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Distribution of ^{14}C-labeled photosynthate in loblolly pine (*Pinus taeda*) seedlings as affected by season and time after exposure

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Summary

Distribution of ^{14}C-labeled photosynthate was determined in field-grown loblolly pine (*Pinus taeda* L.) seedlings on August 9 and October 15, 1984 and January 15 and March 12, 1985. Leaves on a lateral branch fixed ^{14}C photosynthetically and amounts of ^{14}C in seven biochemical fractions in each of six plant parts were determined 8, 24, and 72 h later. In all treatments, ^{14}C uptake was approximately 96% of that originally presented. Respiratory loss of ^{14}C ranged from 22 to 87% of uptake and increased sharply with increasing time after exposure and as the seedlings grew larger later in the study. Most ^{14}C was found in exposed leaves and very little occurred above the exposed branch. Amounts of ^{14}C decreased in the exposed leaves and increased in the roots with time after exposure and date. Sugars were generally the most heavily labeled fraction. Labeled sugar content of exposed leaves decreased by more than half between 8 and 72 h as sugars were metabolized and translocated to other parts, primarily the roots. In roots, the labeling of starch and residue (structural compounds) increased greatly with transport time and season. In all plant parts, proteins and amino acids contained very little ^{14}C regardless of date or time.

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Introduction

Photosynthate distribution in a plant is determined by the relative strengths of carbon sources and sinks (areas of net carbon export and import, respectively). Source and sink strengths can be greatly affected by season (Kocher and Leonard 1971), as well as by other factors. Seasonal changes in photosynthate allocation have been studied in several coniferous species, including loblolly pine (Chung and Barnes 1977, 1980*a*, 1980*b*).

A pattern of seasonal variation in source and sink strengths observed in many conifers and other species is as follows. As the soil warms in early spring before budbreak, roots begin to grow and they become the primary users of stored carbohydrates and current photosynthate (Rook and Hobbs 1976, Teskey and Hinckley 1981). At budbreak, root growth decreases and new shoots become the main sinks (Dickson 1989, Loesscher et al. 1990). Most of the starch stored in the tree is used at this time. Cambial growth also begins at about budbreak (Wareing and Phillips 1981), but is slow until new needles mature and become exporters (Gordon and Larson 1968). As new shoots develop, most assimilate produced by expanding leaves is used locally for tissue formation and respiration (Ursino et al. 1968). Considerable

sugar transfer from old to new foliage also occurs (Chung and Barnes 1980*a*). At maturity, new leaves become the primary exporters of photosynthate. Root growth usually increases after new needles mature, and decreases or stops later in the summer because of insufficient soil moisture (Merritt 1968, Kuhns et al. 1985). Late in the season, roots again become the main carbon sink due to growth and starch accumulation (Schier 1970). Although productivity of old needles declines with age, photosynthate export normally continues until senescence (Chung and Barnes 1980*b*).

The objective of this study was to determine the effect of season on photosynthate distribution in loblolly pine seedlings within 72 h after initial carbon uptake. We hypothesized that photosynthate would move preferentially to areas of fast growth or carbon storage, which would vary by season, with sinks drawing most carbon from nearby sources. Photosynthate distribution was also expected to vary with translocation time, with carbon moving farther and being partitioned into less labile constituents as the translocation time increased. Allocation of ^{14}C from leaves on a lateral branch to each of five other plant parts and partitioning of ^{14}C into seven biochemical fractions was examined on August 9 and October 15, 1984 and January 15 and March 12, 1985, at 8, 24, and 72 h after initial ^{14}C uptake.

Materials and methods

The origin and treatment of the experimental materials have been described in detail previously (Kuhns and Gjerstad 1988). Briefly, 256 9-month-old, half-sib loblolly pine seedlings were planted on December 12, 1983 in 5.7-liter pots containing a 2/1/1 (v/v) mix of ground peat moss, vermiculite, and perlite with 20 g of slow-release granular fertilizer (18/7/10, N/P/K plus iron) added to each pot. After potting, seedlings were placed outside in Auburn, Alabama (longitude 85° W, latitude 33° N) in a bed consisting of 20-cm diameter holes augured in the soil to a depth of 20 cm. The bed was mulched with pine bark and fenced to prevent animal damage. Seedlings were kept well watered until June 18, 1984, and only received water by precipitation after that date.

