at one time, is used and the information organized in the form of a static or time-specific life table (Table 6) such as that described in Krebs (1972, pp. 159-161). This method is based on the assumption that the population possesses a stable age structure, that is, that the proportions of each age class in the population are unchanging from year to year.

Counts of roots from samples collected on all three dates in October 1980 are combined in the life table. Although age structure may have changed somewhat between these dates because of seasonal variation, this possibility was judged to be less important than

Table 6. Size-frequency distribution of roots in cross sections of soil from Tar Swamp.

Diam. class, mm	Midpoint of diam. class	Estimated age (yr)[a]	No. of root ends (n_x)	l_x[b]	d_x[c]	Age-specific mortality (q_x)[d]
0.0-0.5	0.25 mm	0	2759	10,000	8463	0.846
0.5-1.0	0.75	0	424	1537	1106	0.720
1.0-2.0	1.5	0	119	431	224	0.520
2.0-3.0	2.5	4.18	57	207	80	0.386
3.0-4.0	3.5	5.30	35	127	47	0.370
4.0-5.0	4.5	6.40	22	80	38	0.475
5.0-6.0	5.5	7.52	11.5	42	6	0.143
6.0-7.0	6.5	8.63	10	36	11	0.306
7.0-8.0	7.5	9.74	7	25	21	0.840
8.0-9.0	8.5	10.85	1	4		
9.0-10.0	9.5	11.96	7			
10.0-11.0	10.5	13.07	1			
11.0-12.0	11.5	14.18	0			
12.0-13.0	12.5	--	0			
13.0-14.0	13.5	--	1			
14.0-15.0	14.5	--	3			
15.0-16.0	15.5	--	0			
16.0-17.0	16.5	--	1			
17.0-18.0	17.5	--	0			
18.0-19.0	18.5	--	0			
19.0-20.0	19.5	--	0			
20.0-21.0	20.5	--	0			
21.0-22.0	21.5	--	1			
22.0-23.0	22.5	--	2			

[a] Obtained from regression equation (p. 44)

[b] Survivors adjusted to 10,000 original roots

[c] Deaths (losses) between two consecutive size/age classes adjusted to 10,000 original roots

[d] Calculated from $d_x \div l_x$

supplying information for as many size classes as possible in the table.

The extreme left-hand column in Table 6 lists diameter classes of roots which were separately tallied in soil cross sections. The midpoint of each diameter class is given in the next column to the right, and the estimated age of the class, based on the correlation established between diameter and number of growth rings (p. 44 and Figure 8) is given in the column immediately to the right of this. Each growth ring is assumed to represent one year. Because the regression was judged to fit only roots greater than 2 mm diameter, age estimates are not given for smaller roots.

Raw numbers of roots of each diameter class appear in the column headed n_x. These raw numbers are converted for simplicity to proportions of 10,000 by considering the smallest size class to contain 10,000 roots (column headed l_x). The next column (d_x) shows the number of roots based on 10,000 which disappeared in the interval between size classes (deaths). Mortality rates are calculated by dividing d_x by l_x in each size class and appear in the column headed q_x. It can be seen that each size class has a specific mortality rate.

In animal population studies utilizing the size-frequency method (see Hynes and Coleman 1968, Benke 1969, Waters and Hokenstrom 1980) mortality rates for individuals of each size (age) class can be applied to the average weight of an individual in that class. This gives the loss in weight (number of individuals lost times average individual weight) for each class. Totaling the losses over all size classes gives an estimate of total mortality. Assuming that the population is in steady state or applying a correction factor to account for imports and exports, if necessary, the total loss of biomass through mortality will be an estimate equal to the total biomass production. Although losses in numbers are apparent in the life table for roots, an average weight for individual roots is not available. A production estimate from biomass loss is thus not obtainable for the root population in this way.

Numbers of roots of greater than 24 mm diameter are not represented in the life table because of the limited number of samples. Age information on roots of greater than 11.6 mm diameter would be the product of extrapolation of the regression equation and thus invalid. However, roots from 0 to 10 mm diameter represent 80% of the biomass of all lateral roots in the upper 20 cm of soil in Tar Swamp (Table 1).

A survivorship curve based on 10,000 original roots shows the great reduction in the number of roots from the 0-0.5 mm class to the 0.5-1.0 mm class (Figure 9). About 85% of the smallest roots die before they attain the 0.5-1.0 mm size class; almost 98% die before reaching the 2.0-3.0 mm class. Growth rings were only rarely observed in roots of ≤ 1 mm diameter (Figure 8), suggesting that most roots of this size are less than one year old. Thus it can be concluded that about 85% of the roots in this population die within an interval of less than one year, before they reach 1 mm in diameter. The actual turnover time for <1 mm roots is not available from the

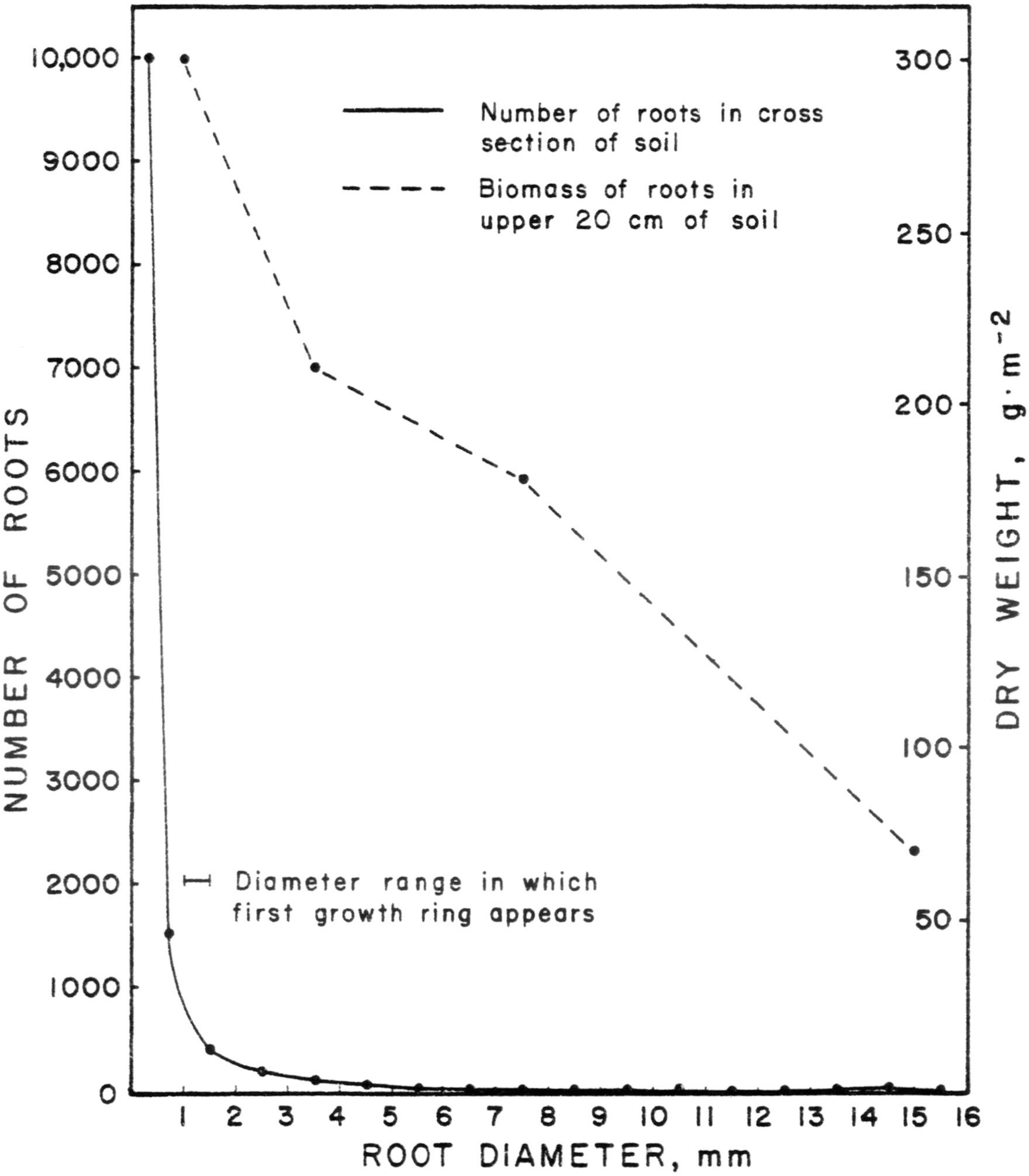

Figure 9. Survival curve of lateral roots in Tar Swamp and biomass of size classes in the upper 20 cm of soil. Diameter is plotted at the midpoint of each diameter class.

life table since there is no method for determining their age. For contrast, values for root biomass per m^2 in the upper 20 cm of soil in Tar Swamp are plotted on this graph.

Fine Root Dynamics in Seedlings

Individually marked root tips of water tupelo seedlings grown in root observation boxes in the greenhouse showed variable and uneven growth rates. Many root tips marked on April 15 showed no growth over the entire period of observation (30 days). Of the root tips which did elongate, rates ranged from 0.07 to 3.75 mm per day in the unflooded plants and from 0.12 to 1.0 mm per day in the flooded plants. These were average rates observed over a variable number of days. Actual growth rates for individual roots were very irregular; in many cases a root might elongate greatly for several days and then show no further elongation.

