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## Patterns of Dry Matter Partitioning and $^{14}\text{C}$ -photosynthate Allocation in 1.5-Year-Old Scots Pine Seedlings

Jukka Lippu

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**Lippu, J.** 1994. Patterns of dry matter partitioning and  $^{14}\text{C}$ -photosynthate allocation in 1.5-year-old Scots pine seedlings. *Silva Fennica* 28(3): 145–153.

Changes in dry matter partitioning,  $^{14}\text{C}$ -incorporation, and sink  $^{14}\text{C}$ -activity of 1.5-year-old Scots pine (*Pinus sylvestris* L.) seedlings grown in growth chamber conditions were studied during a 91-day experiment. On five sampling dates, seedlings were labeled with  $^{14}\text{CO}_2$ , and whole-plant allocation patterns were determined. Intensively growing shoots modified the dry matter partitioning: during shoot growth the proportion of roots decreased but after that it increased. Based on their large proportion of dry matter, the needles (excluding current needles) were the strongest sink of carbon containing 40 % of the incorporated  $^{14}\text{C}$ . Despite their small initial sink size, the elongating shoots (current main shoot + current branch) and their needles were the second strongest sink (30–40 % of the total  $^{14}\text{C}$ ) which reflects their high physiological activity. The proportion of  $^{14}\text{C}$  in the current year's main shoot increased during shoot growth but decreased as the growth began to decline after 70 days. 10–20 % of the total assimilated  $^{14}\text{C}$  was translocated to the roots. Laterals above 2nd order were the strongest sink in the root system, containing twice as much  $^{14}\text{C}$  as the other roots together. Alternation between shoot and root growth can be seen clearly: carbon allocation to roots was relatively high before and after the period of intensive shoot growth. Changes in root sink strength resulted primarily from changes in root sink activity rather than sink size.

**Keywords** *Pinus sylvestris*, carbon,  $^{14}\text{C}$ -incorporation, dry matter partitioning.

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## 1 Introduction

Allocation of photosynthates to different parts of a plant is determined both genetically and by the environment. Genetic factors determine the level of hormones which regulate cellular and tissue growth (Ho 1988). The ability of plant organs and tissues to supply or use a particular metabolic substance (e.g. carbon) is described by the source-sink concept (Ho et al. 1989). Sink strength, or the demand of an organ for assimilate is the product of the rate of incorporation (sink activity) and the volume of the organ (sink size) and may be represented by the proportion of  $^{14}\text{C}$  partitioned to various organs. Sink activity, or the rate of  $^{14}\text{C}$  uptake by an organ, is reflected by the  $^{14}\text{C}$  concentration, or specific activity of that organ. Net photosynthetic production is translocated from sources to sinks by active (phloem loading and unloading) and passive (turgor pressure gradient) mechanisms.

Carbon is allocated to different plant parts and functions. Growth and respiration require the largest part of assimilated photosynthates (see e.g. Lambers 1987). Respiration releases metabolic energy for growth, maintenance and transport processes. A smaller portion of carbon is exuded or consumed by symbiotic associations (Norby et al. 1987, Vogt et al. 1982).

Environmental factors affect source and sink strengths through their effects on photosynthesis, translocation, and growth. Allocation of photosynthates changes during the lifetime of a tree; in the first years of life the needle mass can make up half of the overall dry matter of the plant but in mature trees foliage comprises only 4–5 % of the total mass (Larcher 1975).

The carbohydrate content of a woody plant fluctuates throughout the year. Accumulation of the reserves depends on photosynthesis and the demand for photosynthates in different organs of a plant. In roots, carbohydrates decrease rapidly with budbreak and then increase late in the growing season after cessation of vegetative growth (Krueger and Trappe 1967, Ericsson and Persson 1980). Although the shoot growth of Scots pine (*Pinus sylvestris* L.) is pre-determined (Lanner 1976), the growth of the new shoots depends mostly on current photosynthates and not on reserves (Schier 1970, Ursino and Paul 1973,

Thompson and Puttonen 1992). Wood formation is initially dependent on reserves (first layers of earlywood and the corresponding phloem) and subsequently on current photosynthate (late earlywood and latewood) (Hansen and Beck 1990).