Four treatment dates were chosen to correspond with periods of rapid growth in summer (August 9, 1984), slow growth and very dry conditions in the fall (October 15, 1984), cessation of growth because of cold temperatures and decreased photoperiod in winter (January 15, 1985), and a week after renewed shoot growth in the spring (March 12, 1985). Growth was determined by measuring total seedling height and ground-line diameter to the nearest mm weekly from early July 1984 to mid-March 1985. The presence or absence of actively growing apical regions on the main stem and exposed branch was noted on each treatment date.

On the morning before each treatment date, 12 seedlings were randomly selected from the outdoor bed, lifted with root system and pot intact, brought into a greenhouse, and watered to saturation. At 0400 h on the treatment date, six of these seedlings were placed under six 150-W flood lamps and a centrally located, 175-W mercury-vapor light, all of which were immersed in a water bath to absorb heat. At

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0600 h, one lateral branch from the lowermost whorl of each seedling (formed in the second growing season) was sealed in an exposure chamber made from a 2-liter clear-plastic soda bottle. Tubing was connected to holes in the chamber base and neck for gas circulation. The chamber was sealed to the branch base with modeling clay, plastic sleeves from the chamber, and twist ties. Each chamber was located under one of the flood lamps. Photosynthetic photon flux density (PPFD) in the exposure chambers was approximately 670 μmol m^{-2} s^{-1} and chamber air temperatures ranged from 24 to 26 °C.

Over a 10-min period, 1.1 MBq of $^{14}CO_2$ was injected into each chamber, which was then sealed for 50 min to allow further assimilation. After plants had been exposed for a total of 60 min, gas in each chamber was flushed through a trap containing 15 ml of 1 M NaOH to remove unassimilated $^{14}CO_2$. Branches were removed from the chambers and marked.

The other six seedlings were kept indoors under black plastic until 0800 h. They were then placed under lights until 1000 h when they were exposed to ^{14}C in the same manner as the first six. For details of the exposure system and techniques, see Kuhns and Gjerstad (1988).

After exposure, seedlings were maintained in a 14-h photoperiod. Photosynthetic photon flux density at the top of the seedlings was about 1000 μmol m^{-2} s^{-1} and air temperature was approximately 25–27°C. Sets of four seedlings were harvested at 8, 24, and 72 h after initial exposure to ^{14}C and separated into six parts: (1) a 2-cm section from the plant apex (bud or apical meristem region), (2) all nonexposed stem and branch tissue, (3) all nonexposed leaves, (4) the ^{14}C-exposed lateral branch, (5) the exposed leaves, and (6) the root system. The material was frozen in liquid nitrogen, lyophilized, weighed, ground through a 40-mesh screen in a Wiley mill, and stored in an airtight vial at −20 °C until extraction.

Tissue samples (60 mg dry weight) were extracted and fractionated using a series of solvent, enzymatic, and ion-exchange techniques (Dickson 1979), into seven biochemical fractions: (1) pigments and lipids, (2) free amino acids, (3) organic acids and phosphates, (4) sugars, (5) protein, (6) starch, and (7) residue (mostly cellulose, hemicellulose, and lignin). The amount of ^{14}C in each fraction was determined by liquid scintillation spectrometry. Total ^{14}C in each plant part was calculated as the sum of the ^{14}C in each fraction from that part.

Total radioactivity taken up by each seedling (shown as ^{14}C recovery in Figure 1) was determined by subtracting radioactivity in a seedling's CO_2 trap from that originally placed in the reaction vessel. As a precaution, the liquid remaining in a reaction vessel after labeling was occasionally counted and at no time contained more than 0.19 KBq or 0.02% of the original amount in the reaction vessel.

