

Redistribution of ^{14}C -labelled Reserve Carbon in *Pinus sylvestris* Seedlings during Shoot Elongation

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This study examined the later use of ^{14}C reserves formed in previous autumn in Scots pine (*Pinus sylvestris* L.) seedlings. The seedlings were allowed to photosynthesise $^{14}\text{CO}_2$ in early September when shoot and needle growth was over. The following spring the seedlings were harvested in five samplings during the shoot growth period. The distribution and concentration of ^{14}C were determined and the results were compared with the growth data. It was observed that reserves were not used markedly for the new growth. Most of the ^{14}C was found in one-year-old needles (30–40 %) and in the root system (40–50 %) which was due to both their high activity as a storage sink and their large sink size. The high initial ^{14}C -activity in the finest roots decreased indicating respiration of reserves. Only a small percent of the reserve carbon was found in the new shoots which indicated that reserves are of minor importance in building a new shoot. An allocation of about 15 % of the autumn storage to the stem suggested that in seedlings the stem is of minor importance as a storage organ.

Keywords carbon storage, ^{14}C labelling, photosynthates, root growth, Scots pine, shoot growth

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1 Introduction

Photosynthate storage is formed when production exceeds consumption (growth, respiration, etc.). In conifers, most of the storage is formed in spring before bud break, when a plant photosynthesises but has no strong sinks because growth has not begun, and in autumn, when needle growth is over but photosynthetic rates can be quite high (Kozłowski 1992, Cannell and Devar 1994). In addition, some storage is formed during the growth period (Schier 1970).

Reserve material exists in all parts of a woody plant. In seedlings, however, most of the reserve material is in root tissues or in conifer needles. In winter, the conifer root system possesses the most of the starch (Schier 1970, Ericsson and Persson 1980) because in the shoot, which is exposed to lower temperatures, starch is converted into sugars.

In conifers, shoot elongation seems to be independent of reserve material formed in the previous autumn since the previous year's needles supply the developing shoots with current photosynthates (Ursino and Paul 1973, Hansen and Beck 1990, Fischer and Höll 1992). However, contrasting opinions have been presented (Olofinboba and Kozłowski 1973, Little 1974). Ericsson (1979) observed a decline in needle starch content during rapid shoot elongation in 20-year-old Scots pine (*Pinus sylvestris* L.) trees, which indicates that spring time reserves contribute to shoot growth.

Current photosynthate is the primary carbon source for new roots. Very little of the ^{14}C taken up by seedlings in autumn, and stored in old roots, is available for the growth of new roots (van den Driessche 1987). It is believed that autumn reserves are used mainly for respiration (Glerum 1980) and in situations where current photosynthates cannot supply the amount of carbohydrates necessary for growth (van den Driessche 1987).

However, spring time storage is depleted during root growth, indicating that these reserves are utilized by the new root growth (Ericsson and Persson 1980).

Although the production and use of reserve carbohydrates are quite well known there are still some gaps in the present information. Knowl-

edge is lacking on how autumn reserves are distributed among different roots. In many studies the carbohydrate concentrations alone are measured without detecting whether the carbon is from storage (production in autumn or spring) or from current photosynthesis. Usually the redistribution of autumn reserves has only been measured a few times during the following growing season, which means that accurate time series on dynamics of reserves is lacking. There are few studies on reserve carbon in Scots pine seedlings; most investigations have been made on larger trees (Ericsson and Persson 1980) and in southern latitudes (Hansen and Beck 1990, Fischer and Höll 1991) where the trees may exhibit different carbon dynamics by photosynthesising and growing roots even during the winter.

The aim of this study was to examine where the reserve carbon produced in autumn is located and to produce more accurate information on the use of carbon during the shoot growth period. Special emphasis was put on the root system: how carbon is distributed among different roots.

2 Materials and Methods

In early September 1993, 20 container-grown 2.5-year-old Scots pine seedlings originating in Southern Finland were exposed to ^{14}C -labelled CO_2 (9.25 kBq per seedling) in a 360 liter plexiglas chamber for three hours. $^{14}\text{CO}_2$ was released from $\text{NaH}^{14}\text{CO}_3$ inside the chamber by injecting 1 M HCl through a serum stopper. The photon flux density was $400 \mu\text{mol s}^{-1}\text{m}^{-2}$ (daylight + halogen metal vapour lamps), the temperature was $25 \text{ }^\circ\text{C}$, and the air inside the chamber was circulated with a fan. After the 3-h labelling period, the seedlings were returned to a site under a transparent roof.