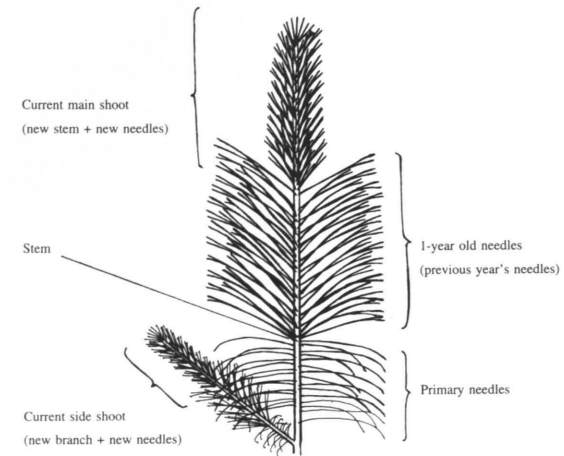
Seasonal changes in carbon allocation are observed in many tree species (Schier 1970, Little 1974, Adams et al. 1989, Schneider and Schmitz 1989). However, there are few studies of current photosynthate allocation and physiological activity (sink activity) in Scots pine seedlings. Better knowledge of allocation dynamics would help in planning nursery operations and tests based on the measurement of seedling vigor. The objective of this study was to determine how the patterns of dry matter partitioning and current photosynthate allocation vary during the season. In addition the sink activities of seedling parts were determined to obtain an estimate of physiological activity.

## 2 Materials and Methods

The study material consisted of 50 container grown 1.5-year-old Scots pine seedlings. The seedlings of southern Finnish origin were lifted at the nursery of the Foundation for Forest Tree Breeding (Haapastensyrjä) two weeks before starting the experiment in spring 1990. Each seedling was transplanted to a one-litre pot containing a mixture of fertilized (ST-peruslannoite: 0.9 kg/m<sup>3</sup>, containing 10 % N, 16.6 % K, 9.4% P and dolomite: 6.5 kg/m<sup>3</sup>, containing 2 % Mg) low humified *Sphagnum* peat (ST-400 Finnpeat B2, Satoturve) and vermiculite (2:1 v/v). The pots

**Table 1.** Sampling according to the developmental stage of the seedlings.

Sample / time after planting, days	Developmental stage	Length of the new needles, mm
I / 15	Bud bursting	-
II / 22	Intense shoot growth	3
III / 39	Intense shoot growth	10
IV / 61	Shoot growth finished	18
V / 91		21



**Fig. 1.** Above ground parts of a 1.5-year-old Scots pine seedling.

were kept in a growth chamber at 13/7 °C (day/night) air temperature, 18 h photoperiod, 200  $\mu\text{mol s}^{-1}\text{m}^{-2}$  photon flux density and 50 % relative humidity.

During a 91-day experiment from March to May 1990, 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). Eight seedlings were exposed to  $^{14}\text{C}$ -labelled  $\text{CO}_2$  (9.25 kBq per seedling) in a 360 liter plexiglass 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. Photon flux density was 300  $\mu\text{mol s}^{-1}\text{m}^{-2}$ , temperature was 28 °C, and the air inside the chamber was stirred with a fan. After the 3-h labelling period, the seedlings were returned to the growth chamber. After 2 days, the roots were washed free of rooting medium and the seedlings were separated into current shoots, 1-year old needles, primary needles, stem (Fig. 1), main root, 1st–2nd order lateral roots, and above 2nd order lateral roots. All plant parts were oven dried at 70 °C for 2 days and weighed. Subsamples were combusted (wet oxidizer Maricont 781, Junitec 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 LKB Rackbeta 1215). The distribution of  $^{14}\text{C}$  (Alloc, % of total incorporated  $^{14}\text{C}$ ) within seedlings, which represents sink strength, was calculated as