Results

Uptake of ^{14}C was high and fairly constant over all treatments (Figure 1). At all dates, ^{14}C recovery, the total amount of ^{14}C in a seedling at harvest, decreased with increasing translocation time, declining by more than half between 8 and 72 h in

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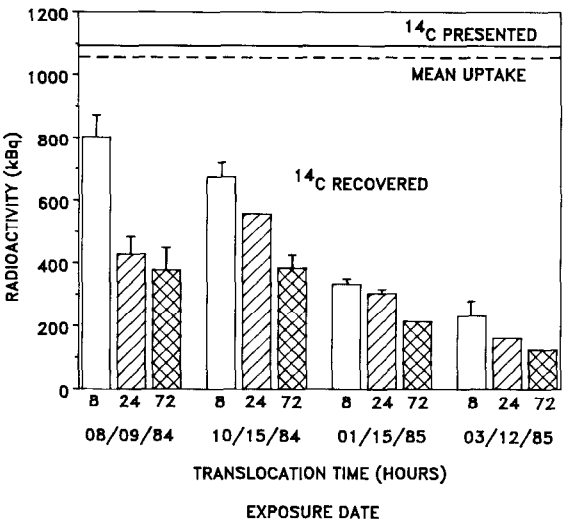

Figure 1. Uptake and recovery of ^{14}C (kBq) by date and time after exposure. The solid horizontal line at about 1.1 MBq indicates the amount of ^{14}C each seedling was exposed to and the dashed line represents average ^{14}C uptake. Plotted values are means of four seedlings (bars indicate standard errors).

August. The rate of ^{14}C loss (loss equals uptake minus recovery) over all dates decreased with increasing time after exposure, averaging 6.5% h^{-1} between 0 and 8 h, 4.1% h^{-1} between 8 and 24 h, and 1.5% h^{-1} between 24 and 72 h.

Total seedling dry weight increased by 146% from August to March (Figure 2). Nonexposed leaves made up most of the dry weight in all but the March treatment, where roots weighed the most. Root dry weight increased greatly during the study, especially between October and January. The nonexposed stem made up a large

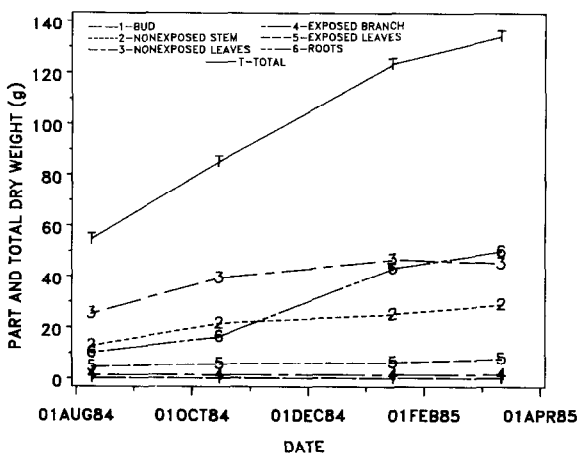

Figure 2. Dry weight (g) for each part and the entire seedling (T) at the four exposure dates. Plotted values are means for twelve seedlings.

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proportion of each seedling's weight, though its increase in dry weight only equalled or exceeded that of the roots between August and October. The bud or seedling apex changed little in dry weight during the study, because only a small, uniformly sized region was harvested. The bud appeared to be actively growing when harvested in August and March. The exposed branch and leaves also changed little in dry weight during the study, though they were just finishing a growth flush in August and just beginning a flush in March. The mean height growth rate of all seedlings was highest in August at 2.9 mm day^{-1}, fell to 0.6 and 0 mm day^{-1} in October, and January, respectively, then rose to 1.5 mm day^{-1} in March. Diameter growth rates followed a similar pattern, although growth at the August and March harvest dates were about equal at 0.07 to 0.08 mm day^{-1}.

