Partitioning of Carbohydrates and Biomass of Needles in Scots Pine Canopy

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The study was aimed at the quantitative evaluation of the temporal and spatial partitioning of non-structural carbohydrates and needle biomass in a canopy of Scots pine (*Pinus sylvestris* L.) growing in a *Myrtillus* site type forest stand (predominant in Estonia). The tree canopy was divided into ten equal layers and the material for the spatial partitioning of the investigated characteristics was sampled from all layers. Our findings revealed a significant variation in morphology and in the partitioning of carbohydrates in needles in different layers of the canopy. The study of the temporal dynamics of carbohydrates showed that starch content in needles started to increase in early spring before budbreak, which was accompanied by a decline in soluble carbohydrates. In October, the starch content of needles was low, but the concentration of soluble sugars started to increase attaining a maximum in winter. Regression analysis indicated that before budbreak, the partitioning of soluble sugars in different canopy layers was relatively weakly correlated with the height of the layer; however, a strong correlation was observed for starch. In autumn, when the growth of trees stopped and daily temperatures decreased, the allocation of soluble sugars was correlated with the height of the canopy layer.

Introduction

Carbohydrates have a highly significant effect on the relationship between photosynthesis and biomass (Gifford *et al.*, 1984), including partitioning between processes of respiration, growth and reproduction as well as morphological partitioning between various structures of plants such as roots, stems and leaves. The effects of assimilates partitioning in trees play an important role in their survival (Kozlowski *et al.*, 1991) as well as in their acclimation to environmental stresses (Wargo and Montgomery, 1983; Gregory *et al.*, 1986). Allocation involves the processes determining the biochemical pathways of carbon that have become available for the distribution or partitioning among plant parts.

The direction of assimilates translocation is primarily regulated by the relative sink strength of an organ. Thus source-sink relationships are not static, and almost all plant organs can act as a sink at some stage of their development.

The content of carbohydrates is characterized by the temporal and spatial dynamics governed by the physiological state and the structural peculiarities of the plant as well as by various environmental factors. It has been found to vary at different evolutionary stages and in different organs of plants (Ericsson, 1978; Hampp *et al.*, 1994; Mandre and Klõšeiko, 1995). The relationship between the temporal and the spatial allocation of photoassimilated carbon and the development of the different plant organs affects significantly the growth pattern of individual trees (Jenkins, 1975; Einig and Hampp, 1990).

Carbohydrate content may vary also considerably in leaves, depending on their location in the canopy. There is strong evidence indicating that the distribution patterns of the photosynthetic properties of the foliage along the canopy are mainly determined by light distribution (Jablonski and Geiger, 1987; Pearcy and Sims, 1994), temperature (Waring, 1991) and availability of nutrients in trees (Field and Mooney, 1986; Vessey and Layzell, 1987). Undoubtedly, the anatomic properties of leaves are affected by their location in the canopy (Kappel and Flore, 1983). For aspen, a relationship was established be-

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tween the variability of carbohydrates and biomass partitioning in the leaves of different canopy layers (Mandre *et al.*, 1998).

Carbon partitioning in plants can be influenced by a variety of factors and the question whether a particular organ is adequately supplied with assimilates and can hence fully realize its growth potential may not have a simple answer. Despite intense research in this area, there is still little information about carbohydrate partitioning in conifer canopies and in the whole tree in field conditions.

Material and Methods

The investigations were performed on 45–55-year-old Scots pine (*Pinus sylvestris* L.) growing in a *Myrtillus* site type pine stand in Central Estonia (Alatskivi, 27°07′ E, 58°35′ N).