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

where  $A_{\text{part}}$  is  $^{14}\text{C}$  (Bq) accumulated in a plant part (needles, stem etc.) and  $A_{\text{tot}}$  is the total incorporated  $^{14}\text{C}$ . The specific  $^{14}\text{C}$ -activity  $A_{\text{sa}}$ , or  $^{14}\text{C}$  concentration (Bq/g dry mass) of a plant part (needles, stem etc.), which reflects sink activity, was calculated as

$$A_{\text{sa}} = A_{\text{smp}} / m_{\text{smp}}$$

where  $A_{\text{smp}}$  is the  $^{14}\text{C}$ -activity of a tissue sample and  $m_{\text{smp}}$  is the dry mass of that sample (0.15–0.2 g). Since plant size increased, and the seedlings fixed different amounts of  $^{14}\text{CO}_2$  depending on their needle mass,  $A_{\text{sa}}$  was related to the specific activity of the entire plant ( $A_{\text{otsa}}$ ) to obtain relative specific activity ( $A_{\text{rsa}}$ ):

$$A_{\text{rsa}} = (A_{\text{sa}} / A_{\text{otsa}}) \cdot 100$$

$A_{\text{rsa}}$  provides an estimate of the demand for photosynthates in different parts of a seedling, i.e. sink activity. However, this is not the “real” sink activity as it does not include  $^{14}\text{C}$ -respiration.

The data were first tested for normality using the Lilliefors test. Some of the data were not normally distributed which required the use of the non-parametric Mann-Whitney U-test to analyze statistical differences between treatment medians. Calculations were performed using SAS statistical software (SAS Institute Inc. 1985).

## 3 Results and Discussion

### 3.1 Dry Matter Partitioning (Sink Size)

Although the dry mass of the current year's shoots and roots increased (from 0.7 g to 3 g and from 2.1 g to 3.5 g, respectively) the total dry mass appeared not to do so (Table 2). This was mainly due to variation in seedling material, especially in the dry mass of 1-year-old needles. Also, the senescence and death of primary (2-year-old) needles decreased the total dry weight at the end of the experiment. Dry weight is the most variable morphological characteristic in Scots pine nursery stock (Jalkanen et al. 1992). Therefore, observing changes in relative dry matter parti-

tioning instead of comparing successive absolute weights of small samples of seedlings gives a more reliable view of seedling development.

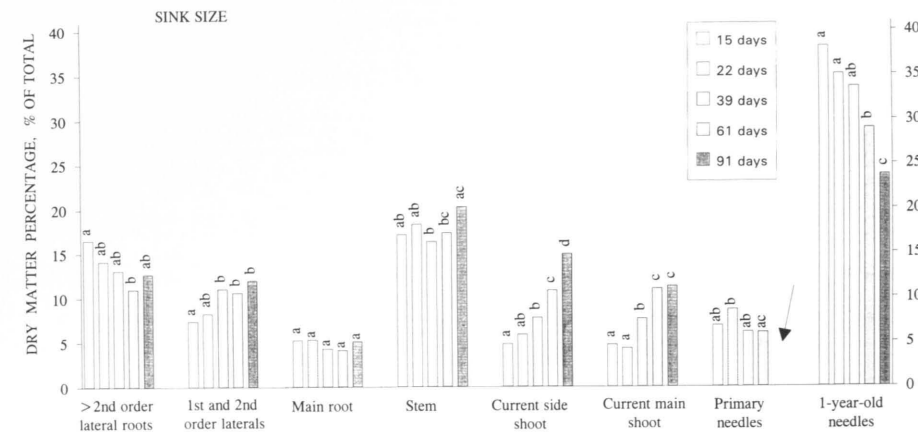
The dry matter partitioning was, as expected, modified by intensive growth of above ground parts (Fig. 2) (see e.g. Leikola and Raulo 1973). The percentage of dry matter partitioned into needles (excluding current needles) compared to other seedling parts was initially highest (45 %) but decreased to 24 % as shoot growth proceeded and primary needles began to senesce and die.

The current year's shoots (main + branch) constituted 10–26 % of total dry weight of the seedlings depending on the stage of growth (Fig. 2). The proportion increased during the experiment but stabilized as growth ceased. The dry matter percentage of the current year's main shoot was about the same as the percentage in the current year's branch. The proportion of stem dry matter in total dry matter was about 20 % and remained at the same level during the experiment.

Roots made up 26–30 % of the total dry matter, which is somewhat higher value usually observed (e.g. Rikala and Huurinainen 1990). In this study, seedlings partitioned 11–16 % of total dry matter to laterals above 2nd order. Partitioning to the main root did not change during the experiment whereas it increased to 1st and 2nd order laterals.