Mapping of the entire visible root systems of two of the flooded seedlings and two of the unflooded seedlings which was started on May 15 gave a more complete indication of overall growth of roots (Figure 10). Measurements of the original root length visible on the longer transparent face of each root box are given in terms of grid intersections (number of intersections of roots with lines on a 0.25 cm grid placed under the transparent tracing) in Table 7. Five-day length increments, which were traced onto the acetate sheet with a different ink color each time, are given in terms of grid intersections and percent of original root length. A separate tracing of the root system visible at the end of 35 days

Figure 10. Photograph of roots visible at transparent face of root observation box.


side 1

Table 7. Production in roots of water tupelo seedlings. Elongation of visible roots is used as a measure of production; the total length increment is a measure of gross production of new root length, while the difference between original and final length is a measure of net production.

	Flooded Seedlings				Unflooded Seedlings			
	1F		4F		1U		2U	
	Length units	Percent of orig. length	Length units	Percent of orig. length	Length units	Percent of orig. length	Length units	Percent of orig. length
Original Length	230	100.0	318	100.0	622	100.0	522	100.0
Length Increments								
No. days								
5	38	16.5	42	13.2	40	6.4	58	11.1
10	34	14.8	28	8.8	51	8.2	48	9.2
15	58	25.2	68	21.4	73	11.7	22	4.2
20	30	13.0	26	8.2	110	17.7	33	6.3
25	30	13.0	41	12.9	94	15.1	22	4.2
30	47	20.4	89	28.0	70	11.2	40	7.7
35	10	4.4	35	11.0	33	5.3	36	6.9
Total length increment (gross production)	247	107.3	329	103.5	471	75.6	259	49.6
Final length	300	130.2	396	124.7	587	94.4	454	86.9
Original length	-230	-100.0	-318	-100.0	-622	-100.0	-522	-100.0
Difference (net production)	70	30.2	78	24.7	-35	-5.6	-68	-13.1

was measured by the grid method and given near the bottom of Table 7 (Final length). In this way both a record of periodic growth increments and overall mortality was obtained. Almost all visible roots were <1 mm in diameter. Exceptions were some segments of the main tap roots which were between 1 and 2 mm in diameter.

Using elongation as a measure of root production, seedlings in the flooded treatment had greater production over the 35 days than plants in the unflooded treatment. Based on the original visible root length, the two flooded plants (1F and 4F) increased by 14.3% to 28% every five days for a total increment of 107.4% (1F) and 103.5% (4F). The two unflooded seedlings (1U and 2U) increased by 4.2% to 17.7% every five days for a total increment of 75.7% (1U) and 49.6% (2U).

In the flooded seedlings, the final root length visible after 35 days was longer than the original length, indicating that root length was increasing in these plants at a faster rate than it was disappearing. Net production, the difference between the original and final length, was about 30% and 25% of the original length in seedlings 1F and 4F, respectively. In the unflooded seedlings, final length of the visible root system was shorter than the original length. Although new root length was being added continually over the 35 days, existing root length was being lost at a slightly faster rate resulting in a net loss of about 6% in 1U and 13% in 2U. Although appearance or disappearance of roots could have resulted from soil shifting, as well as from growth and mortality, this was judged to be minor and these factors should have cancelled each other out. Gross production in the visible root systems would be reflected in the sum of five-day increments in length and is greater in the flooded plants (107.3% and 103.5%) than in the unflooded plants (75.6% and 49.6%).

In order to verify whether a given amount of root elongation would result in similar biomass production in both flooded and unflooded plants, subsamples of ≤ 1 mm diameter roots of both groups were measured for length, dried and weighed. The average dry weight per unit of length in three subsamples of flooded plant roots was 0.0965 $mg \cdot cm^{-1}$ (Table 8). For the unflooded plants the average for three subsamples was 0.0852 $mg \cdot cm^{-1}$. No significant difference at the $p = 0.05$ level was found between the two groups. The pooled average dry weight per cm (0.0908 $mg \cdot cm^{-1}$) could then be used to convert length estimates of production to a dry weight basis (Table 9).

Average root/shoot biomass ratio for the flooded plants obtained after harvest and drying was 0.45 which was half that of the ratio of 0.90 for the unflooded plants (Table 10). This difference in root/shoot ratio was caused by higher shoot dry weight in the flooded treatment (significant, $p < 0.05$) since the difference in average root dry weight in the two sets of seedlings was not significant. In addition, flooded plants had more leaves per plant and a generally healthier appearance. Only the smallest flooded plant, 3F, had a

Table 8. Dry weight/length relations for ≤ 1 mm root subsamples of water tupelo seedlings.

Total length of subsample, cm	Dry weight of subsample, mg	Weight per unit length, $mg \cdot cm^{-1}$
	Flooded Seedlings	
292.0	52.0	0.1781
244.2	15.8	0.0647
214.7	10.0	0.0466
$\bar{x}$		0.0965
	Unflooded Seedlings	
245.1	22.6	0.0922
170.9	12.2	0.0714
203.3	18.7	0.0920
$\bar{x}$		0.0852
Pooled average of all subsamples		0.0908

Table 9. Length and weight conversions for fine roots of tupelo seedlings.

Plant	Measurements	Root length, grid units[a]	Root length, cm[b]	Root dry weight, mg[c]
1F	Original	230	43.28	3.93
	Final	300	56.40	5.12
4F	Original	318	59.77	5.43
	Final	396	74.23	6.74
1U	Original	622	116.74	10.60
	Final	587	110.18	10.00
2U	Original	522	98.00	8.90
	Final	454	85.26	7.74

[a] From Table 7

[b] Length: $y = 0.187x + 0.181$
where y = length in cm
x = length in grid units

[c] Dry weight: $0.0908 \text{ mg} \cdot \text{cm root length}^{-1}$

Table 10. Characteristics of water tupelo seedlings used in greenhouse study at harvest.

Treatment	Plant	Orig. shoot height, cm	Final shoot height, cm	No. leaves	Shoot dry wt., g	Root dry wt., g	Root/shoot ratio	Presence of succulent roots
Flooded	1F		87	23	6.68	2.06	0.31	Several
	2F		95	47	9.17	5.95	0.65	Several
	3F		79	22	5.95	2.69	0.45	No observation
	4F		104	33	10.87	4.37	0.40	Several
	$\bar{x}$	56	91	31	8.17*	3.77	0.45	
Unflooded	1U		70	20	5.98	6.54	1.09	None
	2U		58	17	3.57	3.26	0.91	None
	3U		54	0	2.37	1.87	0.79	No observation
	4U		61	14	4.10	3.38	0.82	None
	$\bar{x}$	53	61	10	4.00*	3.76	0.90	

*Difference between mean shoot dry weight of flooded and unflooded plants was significant at the 0.05 level.

lower shoot weight than any of the unflooded plants, and it also was the only one of the flooded plants with fewer leaves than some of the unflooded plants.

DISCUSSION

Sampling Variation

Between-plot variation for total root biomass was substantially higher for Creeping Swamp roots than for Tar Swamp roots (Figure 4), which may reflect differences in several features. Species diversity was greater in Creeping Swamp than in Tar Swamp, where dominance by one species (water tupelo) was high. Creeping Swamp showed greater spatial variability than Tar Swamp. Excavations in Creeping Swamp revealed a fairly definite organic layer of soil underlain by clayey and sandy layers, varying in depth from one quadrat to another; many roots were generally present in the clayey layers, but very few extended into the light-colored sandy layer under the clay if such a layer was reached. Because of small elevation differences in the floor of the swamp, water depth varied by several cm between quadrats in Creeping Swamp. Tar Swamp, in contrast, had a layer of litter and organic matter at the top of the soil underlain by fairly homogeneous organic mud to the sampling limit of 40 cm; a sandy layer was not encountered (Bradshaw 1977 reports a mineral layer at about 75 cm below the surface in Tar Swamp). Water depth in Tar Swamp appeared to be fairly uniform because of the level swamp floor.

Reliability of estimates of large (20-100 mm diameter) roots is lower than that for smaller root size classes. Sampling frequencies that are adequate for the more evenly distributed smaller size classes may be inadequate for large roots (Karizumi 1968), a factor which needs to be considered when comparing size distribution of roots between the two swamps.

Comparison of Belowground Biomass in Forested Ecosystems

Harris and coworkers (1977) used a combination of soil cores taken $\geq$60 cm from any tree and excavation of individual tree root systems to obtain estimates of lateral (cored) and stump (excavated) root biomass in a 40-year old upland yellow poplar forest in Tennessee. The two root components contributed approximately equal amounts to the total root biomass of the stand, 3600 $g \cdot m^{-2}$. Lateral root biomass estimates obtained from quadrats which were excavated $\geq$50 cm from trees in Tar and Creeping Swamps (2345 and 2702 $g \cdot m^{-2}$, respectively), based on proportions established for the Tennessee forest, may, therefore, approximate half the total root biomass per unit area in these swamps. Root biomass in various forested ecosystems has been measured by soil cores, excavations of soil pits or monoliths, excavations of individual tree root systems, and combinations of these methods. Although the effects of different sampling methods are difficult to evaluate, root biomass in the two North Carolina swamp forests appears to be intermediate in a range of root biomass values for forested ecosystems (Table 11).