At the end of April the first sampling of the 64-day experiment was taken. Samples were taken at random on five dates. The sampling dates were chosen according to the developmental stage of the shoots and needles (Table 1). The roots were washed free of rooting medium and the seedlings were separated into current shoots, one-year old needles, primary needles, stem (see Lipu 1994, Fig. 1), main root, 1st–2nd order lateral

Table 1. Sampling according to the developmental stage of the seedlings. During intense shoot growth the daily growth was 6–7 mm per day. Heat sum data is from the weather station 19 km north-west from the study site.

Sample / time from the beginning, days	Developmental stage	Length of the new needles, mm	Heat sum, degree days
I / 0	Bud bursting	-	27
II / 14	Intense shoot growth	2	134
III / 28	Intense shoot growth	22	260
IV / 51	Shoot growth finished	*	402
V / 64		28	514

* Data missing

roots, and above 2nd order lateral roots. All plant parts were oven dried at 70 °C for two days and weighed. Subsamples were combusted (wet oxidizer Maricont 781, Junitek Co., Finland) and the released $^{14}\text{CO}_2$ was dissolved in a scintillation cocktail. Samples were subsequently counted in a liquid scintillation counter (Wallac 1411). The distribution of ^{14}C (Alloc, % of total recovered ^{14}C) within seedlings, which represents sink strength, was calculated as

$$\text{Alloc} = (A_{\text{part}} / A_{\text{tot}}) \times 100$$

where A_{part} is ^{14}C (Bq) accumulated in a plant part (needles, stem etc.) and A_{tot} is the total ^{14}C recovered.

The data were tested using an analysis of variance (one-way layout) and Tukey's test. Calculations were performed using SAS statistical software (The SAS system... 1992).

3 Results

During the experiment, the total ^{14}C activity of seedlings did not decrease significantly but the concentration of the finest roots did decrease clearly (Figs. 1 and 3). The largest proportion of the storage carbon occurred in the root system (40–50 %) and in old needles (30–40 %) (Fig. 2). The initial ^{14}C concentration of the root system was significantly higher than that of the needles (Fig. 3).

In the beginning of the sampling, most of the root system's ^{14}C was located in the finest roots (24 %, Fig 2), which was due to their greater relative dry mass (Fig. 5). At the end of the experiment the ^{14}C percentage in 1st–2nd order laterals was the highest (22 %). At the first sampling, the concentration of ^{14}C was similar for the different parts of the root system. In >2nd order lateral roots, however, the ^{14}C concentration decreased (Fig. 3) significantly, which was not due to increase in dry mass (Fig. 4). The concentration in coarser roots did not decrease significantly, so they possessed a generally higher ^{14}C concentration than the finest roots (Fig. 3). The concentration of ^{14}C in needles did not change during the experiment. Neither was there a significant change for the stem although the ^{14}C concentration decreased.

The ^{14}C percentage in new shoots (new stem + new branches + new needles) was low and increased only from 2 to 4 % (Fig. 2) of the total ^{14}C whilst the dry matter proportion grew from 2 to 24 % (Fig. 5). In the new shoot, the percentage of ^{14}C did not change markedly at the rapid stage of growth (6–7 mm per day) (Fig. 6). At the first sampling, the ^{14}C concentration in the new shoot was remarkably high but decreased strongly thereafter. There were no significant changes in ^{14}C concentration for the stem although a decreasing trend was observed.