**Table 2.** Dry mass (g) of the seedling parts at the five sampling times during the experiment (mean  $\pm$  SE,  $n = 8$ ).

Seedling part	Time, days after transplanting				
	15	22	39	61	91
	Mean dry mass, g				
1-year-old needles	2.75 $\pm$ 0.29	3.97 $\pm$ 0.45	3.76 $\pm$ 0.36	3.75 $\pm$ 0.37	2.79 $\pm$ 0.23
2-year-old needles	0.52 $\pm$ 0.12	1.02 $\pm$ 0.20	0.68 $\pm$ 0.07	0.82 $\pm$ 0.17	0
Current main shoot	0.33 $\pm$ 0.04	0.46 $\pm$ 0.04	0.84 $\pm$ 0.06	1.39 $\pm$ 0.08	1.27 $\pm$ 0.07
Current side shoots	0.34 $\pm$ 0.04	0.72 $\pm$ 0.16	0.86 $\pm$ 0.11	1.36 $\pm$ 0.13	1.76 $\pm$ 0.16
Stem	1.22 $\pm$ 0.10	2.16 $\pm$ 0.35	1.81 $\pm$ 0.15	2.22 $\pm$ 0.21	2.38 $\pm$ 0.20
Main root	0.37 $\pm$ 0.03	0.59 $\pm$ 0.07	0.48 $\pm$ 0.05	0.51 $\pm$ 0.04	0.58 $\pm$ 0.03
1st and 2nd order laterals	0.55 $\pm$ 0.07	0.93 $\pm$ 0.11	1.20 $\pm$ 0.07	1.34 $\pm$ 0.09	1.41 $\pm$ 0.13
> 2nd order laterals	1.18 $\pm$ 0.14	1.58 $\pm$ 0.18	1.42 $\pm$ 0.09	1.39 $\pm$ 0.15	1.50 $\pm$ 0.13
Mean total dry mass, $\pm$ SE	7.20 $\pm$ 0.59	11.44 $\pm$ 1.38	11.04 $\pm$ 0.74	12.80 $\pm$ 0.79	11.69 $\pm$ 0.65



**Fig. 2.** Proportion of dry matter in different parts of the seedlings, %, mean ( $n = 8$ ). Different letters indicate significant differences at  $p = 0.05$ . New developing needles were included in current shoots. The arrow indicates the death of the primary needles.

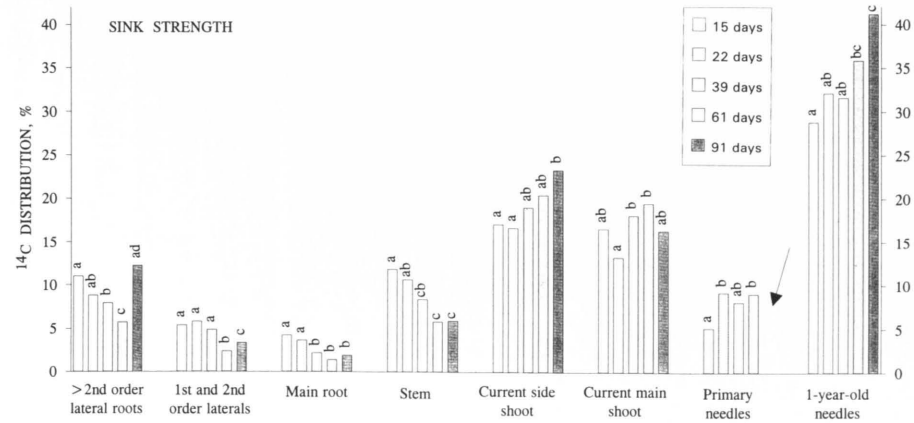
The change in dry matter percentage of a certain seedling part does not necessarily reflect changes in its sink strength because intensively growing parts modify the dry matter percentage of non-growing parts (e.g. previous needles). By measuring  $^{14}\text{C}$  allocation, more information is obtained on the current carbon use in plants.