Most forest stands in which vertical zonation of roots has been observed show a high concentration of roots in the top layer of soil and decreasing proportions with increasing depth, as was noted in the Introduction. Klinge (1976) summarized root zonation in an Amazon

Table 11. Root biomass for selected wetland and upland forested ecosystems.

Community	Maximum sampling depth (cm)	Belowground biomass ($g \cdot m^{-2}$)	Source
Wetlands			
Cypress strand, Fla.	--	2343-9628[a]	Lugo et al. 1978
Cypress strand, Fla.	30	311-808[a] 4291-8358[b]	Burns 1978
Scrub cypress, Fla.	30	783[a]	Brown 1978
Dismal Swamp, Va.			Montague & Day 1980
Cypress	60	1531[a]	
Maple-gum	60	1222[a]	
Melaleuca swamp, Cambodia	--	387[b]	Hozumi et al. 1969
Bog forest, Manitoba	25	2280[a]	Reader & Stewart 1972
Tar Swamp, N.C.	40	2345[a]	This study
Creeping Swamp, N.C.	40	2702[a]	This study
Uplands			
Liriodendron forest, Tenn.	60	1600[b]	Harris et al. 1977
Mixed hardwood, Va.	60	3097[a]	Montague & Day 1980
Mixed deciduous, N.H.	--	1216-2064[a] 2349-3220[b]	Whittaker et al. 1974
Moist tropical, Panama	30	985-1263[a]	Golley et al. 1975
Latosol rain forest, Amazon	107	3974[a]	Klinge 1976
Tropical rain forest ($\bar{x}$ of two sites)	--	10,100[b]	Rodin & Basilevich 1967
Subtropical deciduous ($\bar{x}$ of several studies)	--	8200[b]	Rodin & Basilevich 1967
Douglas fir, Ore.	--	20,900[b]	Santantonio et al. 1977

[a] Lateral roots only, sampled by pit or coring technique.
[b] Total belowground biomass, including stump roots.

rain forest on the basis of soil horizons, finding the greatest concentration of biomass in the H horizon at a depth of 2-6 cm and decreasing biomass with depth to 107 cm. Root excavation sites in a Florida cypress strand, however, showed variability in vertical root distribution. Two out of three pits showed a trend of rapidly decreasing biomass with depth, while a third pit showed the greatest biomass of roots at 12-20 cm with a gradual decrease with depth and extension of roots to a much greater depth (Lugo et al. 1978). Some ecosystems for which comparable data have been established are listed in Table 12. In contrast to Creeping Swamp and other forested communities, Tar Swamp shows a gradual increase in root biomass allocation with depth.

Differences in hydrology and sedimentation of forested wetlands may thus affect the vertical distribution of roots. A high proportion (72%) of all root biomass in Creeping Swamp was found in the upper 20 cm. In Tar Swamp, only 37% of root biomass was present in the upper 20 cm, and the increase of root biomass with depth was due to increased biomass of large (5-100 mm) roots (Table 1). The Tar Swamp forest, located on the alluvial floodplain of a major river, may be near the maximum end of a hypothetical gradient of extent and duration of flooding. Cambial oxygen transport from aboveground parts to roots, a phenomenon which has been demonstrated in flood-tolerant water tupelo (_Nyssa aquatica_ L.) and water ash (_Fraxinus caroliniana_ Mill.) (Hook et al. 1972), may enable these dominant Tar Swamp species to maintain a large biomass of roots at deep levels

Table 12. Vertical distribution of lateral root biomass in several forested communities as percent of lateral root biomass.

Depth interval (cm)	Mixed hardwood[a]	Cypress[a]	Maple-gum[a]	Yellow poplar[b]	Creeping Swamp[c]	Tar Swamp[c]
0-10	45.0	41.0	38.2	35.2	34.0	12.5
10-20	34.3	22.2	30.4	27.6	38.1	24.1
20-30	10.9	12.5	11.2	20.0	22.2	27.2
30-40	4.9	9.6	8.5	9.2	5.7	36.2
40-50	3.3	10.2	6.1	5.7	n.s.[d]	n.s.
50-60	1.5	4.5	5.6	2.3	n.s.	n.s.
Total	100	100	100	100	100	100

[a] Montague and Day (1980). These communities represent different community types found in the Great Dismal Swamp of southeastern Virginia. Cypress and maple-gum communities are intermittently flooded; mixed-hardwood community is rarely flooded.

[b] Harris et al. (1977). Upland yellow poplar forest in eastern Tennessee. Biomass estimated here for 10 cm depth intervals from 15 cm intervals reported in original study.

[c] This study.

[d] Not sampled.

for structural support in the unstable, anaerobic substrate (bulk density, 0.35 $g \cdot cm^{-3}$) which consists of homogeneous fine deposited material to 40 cm or deeper. Creeping Swamp, on the other hand, flooded by the relatively sediment-poor waters of a small headwater stream, appears to retain a soil profile of distinct horizons as well as a vertical root distribution resembling that of upland forests. The constraints of an unstable substrate as well as the absence of molecular oxygen in sediment typical of Tar Swamp may thus restrict diversity to a few species of specialized trees.

Variation in Root Nutrient Concentrations

Root nutrient concentrations have been found to vary for individual tree species (Likens and Bormann 1970) as well as with size class and depth. Cox et al. (1977) found that N and K levels in roots of a yellow poplar forest in Tennessee decreased with increasing root diameter, and Santantonio et al. (1977) showed the same to be true for N, P, and K levels in roots of an old-growth Douglas fir forest. Phosphorus levels measured in roots of a cypress strand in Florida decreased with increasing depth and showed irregular variation with size class (Lugo et al. 1978). Levels of N and K measured in roots of an Amazon rain forest by Klinge (1976), although quite variable, showed no clear trend associated with either size class or depth; concentrations of P, Ca, Mg and Na were found to vary with size class and depth.

Differences in nutrient concentrations in roots may reflect several possible factors. Species differences in nutrient requirements as well as abundance of the nutrient in an available form will affect uptake. Nutrient supplies in the soil at levels in excess of plant requirements may result in "luxury uptake" by plants and storage in organs such as large roots.

In the two North Carolina swamp forests, nutrient concentrations of roots showed substantial variation with size class and depth, although trends were not always consistent. At all levels, concentrations of N in roots in both swamps tended to decrease with increasing root diameter from the finest roots to the 10-20 mm roots (Figure 5). This trend probably reflects higher proportions of metabolically active, growing tissue in smaller roots and the increasing woodiness of progressively larger roots. A similar trend for P concentrations was apparent only in the two top levels of soil in Tar Swamp (Figure 5), as was also true of cation (K, Ca, Mg, and Na) concentrations generally (Figure 6). Knowledge of nutrient concentrations and biomass values for individual size classes of roots is cited by Cox (1972) as important in estimation of rates of nutrient cycling, since various sizes of roots are likely to turn over at different rates.

Comparison of Root Nutrient Concentrations and Stocks in Forested Ecosystems

Concentrations of N in roots of both swamp forests were within the range of N concentrations found in other forested systems, tending to be lower than those found by Cox in the yellow poplar forest but somewhat higher than those of the old-growth Douglas fir stand in

Oregon (Table 13).

Concentrations of P in Tar Swamp roots were high in comparison to Creeping Swamp and roots of a Florida cypress strand and other forested ecosystems. Cation concentrations in roots of the two swamps varied in their rank on the scale of those forests studied, but were generally at the high end. Creeping Swamp showed especially high concentrations of Ca in roots, even omitting from consideration the unusually high peaks of Ca in 10-20 mm roots (Figure 6). Na concentrations were also high in Creeping Swamp roots, while Tar Swamp roots had the highest concentrations of Mg of those forests for which values were available. The high levels of P in Tar Swamp in comparison with other forests may be a reflection of the greater mobility of this element in the more constantly flooded sediment.

Stocks of N in both swamps and stocks of P in Creeping Swamp roots were rather low in comparison to root N and P stocks in other forested ecosystems. Stocks of K and Ca in the two swamps were intermediate, while stocks of Mg and Na were rather high, based on a limited comparison (Table 14).