Twelve trees with a similar canopy and habitus were selected for analysis. Trees for morphometric measurements were felled in October, when the annual growth of needles and shoots had stopped; for biochemical analyses trees were felled twice – in early spring and in autumn. The canopy of each tree was divided into ten equal horizontal layers (L). For each layer the total dry mass of needles (% of the total mass of the crown) was determined. For morphometric measurements of needles and for estimation of their carbohydrate concentration, the apical shoot ($n = 12$) of the largest branch from each canopy layer ($n = 10$) of the sample tree was taken to reduce the variation of the results due to a random selection of shoots. The number of buds on shoots (no shoot^{-1}) was counted, the average length of needles (mm, $n = 200–300$), dry mass (mg, $n = 100$) and needle mass per length (mg mm^{-1}) as well as the density of needle pairs on shoots (no cm^{-1}) were determined. The dry mass of needles was measured after drying at 70 °C.

Needles for the vertical partitioning of non-structural carbohydrates in the canopy were taken from ten canopy layers at the time before budbreak in late March and in early October when the growth of needles had already stopped. The temporal partitioning of carbohydrates was estimated using needles from the 3rd and 4th canopy layers characterized by an average rate of photosynthesis in conifers (Kozlowski *et al.*, 1991). For biochemical analyses, only one-year-old needles were used, as they are the most important source of assimilates for new developing organs (Ericsson, 1978).

All one-year-old needles were removed from the shoots and frozen immediately in liquid nitrogen. Total soluble sugar (SS) and starch (ST) concentrations were estimated according to Ferenbaugh (1976), Marshall (1985) and Arasimovich and Ermakov (1987). Determination of the amounts of soluble sugars and starch in tissues were carried out in three replications using 1–5 g of dried and homogenized plant material of needles. Repeated extraction (3 times, à 10–15 minutes) of soluble sugars was carried out with 80% ethanol. After centrifugation the soluble supernatant was collected. All the residue that remained after the removal of soluble sugars was dried, followed by gelatinization in distilled water and prolonged hydrolysis with 35% perchloric acid, which provide complete hydrolysis of all starch into glucose (Ferenbaugh, 1976; Marshall, 1985). The obtained soluble sugar and hydrolysed starch extracts were reacted separately with anthrone reagent (0.1% anthrone in 72% sulfuric acid) to produce a blue-green color, and the absorbances were measured (Unicam UV-VIS spectrometry, UK) at 620 nm (Ferenbaugh, 1976; Peace *et al.*, 1995). Concentrations (% of dry weight) were calculated using glucose curves as standard.

The regression trendlines and the R-squared values (R^2) at the significance level ($p < 0.01$) for the investigated parameters were calculated using the MS Excel 5.0 package. One-way analysis of variance was tested by ANOVA analysis according to Statgraphics 5.0.

Results and Discussion

Temporal changes of carbohydrates in the needles of Scots pine growing in a *Myrtillus* site type forest stand showed that the starch content of one-year-old needles starts to increase in early spring (March, April) before budbreak (Fig. 1). This is caused by a rapid increase in net photosynthetic activity during spring, observed in several studies of evergreen conifers (Ericsson, 1980; Mattsson and Troeng, 1986). The increase in

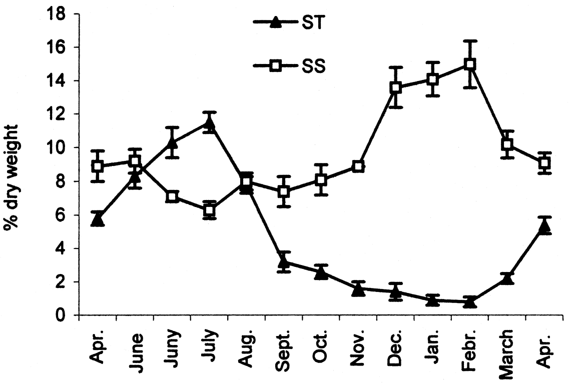

Fig. 1. Annual dynamics of soluble sugars (SS) and starch (ST) in one-year-old needles of Scots pine.