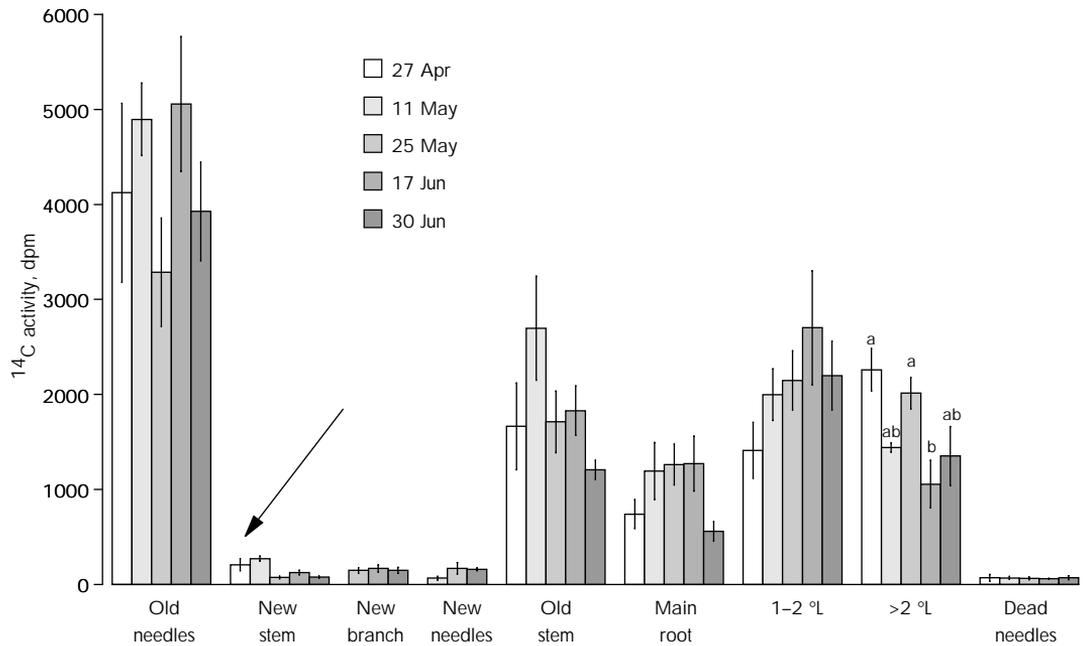


Fig. 1. Absolute amount of ¹⁴C activity in different parts of the seedling. In the first two samplings newly emerging needles were included in the new stem (see arrow). 1 °L and 2 °L are first and second order lateral roots. Vertical bars are ± one standard error, $n = 4$. Different letters indicate significant differences at $p = 0.05$ using Tukey’s Studentized Range (HSD) test.

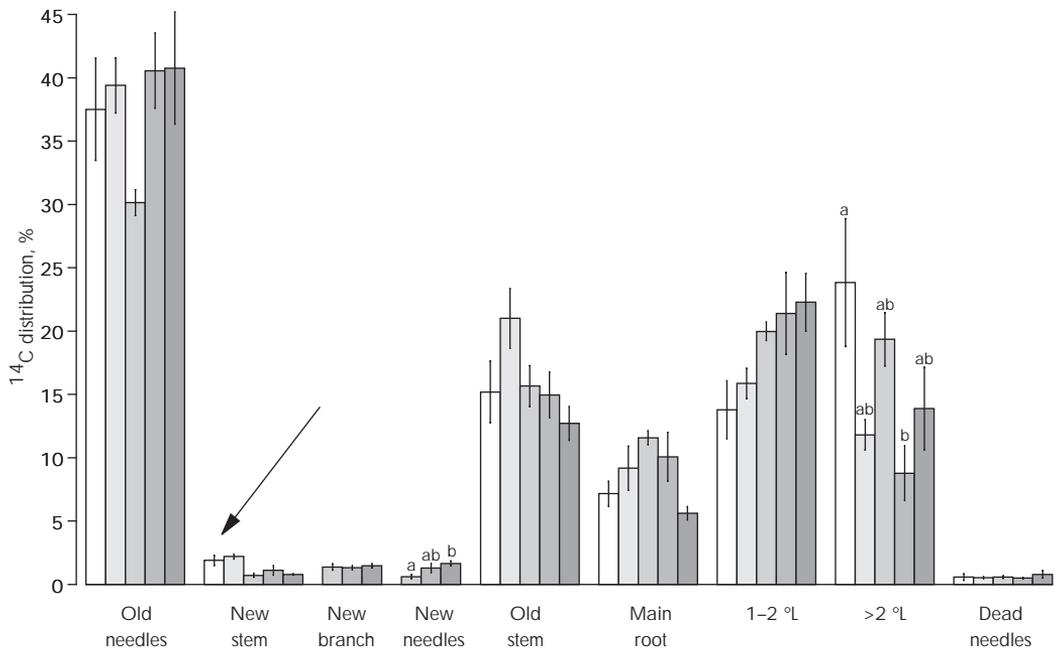


Fig. 2. Proportion of storage ¹⁴C (as a percentage of the total ¹⁴C recovered) representing sink strength of seedling parts during 64-day period. See Fig 1. caption for more detailed explanation.