Findings of unusually high levels of iron in these swamp forest tree roots, particularly fine roots (up to 80,000 $\mu g \cdot g^{-1}$; Figure 7) are surprising in view of the fact that the presence of much lower levels in plant tissues would be highly toxic (Green and Etherington 1977, Chen et al. 1980). For comparison, iron concentrations of upland tree roots ranged from 23-1475 $\mu g \cdot g^{-1}$ (Likens and Bormann 1970) in a New Hampshire forest and 126-592 $\mu g \cdot g^{-1}$ in a local eastern North

Table 13. Ranges of nutrient concentrations in roots of forested ecosystems.

		mg·g dry wt-1					
Community	%N	P	K	Ca	Mg	Na	Source
Yellow poplar forest, Tenn.	0.66-1.18	--	5000-21,500	--	--	--	Cox et al. 1977
Mixed deciduous, N.H.							Whittaker et al. 1979
Acer saccharum	0.71	3700	2700	2500	500	125	
Betula lutea	0.61	800	1400	3700	400	122	
Fagus grandifolia	0.64	1200	2400	3600	500	145	
Latosol rain forest, Amazon	0.70-1.12	60-200	300-2000	200-4000	200-1200	200-2000	Klinge 1976
Douglas fir, Ore.	0.08-0.44	470	300-420	1140-3840	--	--	Santantonio et al. 1977
Cypress strand, Fla.	--	360-1880	--	--	--	--	Lugo et al. 1978
Tar Swamp, N.C.	0.16-0.98	44-3000	200-10,000	800-3800	150-3000	50-3000	This study
Creeping Swamp, N.C.	0.21-1.02	200-1000	300-4000	2500-6200	100-1400	300-400	This study

Table 14. Nutrient stocks in roots of forested ecosystems in $g \cdot m^{-2}$.

Community	N	P	K	Ca	Mg	Na	Source
Mixed deciduous, N.H.	18.1[b]	5.3[b]	6.3[b]	10.1[b]	1.3[b]	0.38[b]	Whittaker et al. 1979
Yellow poplar forest, Tenn.	15.9[a] 21.3[b]	--	21.2[a] 23.9[b]	-- --	-- --	-- --	Cox et al. 1977
Douglas fir, Ore.	6.4[c] 23.0[b]	1.1[c] 2.4[b]	1.8[c] 7.4[b]	7.6[c] 33.0[b]	-- --	-- --	Santantonio et al. 1977
Latosol rain forest, Amazon	37.9[d]	0.42[d]	2.9[d]	5.3[d]	2.5[d]	2.6[d]	Klinge 1976
Cypress strand, Fla.	--	3.54[a]	--	--	--	--	Lugo et al. 1978
Tar Swamp, N.C.	10.0[a]	4.66[a]	9.24[a]	6.89[a]	4.47[a]	4.59[a]	This study
Creeping Swamp, N.C.	14.3[a]	1.52[a]	7.25[a]	14.9[a]	2.65[a]	4.56[a]	This study

[a] Stocks in lateral roots only, sampled by pit or coring technique.

[b] Stocks in total belowground biomass, including stump roots.

[c] Stocks in roots of 0-10 mm diameter only.

[d] Stocks in lateral roots of 0-50 mm diameter.

Carolina upland mixed deciduous woods, much less than most values found in this study. The trend of decreasing Fe concentrations with increasing diameter of roots indicates that Fe levels may be proportional to surface area and thus that Fe is associated with the outer layers of roots.

The significance of high levels of iron in roots of flooded plants is unclear. Some plants poorly adapted to flooding accumulate large quantities of Fe when grown under flooded conditions (Jones and Etherington 1970, Keeley 1979). However, oxidation of reduced compounds such as the soluble Fe^{++} present in the water and sediments of swamp forests and precipitation of the insoluble oxidized compounds can be brought about by oxygen transport from aboveground parts of the plant through the cambium to the roots in flood-tolerant plants such as water tupelo (*Nyssa aquatica* L.), water ash (*Fraxinus caroliniana* Mill.), black gum (*Nyssa sylvatica* var. *biflora*), and rice (*Oryza sativa* L.) (Armstrong and Boatman 1967, Hook et al. 1972, Green and Etherington 1977, Keeley 1979, Chen et al. 1980). It has been suggested that the ability to "oxidize the rhizosphere" and to oxidize and precipitate iron compounds on and in the root cortex may prevent translocation of toxic excesses of iron to other parts of the plant (Armstrong and Boatman 1967, Keeley 1979). However, accumulation of Fe on the cell walls of the root cortex, as observed by Armstrong and Boatman (1967) in the roots of *Menyanthes trifoliata* in bogs, may also represent a stress to the plant by inhibiting gas exchange within the root. The possibility that Fe oxidation and precipitation is associated with the root cortex is suggested by the trend of increasing Fe concentrations with decreasing root diameter (Figure 5) and consequently greater proportion of surface area to volume. Since a greater proportion of the surface area of roots becomes suberized with increasing age (Kramer and Kozlowski 1979, p. 46), large diameter roots presumably have more suberization of cell walls, which may restrict radial oxygen transport. Thus whether Fe precipitation is a means of coping with the stresses of an anaerobic substrate or eventually constitutes a stress in itself is uncertain.

Assessment of Approaches to Determining Root Production

Age Structure Analysis

The usefulness of applying the age structure analysis or life table approach to the problem of root mortality and production is mainly in the information it supplies on the frequency distribution of root diameter classes, giving an approximation of root age distribution in soil and an indication of the maximum length of survival of most fine roots. In the present study soil blocks were found to contain a very large number of the finest roots relative to large roots, implying that only a limited number of these fine roots survive and grow to larger size classes and that a great number of fine roots appear to be very short-lived (Figure 9).

The problem with the use of these techniques as a method for obtaining an estimate of root production is that unlike benthic invertebrates, with which techniques like these have been successful, roots are not separate entities which can easily be assigned an average weight. Estimation of production in invertebrates depends on knowledge of the life history and calculation of an average weight for animals of a particular linear dimension, which are often readily identifiable stages, such as instars. Percent mortality, from losses between successive size classes, is multiplied by the average individual weight to give the biomass loss for each size class and the sum of biomass losses over all size classes gives an estimate of biomass production. Percent mortality between size classes cannot be applied to unit area biomass values which have been determined for roots (Table 1). If a length/weight relation for each class could be worked out within reasonable confidence limits, as has been done for roots $\leq$1 mm (Table 8), figures for average biomass of individual roots would be available for application of mortality rates.

Successful application of this approach would also require a larger number of samples in order to obtain adequate information for each size class including a representative number of large (>20 mm) roots. This would require greater resources for transporting the soil blocks, ample freezing space for storage, and better access to a band saw for cutting the frozen soil blocks. Periodic sample collections throughout the year would also provide more representative information about the relationships among size classes by taking into account potential seasonal changes in numbers of roots in each class. Obtaining samples of soil in intact blocks from below 20 cm depth, especially in waterlogged soil, would pose difficulties.

Age estimates of roots might be improved by use of magnification to determine the number of growth rings directly rather than from diameter measurements.

Fine Root Dynamics

Differences in root/shoot ratios due to differences in shoot dry weight, as well as differences in general appearance, number of leaves, and presence or absence of succulent roots (Table 10) indicate that watering regime affected the growth of tupelo seedlings. Results of root length measurements (Table 7) indicate that net root production was positive in the flooded plants over the period of observation (production exceeded mortality) and negative in the unflooded plants (mortality exceeded production). Because of the young age of the plants and the length of time growth was observed, a balance between new growth and mortality or steady state was not observed; such a situation would not be expected in seedlings as it might be in a mature forest from year to year. Graphs of length increments in fine roots illustrate the processes of production and mortality (Figure 11). In plant 1F the final visible root length (299.5 units) was greater than the initial visible root length (230 units). If all root material had remained visible, addition of root length increments to the initial visible root length would have given a total final length of 477 units instead of 299.5 units. The difference between potential and actual final root length is 177.5 units, the length of roots which disappeared. A line connecting the mortality value of 177.5 at 35 days with the initial length of roots which disappeared represents the