starch is accompanied by a decline in soluble carbohydrates in one-year-old needles, which is affected by several factors. It is clear that respiration processes will intensify in spring, when needles harden (Fisher and Höll, 1991; Amundson *et al.*, 1992). There is evidence that one-year-old needles are the most important sources of assimilates for the functional activity of conifers (Ericsson, 1978). In early spring, the metabolism of buds enhances their attracting effect and the influx of assimilates into developing buds increases. Thus the decrease in soluble carbohydrates in one-year-old needles may result from the translocation into current year needles and from elongation of the axis of new shoots. At the same time, also the accumulation of starch increases in roots (Kozlowski *et al.*, 1991). Although the total content of soluble carbohydrates in the needles decreases in spring, the dynamics of individual representatives of carbohydrates is variable. Differently from the content of fructose, glucose (predominant soluble sugars), galactose, raffinose etc., the content of sucrose has been found to increase somewhat 10–20 days after budbreak in the needles of Scots pine (Fisher and Höll, 1991) and Norway spruce (Hampp *et al.*, 1994), however, in 30–40 days its content decreases again. Moreover, Einig and Hampp (1990) did not detect large fluctuations in needles' sucrose content between May and October in contrast to their starch content.

Intensified photosynthesis in conifers in May (Troeng and Linder, 1982; Adams *et al.*, 1990; Kull and Koppel, 1992) is reflected in the accumulation of starch in Scots pine needles. The starch content of needles is at maximum from July to August accounting for up to 12–15% of dry weight at this time. Photosynthesis starts to decline in late autumn due to lower photosynthetic photon flux density as well as low temperatures (Troeng and Linder, 1982). This brings about important physiological changes in trees, related to resistance to unfavourable winter conditions. From September starch content decreases gradually and the concentration of soluble sugars starts to increase.

Hansen (1992) showed that the decrease in starch content in winter is due to a higher rate of starch degradation compared with the rate of its synthesis. In December-January, starch is almost completely exhausted (0.8–0.9% of d.w.), and the content of soluble sugars attains a maximum level in January-February (14–15% of d.w.). The content of soluble sugars serves as an important factor in the development of resistance of trees to low temperatures in winter. Usually, the lowest temperatures in Estonia are registered in January and February. In the studied area the mean temperature in January is −2.1 °C and in February −5.5 °C. This period is characterized by a pronounced depression of the photosynthetic capacity of conifers in Estonia (Kull and Koppel, 1992).

However, transformation of organic substances does not stop in winter. Temperature variation may change certain enzyme pathways, so that the kinetics of enzymes affects carbon partitioning and allocation. Low temperatures influence particularly the ability of roots to take up water and nutrients (Kramer, 1983; Waring, 1991).

As temperature rises in March-April, the content of soluble sugars in needles falls, photosynthesis intensifies, and various metabolic changes take place in preparation for budbreak and a new vegetation period.

The strength and direction of the transport and partitioning of carbohydrates in different plant organs has been shown to be regulated by source-sink relationships. It was demonstrated earlier that foliar photosynthetic properties vary vertically in canopies for both broad-leaf and coniferous trees (Woodman, 1971; Kozlowski *et al.*, 1991; Mandre *et al.*, 1998). Indeed, our study showed a high variability of the accumulation of