Allocation (movement between plant parts) of ^{14}C among the five plant parts that contained most of the ^{14}C changed as the study progressed (Figure 3). Exposed leaves contained more than 50% of a seedling's ^{14}C and more than any other plant part in all cases except the 72-h treatment in March, when roots contained more. Labeled carbon in the exposed leaves declined sharply with increasing translocation time except in the August treatment, and decreased from one date to the next, reaching the lowest amount at the 72-h treatment in March. As ^{14}C decreased in exposed leaves it increased in the roots, with roots generally containing more ^{14}C than any other plant part except the exposed leaves.

Labeled carbon in the exposed branch was highest at 24 h on all dates except October. Activities of ^{14}C in nonexposed stem were similar to those of the exposed branch and generally increased with time after exposure. Nonexposed leaves in most treatments contained little ^{14}C.

Eight h after exposure, most of a seedling's ^{14}C was located in the sugar fraction of the exposed leaves, except in October when organic acids contained slightly more (Figure 4). The activity of ^{14}C-labeled sugar in exposed leaves decreased by more than half between 8 and 72 h on all dates. Labeled carbon in starch in the exposed leaves was generally low (7% or less), with a peak of 15% at 24 h in October. The ^{14}C content of amino acids and organic acids in the exposed leaves also consistently decreased with time, whereas the ^{14}C content in lipids and residue increased. Proteins and amino acids in the exposed leaves of all treatments contained less than 3% of seedling ^{14}C, less than all other fractions.

In parts other than the exposed leaves, sugars were generally the most heavily labeled fraction at all dates and times, and amino acids and proteins were the least labeled fractions (Figures 5–7). In the exposed branch (Figure 5) and nonexposed stem (Figure 6), ^{14}C in sugars was generally low at 8 h, increased by 24 h, and decreased or levelled off by 72 h. Labeled carbon in lipids, protein, starch, and residue generally increased with time in these plant parts, though little ^{14}C was found in these fractions in January.

For nearly all fractions and dates, ^{14}C in roots increased with time after exposure, averaging about 34 times as much at 72 h as at 8 h (Figure 7). In roots, ^{14}C in all fractions except sugars was highest at 72 h in March. In all treatments, most of the ^{14}C in roots was in sugars, and was fairly low for all dates at 8 h and highest at 72 h.

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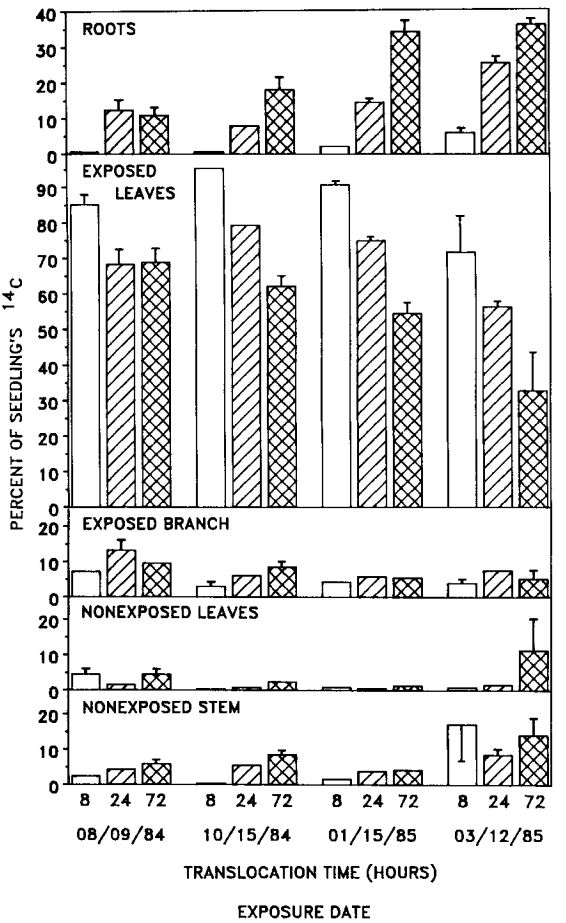

Figure 3. Radioactivity in each seedling part as a percent of total ^{14}C recovered from the seedling, by date and time after exposure. Plotted values are means of four seedlings (bars indicate standard errors). At a given time and date, the sum of the percentages for all parts equals approximately 100%. Data for the bud are not shown because the bud never contained more than 0.1% of the seedling's ^{14}C in any of the treatments.