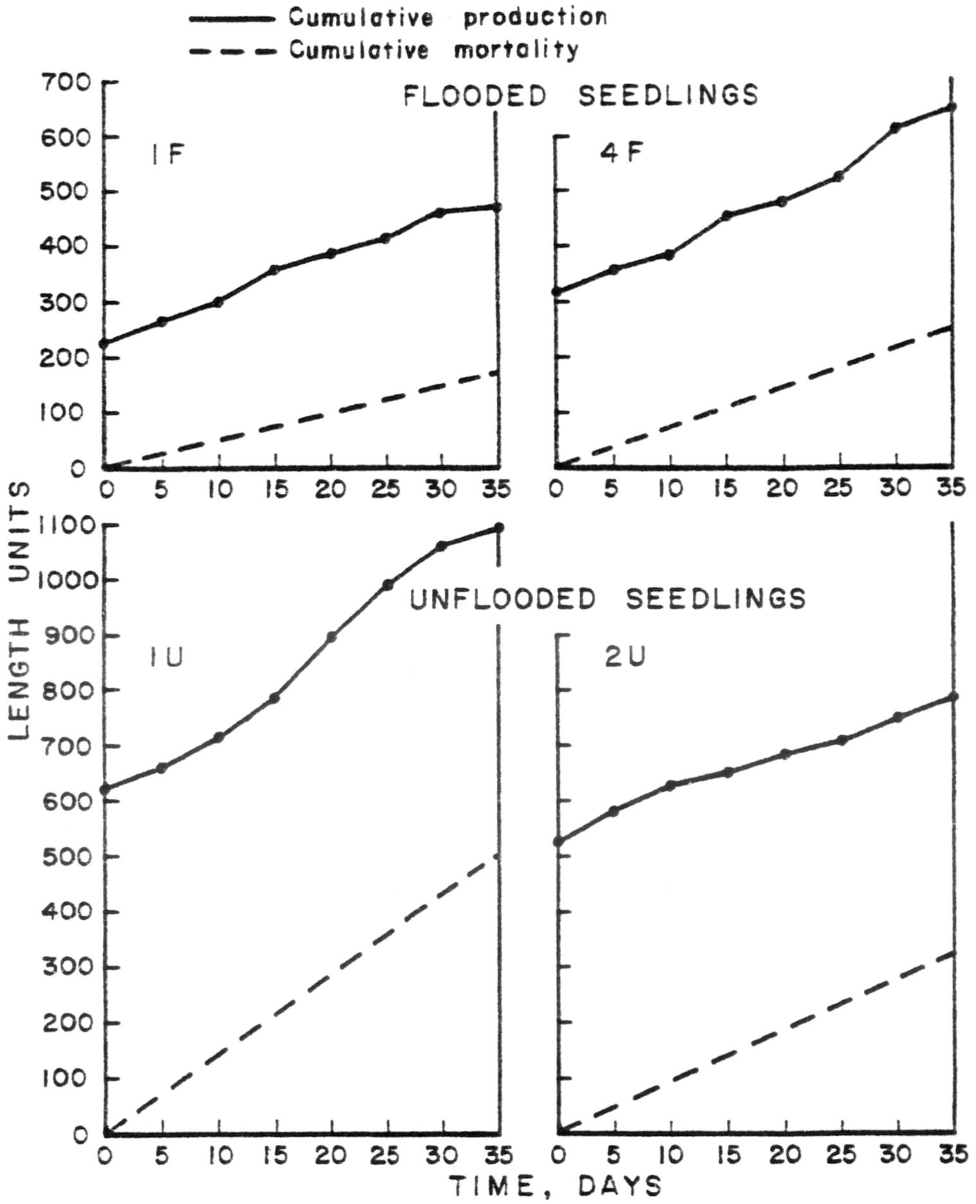

Figure 11. Production and mortality of visible roots of water tupelo seedlings.

average disappearance or mortality rate of roots during 35 days. Gross production is represented by the total length of increments which were added in 35 days (247 units). If only the net change in root length over 35 days were considered, the magnitude of production would appear to be smaller than that seen in these results. For example, in the unflooded plants periodic measurement of length increments shows that a considerable amount of root elongation was taking place even though the net change was negative (Figure 11). In the flooded plants, the net increase in length shown by original and final measurements reflects only about one-fourth of the actual production that was occurring. These observations tend to support the hypothesis that opposing changes in fine root biomass take place simultaneously over short intervals of time and that mortality as well as new growth may be a continual process which may result in high production values for fine roots if carried on over much of the year. Thus methods involving periodic coring and biomass measurements may underestimate fine root production severalfold.

The turnover rate of <1 mm roots in the flooded seedlings can be calculated by using the average of rates of gross production and mortality to equal throughput and original length to equal content as follows:

Plant 1F:

Average daily gross production rate = 7.06 units per day

Average daily mortality rate = 5.09 units per day

Average of gross production and mortality rates = 6.06 units per day

Turnover rate = $\frac{6.06}{230}$ = 0.026 per day

Residence time = $\frac{230}{6.06}$ = 38 days

Plant 4F:

Average daily gross production rate = 9.40 units per day

Average daily mortality rate = 7.16 units per day

Average of gross production and mortality rates = 8.28 units per day

Turnover rate = $\frac{8.28}{318}$ = 0.026 per day

Residence time = $\frac{318}{8.28}$ = 38 days

Thus the residence time for <1 mm roots under favorable conditions in these seedlings is 38 days, or about 5 wk. Similar calculations for the unflooded seedlings gave an average residence time of 53 days. It is reasonable to expect residence time and turnover rate to vary with the season of the year, using differences seen between flooded and unflooded seedling root growth to represent more or less favorable environmental conditions. The gap between production of new root material and mortality would be expected to widen under favorable seasonal conditions and to narrow under less favorable conditions, leading to changes in standing crop biomass. Under semi-controlled conditions and assuming a constant daily mortality rate (calculated by dividing total cumulative mortality by 35 days), there is great variation in net production of fine roots even during the 35-day observation period (Figure 12).

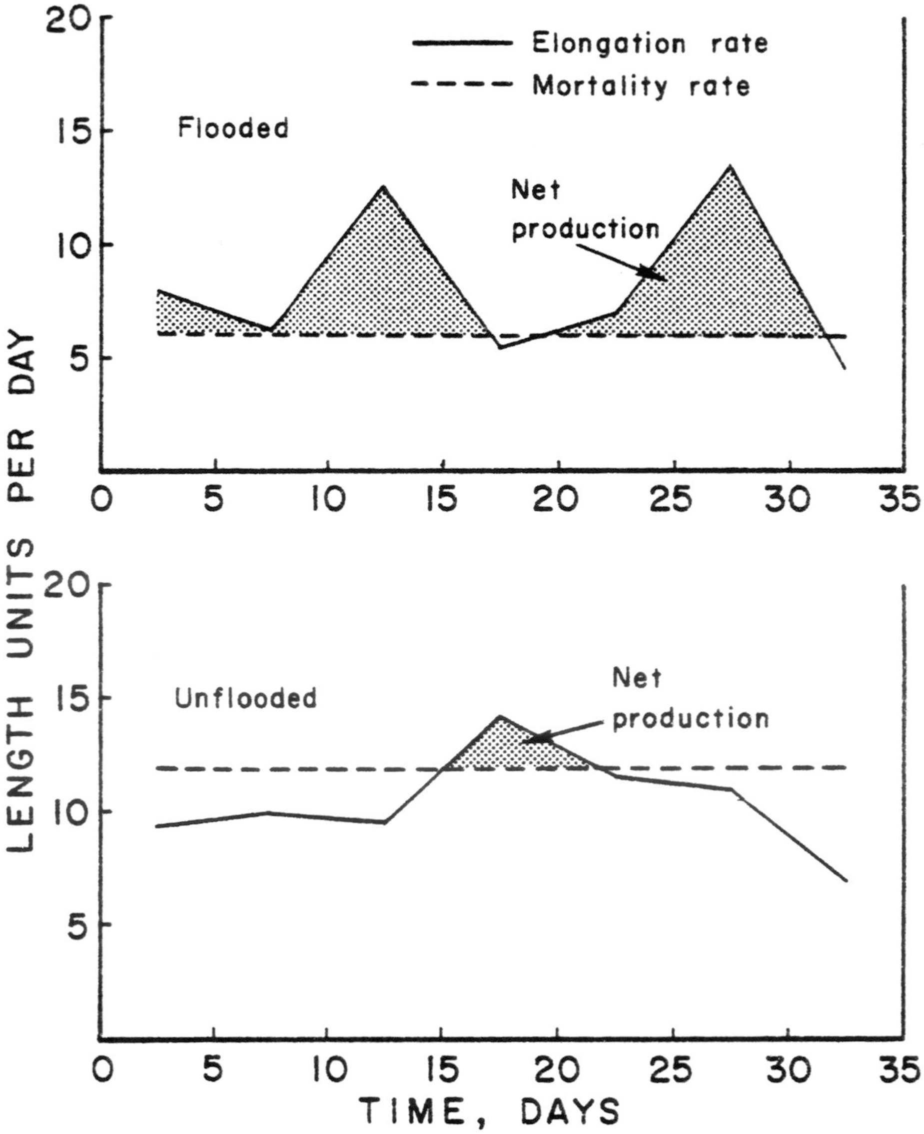

Figure 12. Average daily rates of elongation and mortality for flooded and unflooded tupelo seedlings. Daily elongation rates are calculated from five-day rates and averaged for two plants in each treatment; daily mortality rates are calculated from total cumulative mortality over 35 days, averaged for plants in each treatment.

Nutrient Cycling

If roots are important in nutrient cycling, as has been suggested by Cox et al. (1977), determination of organic matter and nutrient content for various size classes of roots is necessary for estimation of turnover rates of these materials in forested ecosystems. Standing stocks of organic matter (as ash-free dry weight) and nutrients in lateral roots at the 0-10 cm depth in Tar and Creeping Swamp can be compared with stocks in sediments of Tar Swamp (Brinson et al. 1981) and Creeping Swamp (soil sampled in the area of the root excavation pits in January 1979; unpublished data). Results of analyses for the top 5 cm of soil, from which samples were taken, are here assumed to be true for the top 10 cm. Results reported in terms of weight of organic matter and nutrients per dry weight of soil were converted to an area basis by multiplying by the bulk density (0.35 $g \cdot cm^{-3}$, Tar Swamp; 0.52 $g \cdot cm^{-3}$, Creeping Swamp) to make them comparable to standing stocks in roots at 0-10 cm depth.

Roots in the top 10 cm of soil comprised a small fraction of organic matter in soil in both swamps, but this was about twice as high in Creeping Swamp (5%) as in Tar Swamp (2.5%). Organic matter in the top 10 cm of soil in the Creeping Swamp study site was about 1.5 times the amount in Tar Swamp (17,450 $g \cdot m^{-2}$ vs. 11,020 $g \cdot m^{-2}$) (Figure 13a).