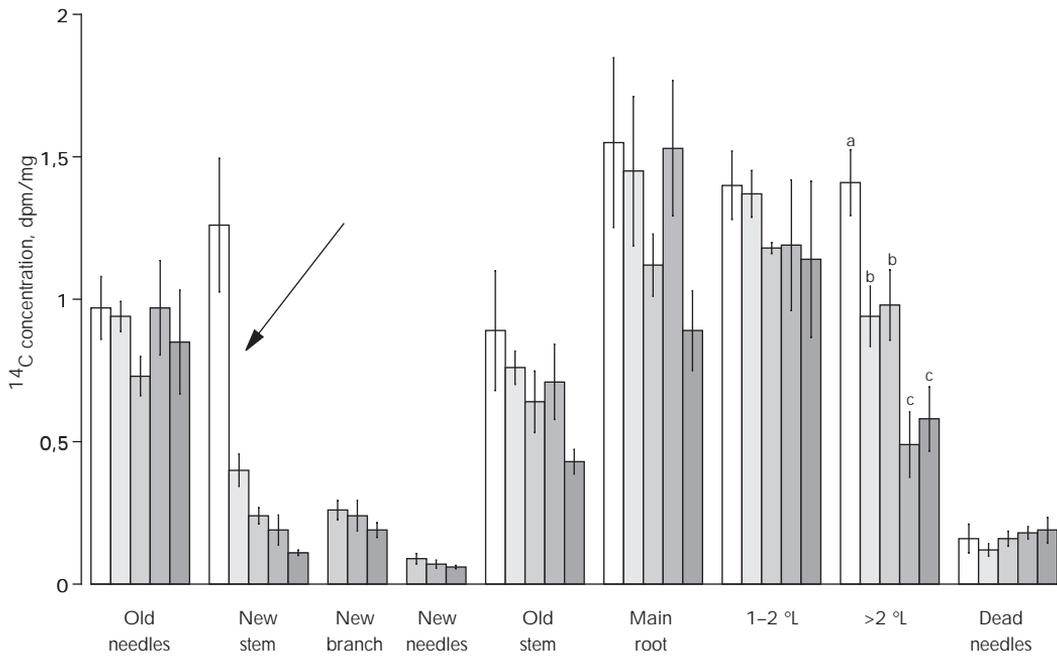


Fig. 3. ^{14}C concentration of the plant part. See Fig 1. caption for more detailed explanation.

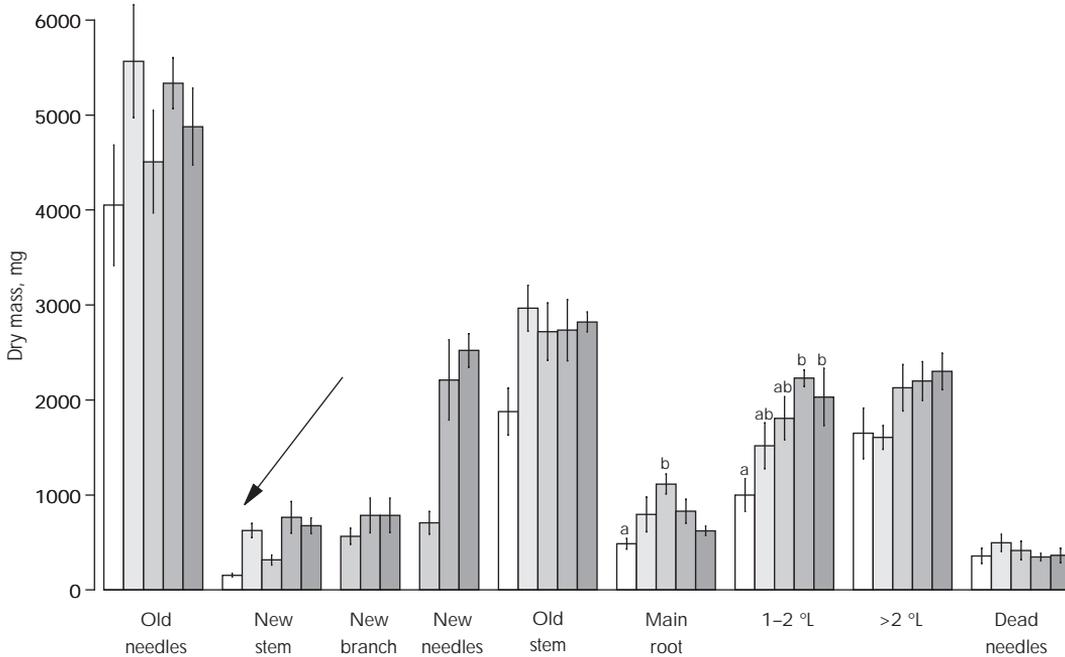


Fig. 4. Absolute amount of dry matter in seedling parts during 64-day period. See Fig 1. caption for more detailed explanation.