Amounts of ^{14}C in residue and lipids were generally higher in roots than in other plant parts except exposed leaves.

The nonexposed leaves had little ^{14}C in any fraction at any date or time except the 72-h treatment in March, when most fractions showed a marked increase in labeling and sugars contained over 5% of the total ^{14}C of the seedling (data not shown).

Discussion

Labeled carbon loss was most likely due to respiration because tissue loss was minimal (Ericsson 1978), though some loss by root exudation may have occurred. The 8-h respiration values obtained early in our study are similar to those reported

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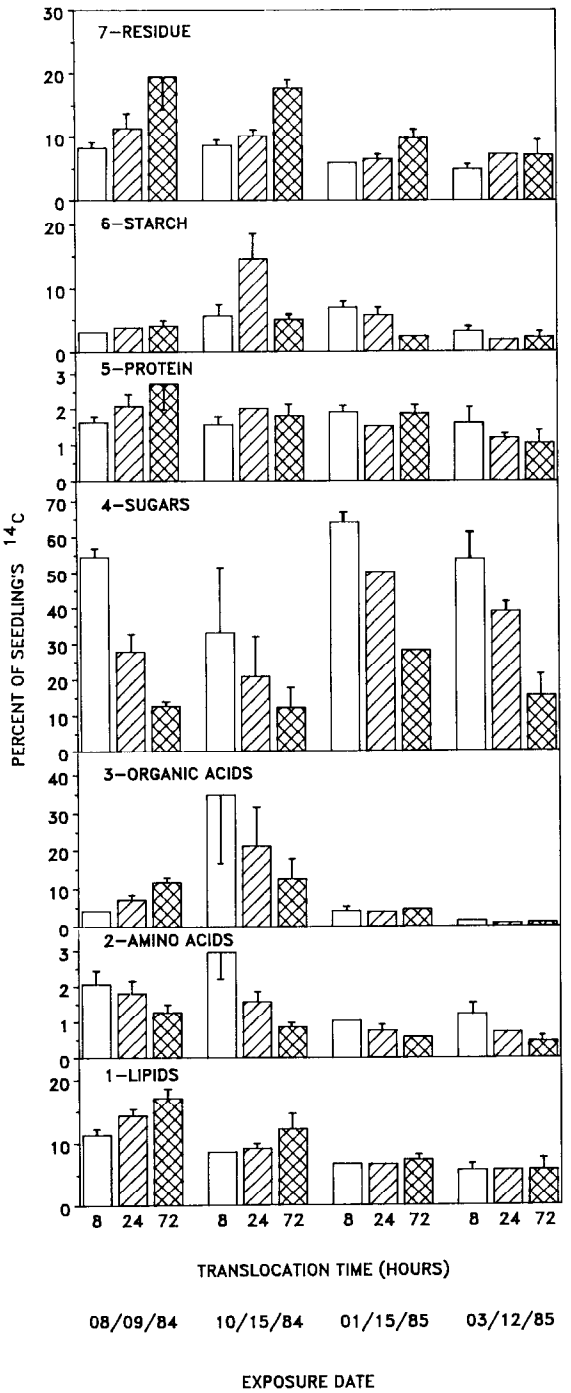

Figure 4. Radioactivity in each chemical fraction in the exposed leaves expressed as a percent of the total radioactivity in the seedling, by date and time after exposure. Plotted values are means of four seedlings (bars indicate standard errors).