Roots made up a very small fraction of total nitrogen in the sediments of both swamps, but more in Creeping (0.8%) than in Tar Swamp (0.5%). Sediment total N was twice as high in Creeping as in

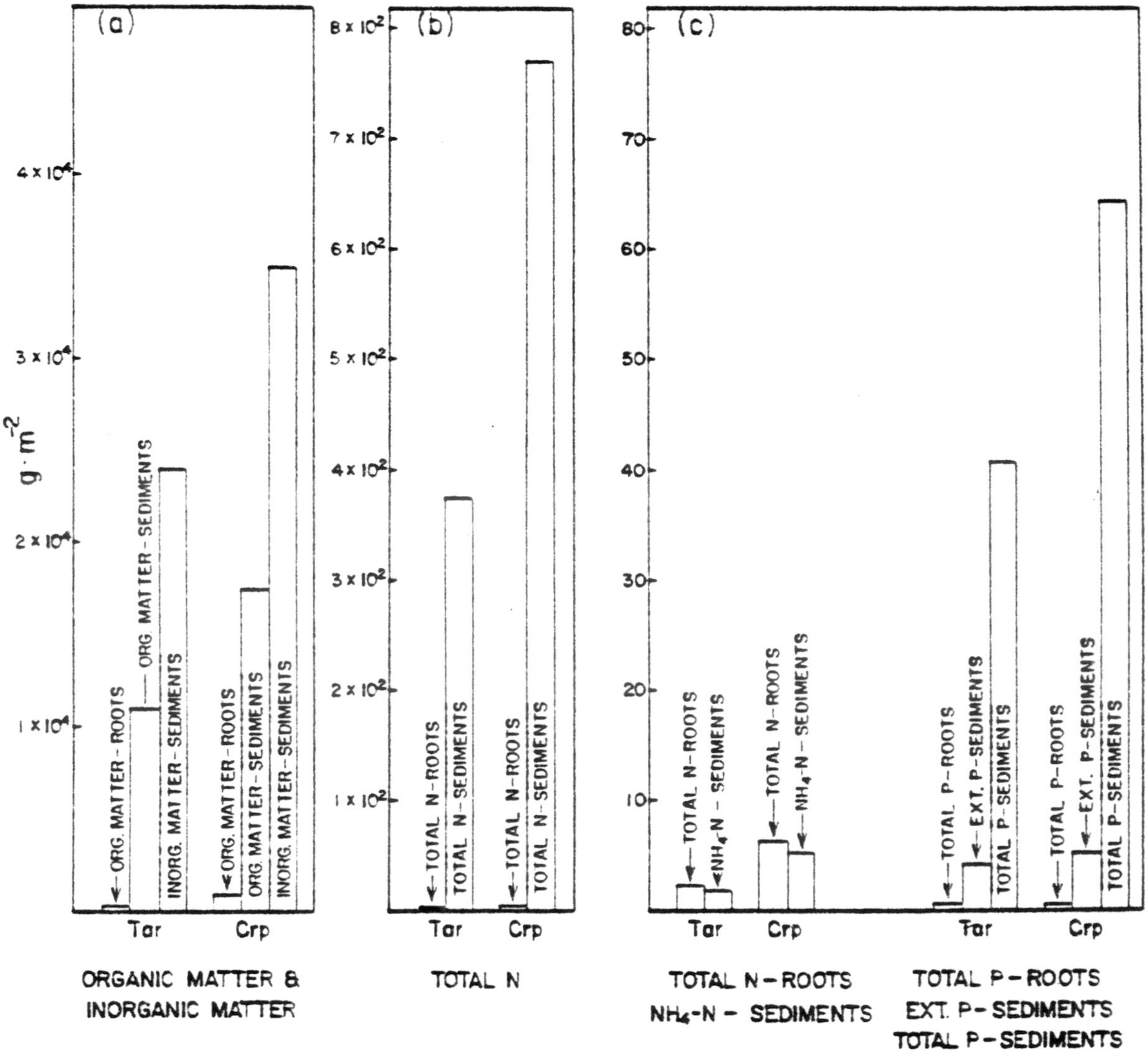

Figure 13. Comparison of standing stocks of nutrients and organic matter in lateral roots and sediments to 10 cm depth.

Tar (770 vs. 378 $g \cdot m^{-2}$ in the top 10 cm) (Figure 13b). About 0.5% of the total N in the sediments of Tar Swamp is in the form of NH_4-N, which is the major fraction of inorganic N available to plants in this swamp, where NO_3-N levels are very low because of anaerobic conditions (Brinson et al. 1981). Roots in the top 10 cm in this swamp contained slightly more total N than the NH_4-N in the sediments. In Creeping Swamp, NH_4-N is about 0.7% of the sediment total N; roots at 0-10 cm also contained slightly more total N than the NH_4-N component of the sediment (Figure 13c).

Root total P stocks were only a small fraction of the total P in the sediments in both swamps (0.6 $g \cdot m^{-2}$ of 41 $g \cdot m^{-2}$, or 1.6%, in Tar Swamp; 0.7 $g \cdot m^{-2}$ of 64 $g \cdot m^{-2}$, or 1%, in Creeping Swamp). Root total P represented less than the extractable fraction of P in the sediments of each swamp (about 5%).

Total nitrogen and phosphorus stocks in roots per square meter in each swamp (Tables 4 and 5) were converted to gram-atoms for comparing atomic ratios. The N:P ratios in roots were similar to those in sediments for each swamp, respectively (Table 15). Nitrogen and phosphorus concentrations in roots thus appear to reflect the proportions present in the swamp sediments. The lower ratio in Tar Swamp is probably due to the much larger watershed providing a greater supply of phosphorus. Similarity of concentrations of these nutrients in roots to soil concentrations suggests that luxury uptake of nutrients in excess of plant requirements was taking place.

Table 15. Atomic ratios of N and P in lateral roots and swamp sediments, based on nutrient stocks per square meter.

	N:P Ratio	
	Tar Swamp	Creeping Swamp
Sediment	4.2[a]	26.5[b]
Lateral roots	4.8[c]	20.9[c]

[a] Brinson et al. 1981, p. 49.

[b] Analyses of soil in root sampling area, 1979; unpublished data.

[c] Tables 4 and 5, this study.

Cox (1972) estimated that 90% of dead roots of yellow poplar seedlings were <5 mm in diameter and that 75% of these were <1 mm. If the same is true of water tupelo seedlings, 67.5% of dead roots are <1 mm in diameter. Thus <1 mm roots would account for most of the organic matter and nutrients of root origin present in the soil at any one time.

Residence time for <1 mm roots has previously been estimated at 38 days or 0.1 yr in seedlings under favorable soil moisture conditions over a short period of time (5 wk) during May and June, when fine root growth could be expected to be optimum relative to other seasons of the year. Residence time of <1 mm roots of seedlings under less favorable, unflooded conditions was estimated at 53 days or 0.15 yr over the same period of time. Turnover rates could be expected to vary during the year. Using indications from the literature, two periods of optimum root growth annually, with maximum turnover rate, might be expected, alternating with less intense periods of growth during the growing season. During the 200-day growing season characteristic of eastern North Carolina, therefore, <1 mm roots might be expected to undergo about four complete turnovers (two of 38 days each and two of 53 days each). Fine root contributions of organic matter and important nutrients (based on an estimate by Cox 1972 that <1 mm roots represent about half the biomass of <5 mm roots) could thus be calculated.

Organic matter in <1 mm roots in the upper 40 cm of Tar Swamp (calculated as one-half the biomass of <5 mm roots times percent organic matter in <2 mm roots) (Table 4) is 482.3 $g \cdot m^{-2}$. Four turnovers per year would thus result in a return of 1929 $g \cdot m^{-2} \cdot yr^{-1}$ from <1 mm roots to the soil. Organic matter in annual litterfall to the Tar Swamp floor was 617.5 $g \cdot m^{-2} \cdot yr^{-1}$ (Brinson et al. 1980, based on total dry wt of litterfall and average ash content of 3.94%). Thus the annual contribution of <1 mm root organic detritus of the upper 40 cm is roughly three times that of litter. Similarly, return of nitrogen from <1 mm roots in the top 40 cm (calculated by multiplying one-half the biomass of <5 mm roots times N concentrations of <2 mm roots) is 14.9 $g \cdot m^{-2} \cdot yr^{-1}$, or about twice that of litter N input of 7.27 $g \cdot m^{-2} \cdot yr^{-1}$. Return of phosphorus from death of <1 mm roots in the upper 40 cm, calculated as above, is 4.67 $g \cdot m^{-2} \cdot yr^{-1}$, about nine times as much as the amount contributed by litter, 0.54 $g \cdot m^{-2} \cdot yr^{-1}$. For potassium, <1 mm root return would be 7.90 $g \cdot m^{-2} \cdot yr^{-1}$, almost four times as much as the 2.11 $g \cdot m^{-2} \cdot yr^{-1}$ from litter.