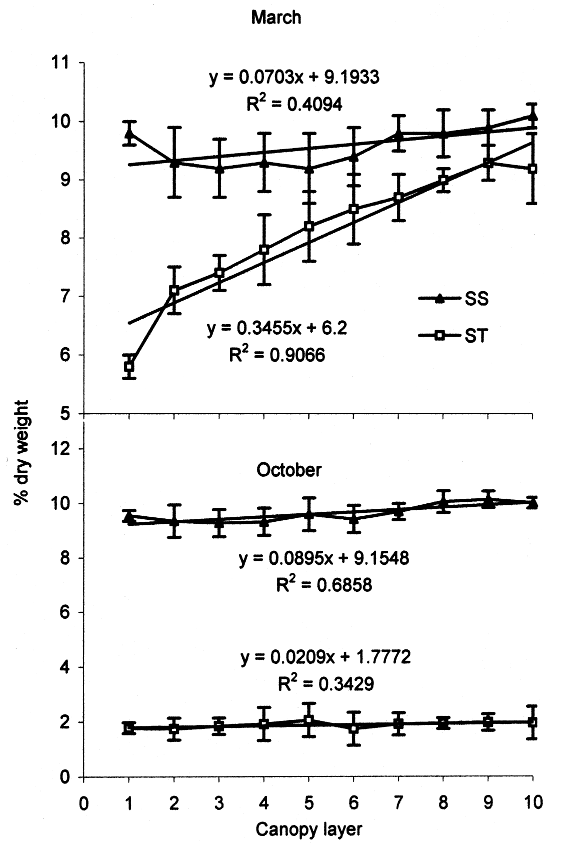

Fig. 2. Vertical distribution of starch (ST) and soluble sugars (SS) in one-year-old needles of Scots pine from different canopy layers.

non-structural carbohydrates in the needles of Scots pine in different canopy layers. In March, before budbreak, and in October, after growth processes had stopped, variability in the dynamics was observed and partitioning of soluble sugars and starch (Fig. 2). At the beginning of budbreak, soluble sugars are mobilized and possibly transported to newly developing organs acting as a powerful sink. Regression analysis indicated that at this time the partitioning of soluble sugars between different layers of the canopy of Scots pine is rather weakly correlated with the height of the layer ($R^2_{\mathrm{SS/L}} = 0.409$, $p < 0.01$). However, a strong correlation was observed between the content of starch and the height of the canopy layer ($R^2_{\mathrm{ST/L}} = 0.907$, $p < 0.001$). In March, the upper layers of the canopy contained 30–69% more starch than the lower layers, and in October, the starch content of the needles was low and relatively stable over the whole canopy ($R^2_{\mathrm{ST/L}} = 0.343$, $p < 0.05$). However, by this time the content of soluble sugars reveals the 10–15% difference between the lower and the upper canopy layers and their concentration is significantly correlated with the height of the canopy layer ($R^2_{\mathrm{SS/L}} = 0.686$, $p < 0.005$) (Fig. 2).

As studied by us, the 5th-6th layers account for almost 35% of total needle mass. Needle mass in the top of the canopy and in its lowermost layer makes up 10% and 24% of total needle mass, respectively. A similar allocation of assimilating mass has been observed in canopies of *Picea glehnii*, as well as in the broad-leaved

Table I. Variation of the morphological parameters of needles in different canopy layers of Scots pine (±SD).

Canopy layer	Dry mass of needles per layer, % of total in canopy	Dry mass of needle [mg]	Length of needle [mm]	Mass per unit needle length [mg mm^{-1}]	Density of needles on shoot, no cm^{-1}*	Needle dry mass per shoot unit length [g cm^{-1}]	No of buds on shoots, no shoot^{-1}
1st	1.7±0.06	9.2±0.1	44.9±3.6	0.200±0.02	10.0±2.2	0.18±0.01	1.3±0.0
2nd	5.3±0.14	8.9±0.1	45.6±3.2	0.195±0.02	10.5±1.2	0.18±0.02	1.7±0.1
3rd	8.5±0.16	9.9±0.3	45.5±3.9	0.217±0.04	10.8±1.0	0.21±0.01	1.5±0.3
4th	15.2±0.15	12.7±0.2	50.3±2.4	0.252±0.01	9.2±1.1	0.23±0.01	2.0±0.1
5th	17.5±1.21	17.4±0.6	56.9±1.8	0.306±0.01	9.4±0.8	0.30±0.00	2.9±0.1
6th	17.7±1.14	21.5±0.9	58.6±2.0	0.367±0.02	8.6±0.7	0.32±0.01	1.9±0.1
7th	14.4±0.78	22.0±0.3	62.6±5.4	0.351±0.03	8.0±0.6	0.35±0.00	3.1±0.1
8th	11.5±0.96	22.4±0.9	63.9±5.1	0.351±0.12	8.1±0.4	0.37±0.00	3.9±0.1
9th	5.8±0.71	22.5±1.2	63.7±2.8	0.353±0.07	8.3±0.5	0.40±0.00	4.3±0.2
10th	2.4±0.114	22.0±1.3	61.3±2.9	0.359±0.03	6.5±0.2	0.28±0.00	4.2±0.2