### 3.2 $^{14}\text{C}$ Distribution (Sink Strength)

Needles contained more  $^{14}\text{C}$  than any other plant part; about 30–40 % of  $^{14}\text{C}$  remained in 1-year-old needles and 0–9 % in 2-year-old (primary) ones (Fig. 3). In allocation studies the proportion of total  $^{14}\text{C}$  in needles has usually been reported to be about half (Gordon and Larson 1970, Arovaara and Ilvesniemi 1990) or greater (Kuhns and Gjerstad 1988). Carbon allocation to needles increased slightly during the experiment. At the end of the experiment, the percentage of  $^{14}\text{C}$  in needles (Fig. 3) was greater than the proportion of needle mass in total dry matter (Fig. 2). This indicates that the lack of an active sink (e.g. growing shoot) caused accumulation of reserve substances (see Fischer and Höll 1991). In conifer seedlings, old needles play an important role

as storage for photosynthates. In young trees, the allocation to needles is much less than in small seedlings. Hansen and Beck (1990) reported that, in 8-year-old Scots pine, the allocation to branches and needles was only about 8 % whereas it was 89 % to stem. In mature conifers needles make up 4–5 % of total mass (Larcher 1975) and hence are of minor importance as a storage.

30–40 % of the total  $^{14}\text{C}$  was allocated to the current year's shoots (main + branch) and their needles. Allocation to both the current year's main shoot and the new branches was about the same, between 15–20 % throughout the study period, except at the end of the period when allocation was 14 % and 23 % to new main shoot and new branches, respectively.  $^{14}\text{C}$ -allocation to the current year's main shoot increased during shoot growth but decreased as the growth began to cease after 70 days. Allocation to the current year's branches increased continuously during the experiment. A growing shoot consumes carbohydrates mainly from the previous season's needles which possess high photosynthetic performance (Gordon and Larson 1968). 1-year-old needles are responsible for growth and maintenance of the new shoot but 2- and 3-year-old needles are important sources of energy-rich com-



**Fig. 3.** Proportion of  $^{14}\text{C}$  in seedling parts during the experiment, % of the total  $^{14}\text{C}$  incorporation, %, mean ( $n = 8$ ). Different letters indicate significant differences at  $p = 0.05$ . New developing needles were included in current shoots. The arrow indicates the death of the primary needles.

pounds as well (Fischer and Höll 1991). Both current photosynthates and storage carbohydrates are translocated from needles. Current photosynthates are translocated to the bud before and after bud break, and storage carbohydrates are used in respiration (Gordon and Larson 1968). Only a minor proportion of the reserves from the stem and obviously no material from the roots (Ursino and Paul 1973) are consumed in bud sprouting.

$^{14}\text{C}$  allocation to stems decreased until shoot growth was over (Fig. 3). The decrease of carbon allocation to stems may be due to cessation of wood formation and the increased allocation to roots. Wood formation is dependent on current photosynthate where storage material plays only an indirect role in the process (Glerum 1980). However, stored carbohydrates are used for the production of the first layers of earlywood and the corresponding phloem (Hansen and Beck 1990).

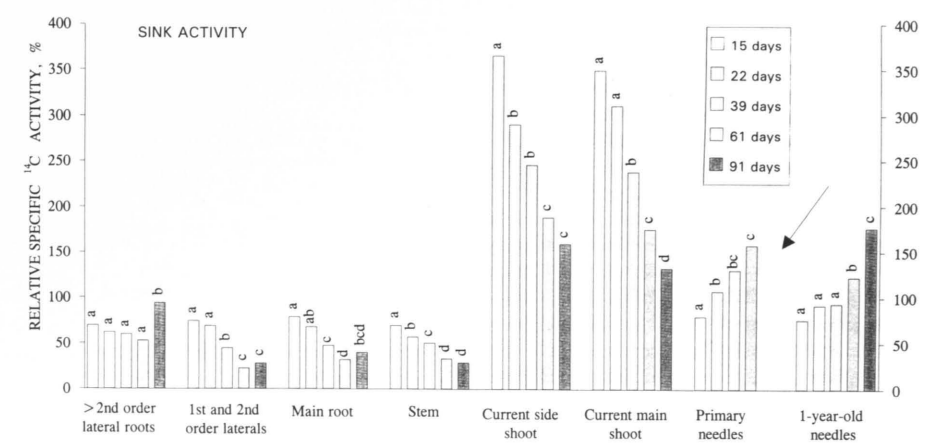
10–20 % of the total assimilated  $^{14}\text{C}$  was translocated to roots. Laterals over 2nd order were the strongest sink in the root system gaining more carbon than the other roots put together (Fig. 3). Before and after shoot elongation, the  $^{14}\text{C}$  allocation to roots was higher than during

shoot growth when the allocation decreased. After shoot growth, the allocation to laterals over 2nd order almost doubled, indicating the beginning of intensive root growth. Seasonal variation in growth and carbohydrate concentration in roots results from interaction of shoot development and current photosynthesis (Loach and Little 1973, Ericsson 1979, van den Driessche 1987).