Values reported by Cox et al. (1977) for biomass and nutrient cycling in an upland Tennessee yellow poplar forest are listed in Table 16. Annual return of N from <5 mm roots in this forest (based on turnover time of less than one yr) was 1.8 times that on N in litter. Annual root return of K in the yellow poplar forest was 12.8 times that of litter and about three times the combined aboveground return of K. Biomass transfer from <5 mm roots in the Tennessee forest was twice that of litter; in Tar Swamp, this was three times that of litter and exceeded root biomass transfer in the upland forest by three times. Since these annual returns are based

Table 16. Comparison of organic matter and nutrient inputs to the soil from aboveground and belowground sources in two forested ecosystems.

	$g \cdot m^{-2} \cdot yr^{-1}$							
	Upland forest			Swamp forest				
	Biomass[a]	N[a]	K[a]	Biomass	Org. matter[b]	N[b]	K[b]	P[b]
Aboveground								
Dryfall-wetfall	-	0.72	0.36	-	-	0.58	0.30	0.05
Canopy leaching	-	0.23	2.94	-	-	0.45	0.90	0.10
Litterfall	331	4.22	1.00	642.8	617.5	7.27	2.11	0.54
Total aboveground inputs	331	5.17	4.30	642.8	617.5	8.30	3.31	0.69
Belowground								
Mortality and decay	675	7.60	12.80	2104[d]	1929[d]	14.9[c]	7.90[c]	4.67[c]
Consumption	75	0.90	1.40					
Exudation and leaching	-	-	12.80					
Total belowground inputs	750	8.50	27.00					

[a] Cox et al. 1977. Root transfers based on 0-5 mm roots representing the greater part of root turnover; turnover time of <1 yr.

[b] Tar Swamp, Brinson et al. 1980. Precipitation values assumed to represent dryfall-wetfall.

[c] Tar Swamp, this study. Root transfers based on <1 mm roots undergoing four turnovers per year.

[d] Biomass and organic matter of <1 mm roots to 40 cm depth are based on the assumption that <1 mm roots = ½ the biomass of <5 mm roots (see Cox 1972) and percent organic matter for <1 mm roots = that for <2 mm roots.

on estimates of production calculated from seasonal differences in biomass, which do not take into account increases and decreases in biomass within sampling intervals, they may underestimate actual returns of organic matter and nutrients.

Thus, if root turnover rates can be extrapolated from water tupelo seedlings to the swamp forest, the annual contributions to the soil of organic matter and major nutrients from mortality of <1 mm roots are at least twice as much as those of aboveground inputs from litter and aqueous sources. The potential contributions of larger size classes up to 5 mm, which have not been considered, would increase these estimates. Inputs from root turnover given above for Tar Swamp also do not take into account the quantities of nutrients which may be leached, exuded, or utilized by microorganisms from living roots. These processes are believed to be responsible for as much as half of root element contributions to soil (Cox et al. 1977).

Focusing on visible dynamics of specific root size classes for which nutrient content has been established may add to information about the role of root processes in forested ecosystems. Cox (1972) showed that seasonal cycles of root biomass and concentrations of nutrients in seedling roots paralleled those of roots of a mature yellow poplar forest *in situ*. Investigations of fine root periodicity and production, employing growth measurements at short intervals over the entire annual cycle under a carefully controlled variety of environmental conditions, may be a relatively efficient way of gaining knowledge about belowground production and mortality rates and thus organic matter and nutrient turnover. The results of this study lend support to the suggestion that root processes have an even greater effect than aboveground processes on biogeochemical cycling and must be included in estimates of ecosystem budgets.

LITERATURE CITED

Allen, S. E., H. M. Grimshaw, J. A. Parkinson, and C. Quarmby. 1974. Chemical Analysis of Ecological Materials. John Wiley and Sons, New York. 565 pp.

Arbez, M. 1971. Croissance des racines du pin Laricio de Corse (Pinus nigra Arn., ssp. Laricio), au stade juvénile. Ann. Sci. Forest. 28:259-288.

Armstrong, W. and D. J. Boatman. 1967. Some field observations relating the growth of bog plants to conditions of soil aeration. J. Ecol. 55:101-110.

Benke, A. C. 1979. A modification of the Hynes method for estimating secondary production with particular significance for multivoltine populations. Limnol. Oceanogr. 24:168-171.

Bode, R. H. 1959. Ueber den Zusammenhang zwischen Blattenfaltung und Neubildung der Saugwurzeln bei Juglans. Ber. Dtsch. Bot. Ges. 72:93-98.

Bradshaw, H. D. 1977. Nitrogen Cycling in an Alluvial Swamp Forest. M. S. Thesis. East Carolina University, Greenville, N. C. 89 pp.

Bremner, J. M. 1965. Total nitrogen, pp. 1149-1178, and Inorganic forms of nitrogen, pp. 1179-1237. In C. A. Black (ed.), Methods of Soil Analysis, Part 2. Amer. Soc. Agronomy, Madison, Wisc. pp. 1179-1237.

Brinson, M. M. 1977. Decomposition and nutrient exchange of litter in an alluvial swamp forest. Ecology 58:601-609.

Brinson, M. M., H. D. Bradshaw, R. N. Holmes, and J. B. Elkins, Jr. 1980. Litterfall, stemflow, and throughfall nutrient fluxes in an alluvial swamp forest. Ecology 61:827-835.

Brinson, M. M., H. D. Bradshaw, and E. S. Kane. 1981. Nitrogen Cycling and Assimilative Capacity of Nitrogen and Phosphorus by Riverine Wetland Forests. Report 167, Water Resources Research Institute of the Univ. of North Carolina, Raleigh. 90 pp.

Brown, S. 1978. A comparison of cypress ecosystems in the landscape of Florida. Ph.D. Dissertation. University of Florida, Gainesville, Fla. 571 pp.

Burns, L. A. 1978. Productivity, Biomass, and Water Relations in a Florida Cypress Forest. Ph.D. Dissertation. University of North Carolina, Chapel Hill, N. C.

Caldwell, M. M. 1979. Root structure: The considerable cost of belowground function, pp. 408-427. In O. T. Solbrig, S. Jain, G. B. Johnson, and P. H. Raven (eds.). Topics in Plant Population Biology. Columbia Univ. Press, New York. 589 pp.

Chapman, D. W. 1978. Production, pp. 202-217. In T. Bagenal. Methods for Assessment of Fish Production in Fresh Waters. Third Edition. IBP Handbook No. 3. Blackwell Scientific Publications, Oxford. 365 pp.

Chen, C. C., J. B. Dixon, and F. T. Turner. 1980. Iron coatings on rice roots: Morphology and models of development. Soil Sci. Soc. Am. J. 44:1113-1119.

Cox, T. L. 1972. Production, Mortality, and Nutrient Cycling in Root Systems of Liriodendron Seedlings. Ph.D. Dissertation. Univ. of Tennessee, Knoxville.

Cox, T. L., W. F. Harris, B. S. Ausmus, and N. T. Edwards. 1977. The role of roots in biogeochemical cycles in eastern deciduous forests, pp. 321-325. In J. K. Marshall (ed.). The Belowground Ecosystem: A Synthesis of Plant-associated Processes. Colorado State University, Fort Collins. 351 pp.

de la Cruz, A. A. and C. T. Hackney. 1977. Energy value, elemental composition, and productivity of belowground biomass of a Juncus tidal marsh. Ecology 58:1165-1170.

Edwards, N. T. and W. F. Harris. 1977. Carbon cycling in a mixed deciduous forest floor. Ecology 50:431-437.

Epstein, E. 1977. The role of roots in the chemical economy of life on earth. Bioscience 27:783-787.

Golley, F. B., J. T. McGinnis, R. G. Clements, G. I. Child, and M. J. Duever. 1975. Mineral Cycling in a Tropical Moist Forest Ecosystem. Univ. of Georgia Press, Athens, Ga. 248 pp.

Green, M. S. and J. R. Etherington. 1977. Oxidation of ferrous iron by rice (Oryza sativa L.) roots: A mechanism for waterlogging tolerance? J. Expt. Bot. 38:678-690.

Hamilton, A. L. 1969. On estimating annual production. Limnol. Oceanogr. 14:771-782.

Harris, W. F., R. S. Kinerson, Jr., and N. T. Edwards. 1977. Comparison of belowground biomass of natural deciduous forests and loblolly pine plantations, pp. 29-36. In J. K. Marshall (ed.). The Belowground Ecosytem: A Synthesis of Plant-associated Processes. Colorado State University, Fort Collins. 351 pp.

Hermann, R. K. 1977. Growth and production of tree roots: A review, pp. 7-28. In J. K. Marshall (ed.). The Belowground Ecosystem: A Synthesis of Plant-associated Processes. Colorado State University, Fort Collins. 351 pp.

Hook, D. D., C. L. Brown, and R. H. Wetmore. 1972. Aeration in trees. Bot. Gaz. 133:443-451.

Hozumi, K., K. Yoda, S. Kokawa, and T. Kira. 1969. Production ecology of tropical rain forests in SW Cambodia. I. Plant biomass. In T. Kira and K. Iwata (eds.). Nature and Life in Southeast Asia (Kyoto) 6:1-51.