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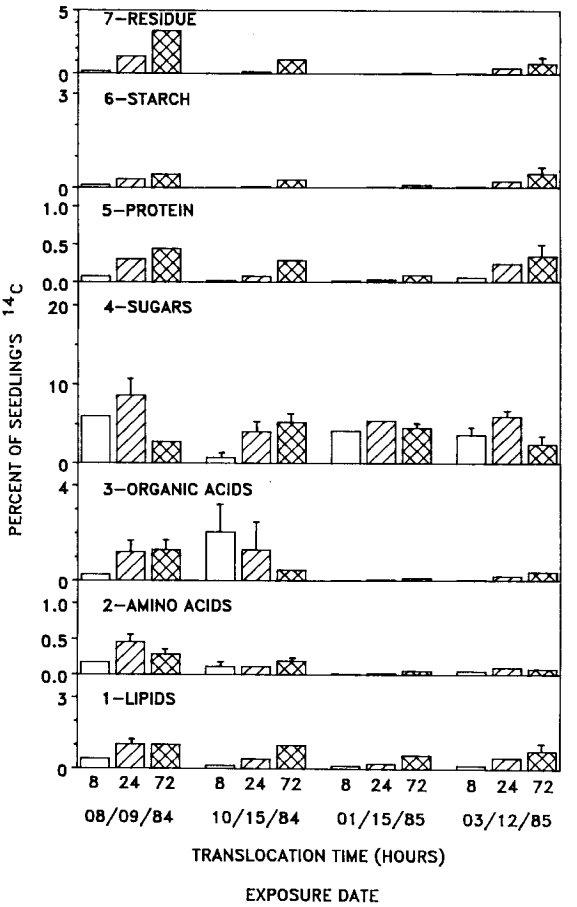

Figure 5. Radioactivity in each chemical fraction in the exposed stem, expressed as a percent of the total radioactivity in the seedling, by date and time after exposure. Plotted values are means of four seedlings (bars indicate standard errors).

by Lister et al. (1967) and Ursino and Paul (1973) in white pine (*Pinus strobus* L.) seedlings, but our respiration values at 24 and 72 h at all dates, and at 8 h in January and March are much higher than those reported by others (Kinerson 1975). High ^{14}C respiration values later in the study may be associated with the increasing size of the main ^{14}C sink, the roots (Norby et al. 1987). The decrease in respiratory ^{14}C loss between 24 and 72 h was probably due to conversion of labeled and readily hydrolyzable products, like sugars, to less available forms, especially in the roots. Additional ^{14}C loss would probably occur for weeks or months after labeling (Ursino and Paul 1973, Smith and Paul 1988).

Photosynthate allocation is generally determined by the relative strengths and locations of carbon sources and sinks (i.e., the rates of assimilate production and use in various plant parts). In this study allocation was strongly affected by a 400% increase in root system dry weight that was not accompanied by a comparable

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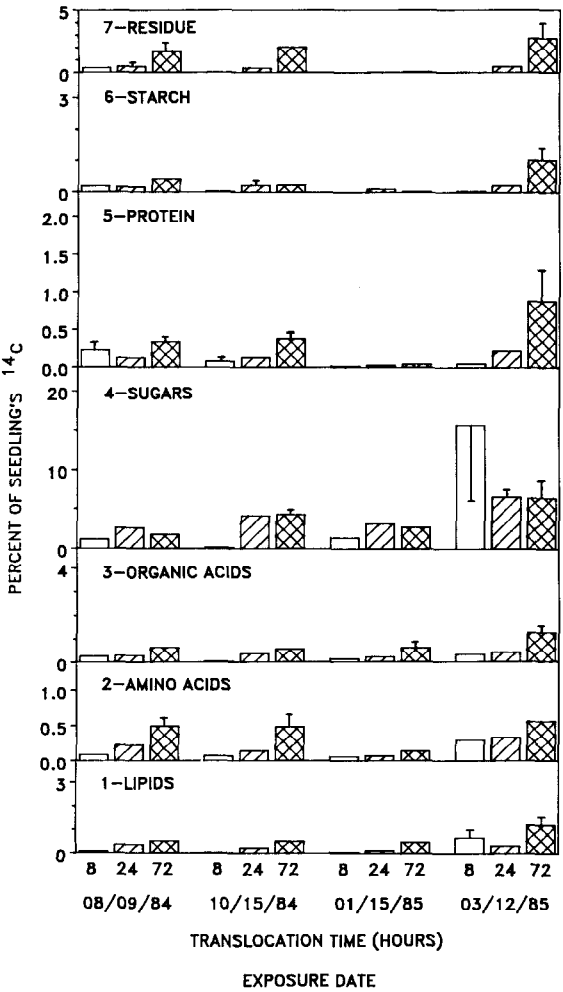