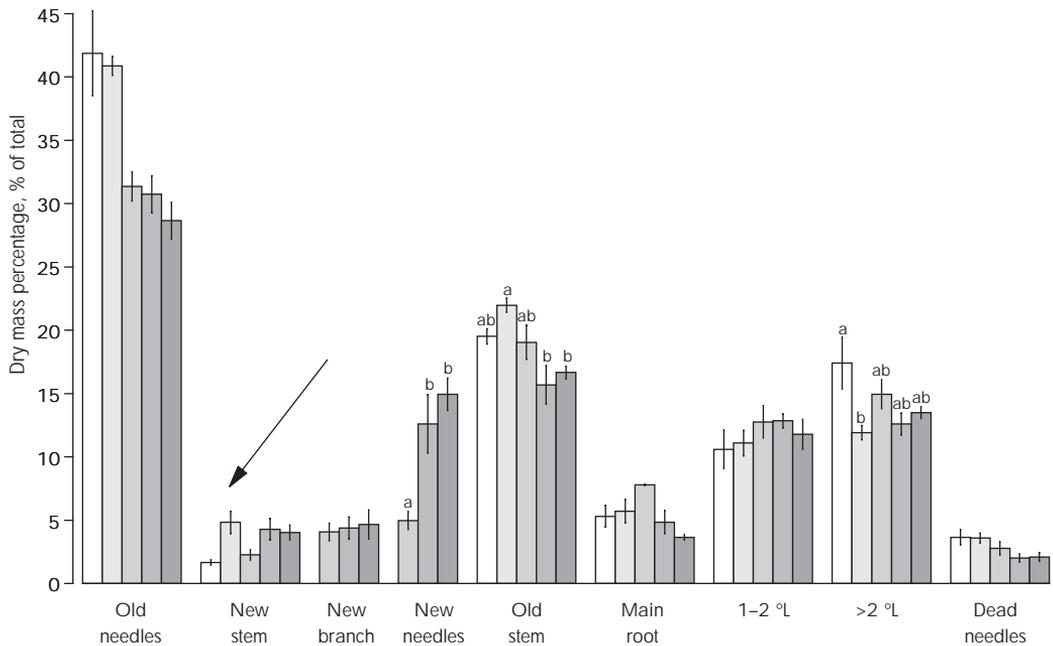


Fig. 5. Proportion of dry matter in seedling parts during 64-day period. See Fig 1. caption for more detailed explanation.

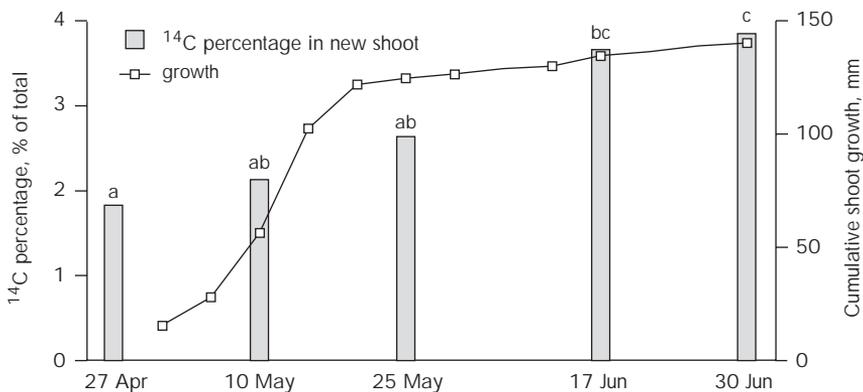


Fig. 6. Proportion of storage ¹⁴C (as a percentage of the total ¹⁴C recovered) and length growth of new shoot during the experiment.