Hynes, H. B. N. and J. M. Coleman. 1968. A simple method of assessing the annual production of stream benthos. Limnol. Oceanogr. 13:569-573.

Jones, H. E. and J. R. Etherington. 1970. Comparative studies of plant growth and distribution in relation to waterlogging. J. Ecol. 58:487-496.

Jordan, C. F. and G. Escalante. 1980. Root productivity in an Amazon rain forest. Ecology 61:14-18.

Karizumi, N. 1968. Estimation of root biomass in forests by soil block sampling, pp. 79-86. In M. S. Ghilarov, V. A. Kovda, L. N. Novichkova-Ivanova, L. E. Rodin, and V. M. Sveshnikova (eds.). Methods of Productivity Studies in Root Systems and Rhizosphere Organisms. International Symposium. USSR Academy of Sciences, Leningrad. 240 pp.

Keeley, J. E. 1979. Population differentiation along a flood frequency gradient: Physiological adaptations to flooding in Nyssa sylvatica. Ecol. Monogr. 49:89-108.

Klinge, H. 1976. Root mass estimation in lowland tropical rainforests of Central Amazonia, Brazil: IV. Nutrients in fine roots from latosols. Tropical Ecology 17:79-88.

Kozlowski, T. T. 1971. Growth and Development of Trees. Academic Press, New York. Two vol.

Kramer, P. J. and T. T. Kozlowski. 1960. Physiology of Trees. McGraw-Hill, New York. 642 pp.

Kramer, P. J. and T. T. Kozlowski. 1979. Physiology of Woody Plants. Academic Press, New York. 811 pp.

Krebs, C. J. 1971. Ecology: The Experimental Analysis of Distribution and Abundance. Harper and Row, New York. 694 pp.

Lieth, H. 1968. The determination of plant dry-matter production with special emphasis on the underground parts, pp. 179-186. In F. E. Eckardt (ed.). Functioning of Terrestrial Ecosystems at the Primary Production Level. UNESCO, Paris.

Likens, G. E. and F. H. Bormann. 1970. Chemical analyses of plant tissues from the Hubbard Brook ecosystem in New Hampshire. Yale University School of Forestry Bulletin No. 79. New Haven, Conn. 25 pp.

Lugo, A. E., J. Nessel, and T. Hanlon. 1978. Studies on root biomass, phosphorus immobilization by roots and the influence of root distribution on plant survival in a north-central Florida cypress strand, pp. 802-826. In H. T. Odum and K. C. Ewel (eds.). Cypress Wetlands for Water Management, Recycling and Conservation. Fourth Annual Report to National Science Foundation. Center for Wetlands, Univ. of Florida, Gainesville, Fla.

Lyr, H. and G. Hoffmann. 1967. Growth rates and growth periodicity of tree roots, pp. 181-235. In J. A. Romberger and P. Mikola (eds.). International Review of Forestry Research. Academic Press, New York.

Mathews, C. P. and D. F. Westlake. 1969. Estimation of production by populations of higher plants subject to high mortality. Oikos 20:156-160.

Merritt, C. 1968. Effect of environment and heredity on the root growth pattern of red pine. Ecology 49:34-40.

Moir, W. H. and E. P. Bachelard. 1969. Distribution of fine roots in three Pinus radiata plantations near Canberra, Australia. Ecology 50:658-662.

Montague, K. A. and F. P. Day, Jr. 1980. Belowground biomass of four plant communities of the Great Dismal Swamp, Virginia. Am. Midl. Nat. 103:83-87.

Mulholland, P. J. 1979. Organic Carbon Cycling in a Swamp-Stream Ecosystem and Export by Streams in Eastern North Carolina. Ph.D. Dissertation. Univ. of North Carolina, Chapel Hill. 151 pp.

Newbould, P. J. 1968. Methods of estimating root production, pp. 187-190. In F. E. Eckardt (ed.). Functioning of Terrestrial Ecosystems at the Primary Production Level. UNESCO, Paris.

Newman, E. I. 1966. A method of estimating the total length of root in a sample. J. Appl. Ecol. 3:139-145.

Ovington, J. D. and G. Murray. 1968. Seasonal periodicity of root growth of birch trees, pp. 146-154. In M. S. Ghilarov, V. A. Kovda, L. N. Novichkova-Ivanova, L. E. Rodin, and V. M. Sveshnikova (eds.). Methods of Productivity Studies in Root Systems and Rhizosphere Organisms. International Symposium. USSR Academy of Sciences, Leningrad. 240 pp.

Persson, H. 1978. Root dynamics in a young Scots pine stand in central Sweden. Oikos 30:508-519.

Persson, H. 1979. Fine-root production, mortality and decomposition in forest ecosystems. Vegetatio 41:101-109.

Ponnamperuma, F. N. 1972. The chemistry of submerged soils. Advances in Agronomy 24:29-95.

Reader, R. J. and J. M. Stewart. 1972. The relationship between net primary production and accumulation for a peatland in southeastern Manitoba. Ecology 53:1024-1037.

Reichle, D. E., B. E. Dinger, N. T. Edwards, W. F. Harris, and P. Sollins. 1973. Carbon flow and storage in a forest ecosystem, pp. 345-365. In G. M. Woodwell and E. V. Pecan (eds.). Carbon in the Biosphere, Brookhaven Symposium in Biology, AEC Conf. No. Conf.-720510. 392 pp.

Richardson, S. D. 1968. The study of root development in controlled environments, pp. 168-176. In M. S. Ghilarov, V. A. Kovda, L. N. Novichkova-Ivanova, L. E. Rodin, and V. M. Sveshnikova (eds.). Methods of Productivity Studies in Root Systems and Rhizosphere Organisms. International Symposium. USSR Academy of Sciences, Leningrad. 240 pp.

Rodin, L. E. and N. I. Basilevich. 1967. Production and Mineral Cycling in Terrestrial Vegetation. Oliver and Boyd, Edinburgh and London.

Rogers, W. S. and G. C. Head. 1968. Studies of roots of fruit plants by observation panels and time-lapse photography, pp. 176-186. In M. S. Ghilarov, V. A. Kovda, L. N. Novichkova-Ivanova, L. E. Rodin, and V. M. Sveshnikova (eds.). Methods of Productivity Studies in Root Systems and Rhizosphere Organisms, International Symposium. USSR Academy of Sciences, Leningrad. 240 pp.

Santantonio, D., R. K. Hermann, and W. S. Overton. 1977. Root biomass studies in forest ecosystems. Pedobiologia 17:1-31.

Scheiner, D. 1976. Determination of ammonia and Kjeldahl nitrogen by indophenol method. Water Research 10:31-36.

Shaver, G. R. and W. D. Billings. 1975. Root production and root turnover in a wet tundra ecosystem, Barrow, Alaska. Ecology 56:401-409.

Tennant, D. 1975. A test of the modified line intersect method of estimating root length. J. Ecol. 63:995-1001.

Trent, A. W. 1972. Measurement of Root Growth and Respiration in Arctic Plants. M. A. Thesis. Duke University, Durham, N. C. 75 pp.

U.S. Environmental Protection Agency. 1979. Methods for chemical analyses of water and wastes. Environmental Monitoring and Support Laboratory, Offie of Research and Development, U.S. Environmental Protection Agency, Cincinnati, Ohio.

U.S. Geological Survey. 1979. Water Resources Data for North Carolina. Raleigh, N. C. 541 pp.

Valiela, I., J. M. Teal, and N. Y. Persson. 1976. Production and dynamics of experimentally enriched salt marsh vegetation: Belowground biomass. Limnol. Oceanogr. 21:245-252.

Waters, T. J. and J. C. Hokenstrom. 1980. Annual production and drift of the stream amphipod *Gammarus pseudolimnaeus* in Valley Creek, Minnesota. Limnol. Oceanogr. 25:700-710.

White, E. H., W. L. Pritchett, and W. K. Robertson. 1971. Slash pine root biomass and nutrient concentrations. Forest Biomass Studies, XVth IUFRO Congress, University of Florida, Gainesville, Florida.

Whittaker, R. H., F. H. Bormann, G. E. Likens, and T. G. Siccama. 1974. The Hubbard Brook ecosystem study: Forest biomass and production. Ecol. Monogr. 44:233-252.

Whittaker, R. H., G. E. Likens, F. H. Bormann, J. S. Eaton, and T. G. Siccama. 1979. The Hubbard Brook ecosystem study: Forest nutrient cycling and element behavior. Ecology 60:203-220.

Wilcox, H. E. 1962. Growth studies of the root of incense cedar, *Libocedrus decurrens*. II. Morphological features of the root system and growth behavior. Am. J. Bot. 49:237-245.

Wilcox, H. E. 1968. Morphological studies of the root of red pine, *Pinus resinosa*. I. Growth characteristics and patterns of branching. Am. J. Bot. 55:247-254.

Yarbro, L. A. 1979. Phosphorus Cycling in the Creeping Swamp Floodplain Ecosystem and Exports from the Creeping Swamp Watershed. Ph.D. Dissertation. Univ. of North Carolina, Chapel Hill. 231 pp.