Figure 6. Radioactivity in each chemical fraction in the nonexposed stem, expressed as a percent of the total radioactivity in the seedling, by date and time after exposure. Plotted values are means of four seedlings (bars indicate standard errors).

increase in dry weight of other plant parts (Lister et al. 1967, van den Driessche 1987, Smith and Paul 1988). Another reason that roots were stronger sinks, on most dates and at most times after exposure, than either the nonexposed branch and leaves or the plant apex is that the the latter were all located at a higher point on the main stem axis than the exposed branch. Leaves that are near the stem apex generally export carbon upward, whereas leaves that are further from the apex export carbon downward (Mooney 1972, Ericsson 1978).

From August to March, the phenology of the exposed branch and leaves may have affected changes in carbon allocation between the exposed leaves and the roots. The presence of many growing, immature needles from a late growth flush in August

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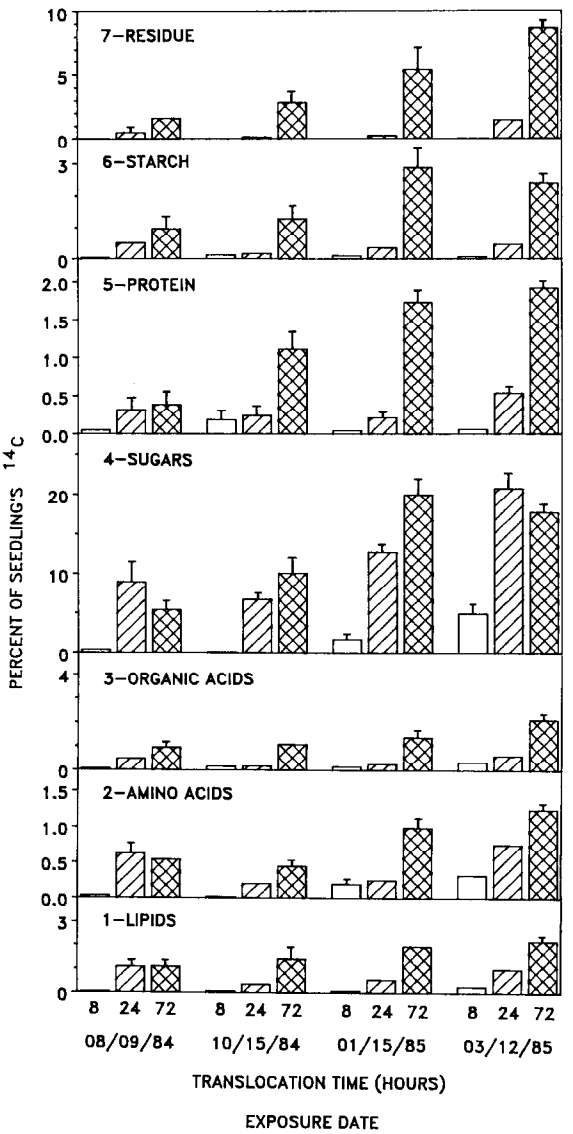

Figure 7. Radioactivity in each chemical fraction in the roots, expressed as a percent of the total radioactivity in the seedling, by date and time after exposure. Plotted values are means of four seedlings (bars indicate standard errors).