### 3.3 Relative Specific $^{14}\text{C}$ Activity (Sink Activity)

Sink activity seems to fluctuate markedly in all parts of the seedling indicating physiological changes and alternation of growth between plant organs (Fig. 4). However, changes in sink activity (relative specific activity) may result more from the change in sink size than physiological activity. In such cases it is a matter of dilution and not a change in physiological activity.

Developing current year's shoots were the most active sinks, reflecting the high rate of cell division which is crucial in attracting new assimilates (Ho 1988). The sink activity was initially 3–6-fold greater in new shoots compared to stem, main root and 1st and 2nd order lateral roots, and



**Fig. 4.** Sink  $^{14}\text{C}$ -activity (%) or relative specific activity of seedling parts, obtained by relating the specific activity of a seedling part to the specific activity of the entire plant, %, mean ( $n = 8$ ). Different letters indicate significant differences at  $p = 0.05$ . New developing needles were included in current shoots. The arrow indicates the death of the primary needles.

2–3-fold greater compared to old needles. However, shoot sink activity decreased gradually to half of its initial value as shoot growth began to cease (Fig. 4 and Table 2). Most of the decrease was the result of an increase in sink size. The developing new needles demanded, relatively, 3 times as much carbon as the new shoot itself (data not shown here). New needles do not photosynthesize in the early stages of development (Troeng and Linder 1982). In Scots pine needles, the change of translocation direction from import to export of carbohydrates occurs for the current needles in the middle of July when they have reached half of their final length (Ericsson 1978). The activity of the 1-year-old needles as a sink increased at the end of the experiment coincident with shoot growth termination. The increase seems to be the result of  $^{14}\text{C}$  accumulated as storage. Glerum (1980) found that a considerable portion of the photosynthate retained in needles occurred in non-structural components which suggests that the needles are important for storage of reserves. Considering source-sink relationships, needles are a complicated part of a plant. They act both as a source and a sink at the same time, and, in addition, their source-sink status changes during needle development. New

developing needles are a utilization sink because most of the imported carbon would be used for growth or respiration. Old needles are a storage sink because a substantial proportion of the assimilates is stored rather than consumed. These aspects should be borne in mind when comparing needles to other organs of a seedling.

The sink activity generally decreased in stem, main root and in first and second order lateral roots during the experiment. Sink activity followed a similar pattern in all roots: activity decreased initially but finally increased. The increase was more pronounced in laterals over 2nd order. Sink activity of the whole root system was relatively high before and after intense shoot growth indicating alternation between shoot and root. In the root system, changes in root sink activity (and not so much sink size) appeared to be responsible for the changes in root sink strength.

### 3.4 Conclusions

All the measured parameters give valuable information on seedling status from different viewpoints. Mass relations can be used to evaluate

the balance between carbon assimilation by foliage and water acquisition by roots. It is possible to find values of shoot to root ratio that maximize whole plant carbon gain (Givnish 1986). However, mass relations are a result of an integral of growth rate over a longer period. By measuring  $^{14}\text{C}$  allocation, more accurate information is obtained on the current carbon use in plants. For example, the length of fine roots may increase markedly without a substantial change in dry weight whilst, at the same time, an increase in allocation of  $^{14}\text{C}$  to the fine roots may be more pronounced. The percentage of  $^{14}\text{C}$  in a certain plant part is strongly affected by the size of that part which means that the allocation percentage is not a purely physiological character. A considerable proportion of carbon may be allocated to a large but yet physiologically weak part of a plant. Therefore, of the three measured characters, sink activity is the best indicator of the internal status of seedling parts giving an estimate of the physiological demand for photosynthates.

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