* Number of needle pairs on shoot.

species *Betula platyphylla* (Kikuzawa and Umeki, 1996), *Populus tremula* L. (Mandre *et al.*, 1998) and *Salix viminalis* (Ross and Ross, 1996). Thus it is evident that the assimilating mass and the photosynthetic productivity of trees is allocated predominantly in the middle layers of the canopy. For conifers, this conclusion is supported by studies of Woodman (1971), Ågren *et al.* (1980) and Troeng and Linder (1982).

We established differences not only in the biochemical but also in the morphological parameters of needles located in different layers of the canopy (Table I). Needle length and mass, the ratio of needle mass to the length of an individual needle as well as needle mass per shoot unit length increase toward the top of the tree canopy. Such a dynamics of needle parameters is considered normal for Scots pine (Flower-Ellis and Persson, 1980). Also, the number of buds is significantly larger in the upper layers. At the same time, the density of needles on shoots, which may reflect light conditions for growing needles in the canopy (Thompson, 1985), decreases towards the top of the tree. Lower needle density can enhance penetration of light into the canopy. Differences in this parameter reflect differences in both photosynthetic capacity and adaptation to various water and temperature regimes between different canopy layers (Margolis *et al.*, 1995). Dispersion analysis revealed significant differences in the investigated parameters between different canopy layers, and regression analysis indicated the dependence of their values on the location of the corresponding layers in the canopy (Table II).

Formation of buds in late summer and their number on the shoots, which determine foliage density and assimilation area, displayed a significant correlation with the content of carbohydrates in the needles in spring and especially in autumn (Table III). At the onset of bud sprouting in one-year-old needles of Scots pine, the amount of starch was at maximum, which provided initial material for bud development. Ursino and Paul (1973) suggested that the reserve of soluble carbohydrates, deposited in the needles during autumn, plays an important role in the development of new shoots, while Hansen and Beck (1990) showed that only 0.4% of the existing pool of soluble carbohydrates in Scots pine contributed to sprouting. Our experiments showed that needle mass and length and even the number of buds on shoots depend significantly on the amount of soluble sugars deposited in the needles in autumn. Undoubtedly, the increase in the concentration of soluble sugars in conifers in autumn is important for building resistance to unfavourable conditions in winter.

Table II. Differences between the morphological parameters of pine in different layers of the canopy and the dependence of the values of the parameters on the location of the layer in the canopy.

Parameter	Layer of canopy			
	One-way analysis of variance		Regression analysis	
	F-ratio	Significance	R^2	Significance
Length of needles	7.002	0.0000	0.871	0.011
Dry mass of needles	8.314	0.0000	0.872	0.050
Mass per unit needle length	16.209	0.0000	0.894	0.005
Density of needles on shoot	2.486	0.0159	0.803	0.042
Number of buds on shoot	10.507	0.0000	0.860	0.038
Needle dry mass per unit of shoot	7.028	0.0001	0.744	0.005

Table III. Relationship of the average values of the morphological parameters of needles and the formation of buds on shoots with the content non-structural carbohydrates. Regression analysis and determination coefficient (R^2) value were calculated for the significance level $p < 0.01$.

Parameter	Soluble sugars		Starch	
	March	October	March	October
Length of needles	0.328	0.642	0.843	0.336
Dry mass of needles	0.316	0.568	0.832	0.249
Mass per unit needle length	0.755	0.573	0.754	0.224
Number of buds on shoots	0.458	0.869	0.792	0.596

However, the relationship between the role of soluble carbohydrates, the growth of needles and the number of buds formed on the shoot are not yet fully understood.

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