4 Discussion

In conifers, some autumn storage is utilized for initiation of the first layers of xylem during early spring (Hansen and Beck 1990) and for respiration especially in the absence of photosynthesis

(Glerum 1980, Hansen et al. 1996). Some of the springtime storage is used for shoot and root growth (Ericsson and Persson 1980) but the main portion of the growth is dependent on current photosynthates (van den Driessche 1987). Thus, if the critical standard about the importance of

these carbon pools is the amount of carbon allocated to new growth, then the current photosynthates are the most important.

In agreement with earlier studies (Schier 1970, Glerum 1980), the major part of the reserves was stored in old needles and roots. This high percentage is attributable not only to the high volume of these organs, but also to the high concentration of labelled carbon. Due to their higher initial concentration the roots seem to be more active storage sinks than the needles. However, root sink activity is strongly dependent on soil temperature. At low soil temperatures conifers favour allocation to the shoots (Heninger and White 1974, Kuhns and Gjerstad 1988). The observation that ^{14}C concentration in the old needles did not decrease despite the active sinks nearby is supported by Driessche (1987) and Schier (1970), who showed that much of carbon assimilated in autumn is incorporated into needle structural material and does not contribute to the labile storage pool to the same extent as the root system's reserve carbon. Thus, it can be assumed that the root system is an important storage organ of autumn-formed reserve carbon and this importance is based on its large relative sink size, high concentration of reserve carbon, and on the form of storage carbohydrates. In addition, warm soil in the early autumn favours translocation of storage carbon to root system.

The concentration of storage carbon that accumulates in the roots in the autumn is often higher than in the stem (Kozlowski 1992) which was observed in this experiment also. Thus, in seedlings, the stem with a small relative sink size is of minor importance as a storage organ.

In general, the total ^{14}C activity of seedlings did not decrease significantly, which means that respiration loss of storage carbon was small. Only in the finest roots there was a significant decrease in ^{14}C activity together with a slight increase in dry mass. This decrease is an indication of either translocation to other parts of a seedling or respiration. It is unlikely that carbon was translocated because the finest roots are an active sink of carbon. When carbohydrates are limiting, storage carbon may be translocated from coarser roots to finer ones (Ericsson and Persson 1980), not vice versa. It is even more improbable that carbon is translocated further to above

ground parts of a seedling (Ursino and Paul 1973, Marshall and Waring 1985). Thus, it seems that carbon is lost from the finest roots through respiration. The respiration loss of carbon becomes even more notable later when shoot growth is over (Gordon and Larson 1968, Marshall and Waring 1985).

No ^{14}C was translocated for the new root growth, otherwise the activity of ^{14}C would have increased in the finest roots. Although roots contain a substantial amount of storage carbon accumulated in autumn, it is not used markedly for the new root growth (van den Driessche 1987). Roots grow using mainly the current photosynthates (van den Driessche 1987, Lippu 1994) or storage photosynthates accumulated in spring before bud break (Ericsson and Persson 1980, Ford and Deans 1977).

Hansen and Beck (1990) observed that autumn reserves play a minor role in the development of new shoot in eight-year-old Scots pine. This was explained by the rapid consumption of the stored material for production of the stem tissue. The results of the present experiment with two-year-old seedlings indicate that storage carbon formed in the previous autumn is used for initiation of shoot growth, but not markedly for shoot elongation. Although the increase in the new shoot's ^{14}C percentage and in absolute ^{14}C activity was statistically significant the final amount remained low. However, this amount is probably an underestimate because a certain amount of storage carbon may have been allocated to the respiration of the elongating shoot (see Gordon and Larson 1968). New shoot is in turn a very strong sink of currently assimilated carbon (Glerum 1980). In Scots pine seedlings 50–60 % of current photosynthates is allocated to new shoot growth (Lippu 1994). Carbon demand of the growing shoot is in part ensured by the springtime storage formed before bud break in the older needles.

Fischer and Höll (1992) did not find any significant changes in the amounts of reserve materials (autumn + spring storage) in the sapwood of 30-year-old Scots pine during shoot expansion. However, in their experiment, the amount of starch in needles decreased slightly. In the present experiment it was also found that in the stem the concentration of ^{14}C storage carbon

formed in the previous autumn decreased but not significantly. It is possible that labelled reserves stored in the stem were utilized for initiation of diameter growth (Hansen and Beck 1990) but this utilization cannot be detected from the present data because the different types of carbohydrates were not measured.

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