1984 probably increased the ^{14}C retained by the exposed leaves, whereas the predominance of mature exposed needles in March 1985 allowed more carbon to be exported (Ursino et al. 1968, Dickmann and Kozlowski 1970). Studies with loblolly pine (Chung and Barnes 1980*a*), red pine (*Pinus resinosa* Ait.) (Gordon and Larson 1968), and Scots pine (*Pinus sylvestris* L.) (Ericsson 1978) confirm that pine needles only export carbon when they near maturity.

The slowing of the rate of ^{14}C translocation from exposed leaves to the roots

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between 24 and 72 h indicates that most labeled photosynthate had reached its final (short-term) destination by 72 h, though some translocation probably would have occurred for several days. Similar findings have been reported by Ziemer (1971) in ponderosa pine, and Rangnekar and Forward (1972) and Dickmann and Kozlowski (1970) in red pine.

Sometimes partitioning of labeled photosynthate was preferentially into chemical fractions involved in growth (residue, protein, lipids), whereas at other times it was used for respiration (mainly sugars). For example, in January when little growth should have occurred in aboveground parts (Garber 1983), most ^{14}C in the aboveground parts was in sugars and little went into structural compounds. Partitioning into structural compounds in the roots, the parts most likely to be growing in January, was fairly high. Another example of partitioning to growth *versus* respiration or maintenance was in March, when the roots, exposed stem, nonexposed stem, and nonexposed leaves were actively growing and partitioning considerable amounts of carbon to structural compounds, compared with the amount partitioned to structural compounds in January. In March, few new exposed leaves were forming and partitioning into structural compounds in those leaves was lowest.

As with structural compounds, relatively large amounts of ^{14}C in organic acids in a plant part at certain dates and times may indicate active growth. Shikimic and quinic acids, precursors of aromatic amino acids and lignin (Chung and Barnes 1980*a*, Hall et al. 1981), are the main organic acids present in loblolly pine (Chung and Barnes 1977) and red pine (Rangnekar and Forward 1972). Rangnekar and Forward (1969) found that 25% of all ^{14}C in actively growing red pine buds exposed to $^{14}CO_2$ was in these acids. Times and dates of high organic-acid ^{14}C content in the present study generally match periods of high residue (mostly cellulose, hemicellulose, and lignin) labeling.

The low amounts of ^{14}C-labeled amino acids found in roots in this study are similar to or slightly higher than the amounts reported in roots of red pine (Rangnekar and Forward 1972) and orange (*Citrus sinenis* L. Osbeck) seedlings (Kriedemann 1969). The low level of amino acid labeling in roots and other plant parts is probably related to the low nitrogen content, usually less than 2% of dry weight, of woody plant tissues in general (Kramer and Kozlowski 1979). It is likely that the amino acids that were labeled were primarily associated with the reduction of inorganic nitrogen from the soil to organic forms for eventual transport in the xylem to other plant parts. Barnes (1963) found that amino acids (mainly glutamine), presumably synthesized from nitrate in the roots, were the most abundant nitrogen compounds transported in the xylem of loblolly pine and six other pine species.

The ^{14}C content of starch was fairly low in all plant parts, though it increased with time after exposure in several tissues, particularly the roots (cf. Olofinboba and Kozlowski 1973). Carbohydrates in eastern cottonwood (*Populus deltoides* Bartr.), are first stored as starch and later converted to sugars under cold conditions (Dickson and Nelson 1982). This may explain the large amounts of ^{14}C in sugar in roots in January.

In summary, allocation and partitioning of carbon from lower branches of loblolly

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pine seedlings appears to be driven by growth and other metabolic activity in the source branch and other plant parts. Most carbon was kept in the source leaves when they were growing and metabolically active, with roots becoming the dominant sink as the seedlings grew. Though carbon distribution varied with time of year, the effects of the large increase in seedling size, particularly root system size, dominated the carbon distribution patterns. More carbon moved to roots and out of sugars into structural and storage compounds as translocation time increased, though some redistribution would likely have occurred after 72 h. Later in the study, respiration of recently fixed (within 72 h) carbon was much higher than that reported by others, possibly a result of a greatly increased seedling size.

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