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Spatial Variability of Mobile Carbohydrates within *Pinus cembra* Trees at the Alpine Treeline

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With 4 figures

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Summary

LI M., HOCH G. & KÖRNER CH. 2001. Spatial variability of mobile carbohydrates within *Pinus cembra* trees at the alpine treeline. – Phyton (Horn, Austria) 41 (2): 203–213, with 4 figures. – English with German summary.

The size of mobile carbohydrate pools in treeline trees may hold the answer to the carbon limitation hypothesis of tree growth at high elevation. However, a major limitation for the use of such a chemical marker is its potentially large spatial and temporal variability at very small scales. Here we explore this variability in *Pinus cembra L.* at the alpine treeline in the Swiss Central Alps. To our surprise, neither slope exposure (south vs. north) nor position within the tree crown (compass directions and upper, middle and lower part of crown) had a significant influence on the concentration of total non-structural carbohydrates (TNC) in tissues. However, different-aged tissues (needles and branch segments) showed a significant difference in TNC concentration, maybe due to their different tissue dry matter density and activity. There is no indication that these patterns change across the season, despite significant seasonal variation in tissue specific TNC. Hence, any broad assessment of the carbon supply status of trees at the alpine treeline needs to carefully select tissue samples for equal age, but does not require a lot of spatial replication within individual trees.

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Zusammenfassung

LI M., HOCH G. & KÖRNER CH. 2001. Räumliche Variabilität mobiler Kohlenhydrate in *Pinus cembra* an der alpinen Baumgrenze. – Phyton (Horn, Austria) 41 (2): 203–213, 4 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Die Vorräte (Konzentrationen) an mobilen Kohlenhydraten in Bäumen der alpinen Baumgrenze könnten Hinweise auf eine mögliche Kohlenstoff-Limitierung geben. Allerdings würde eine große räumliche und zeitliche Variabilität in der Konzentration solcher Reserven ihre Nützlichkeit als Indikator für die Kohlenstoff-Versorgung in Frage stellen. Mit der vorliegenden Studie sollte diese Variabilität in *Pinus cembra L.* an der alpinen Baumgrenze der Schweizerischen Zentral-Alpen untersucht werden. Überraschender Weise hatten weder die Hang-Exposition (Süd- vs. Nordhang) noch die Position innerhalb einer Baumkrone (Himmelsrichtung und Höhe innerhalb der Krone) einen signifikanten Einfluss auf die Konzentration der gesamten nicht-strukturgebundenen Kohlenhydrate (TNC) in den Geweben. Unterschiedlich alte Nadeln und Zweigholz-Segmente unterschieden sich allerdings signifikant von einander. Dies ist möglicherweise auf die altersbedingt unterschiedliche Gewebedichte und/oder Zellaktivität zurück zu führen. Mit Ausnahme der synchronen saisonalen Veränderungen des TNC-Gehaltes mancher Gewebe, blieb das räumliche Verteilungsmuster innerhalb eines Baumes während der gesamten Vegetationsperiode unverändert. Für eine vergleichende Untersuchung der Kohlenstoffversorgung von Bäumen alpiner Baumgrenzen sollte daher besonders darauf geachtet werden, dass immer gleichaltriges Gewebe beprobt wird, während die Exposition und die Beprobungshöhe innerhalb der Baumkrone eher unbedeutend sind.

Introduction

Among other reserves, non-structural carbohydrates represent a tree's major capital for growth and development. The size of this mobile carbon pool in large reflects the balance between carbon uptake and demand of carbon for structural growth and respiration. Total non-structural carbohydrate (TNC) in tissue of trees growing near the high elevation limit of tree growth may hint at the tree carbon supply status (KÖRNER 1998, 1999), however, the carbohydrate status of treeline trees has not yet been assessed. To become conclusive this would require a broad screening across various alpine treeline ecotones, including many tree individuals, all major plant organs and a high temporal replication, with thousands of samples to be analyzed. This rises the issue of an appropriate sampling strategy.

It is well-known that there is a marked difference in the sum or mean of incident radiation between the S- and N-slope of a mountain (FRANZ 1979, BARRY 1992), and the bioclimate also differs substantially between the sunlit upper parts and the shaded lower parts of a dense conifer canopy (GEIGER 1961). These microenvironmental differences may add to the variability in TNC. Since solar radiation is the major driver of carbon assimilation in plants, and given that trees are modular organisms with their 'modules' (e.g. branch segments) operating quite autonomously, their exposure to different photon flux could be expected to affect the build up of very different mobile C-pools, just as it affects nitrogen and chlorophyll per unit leaf area and net photosynthesis (MCLAUGHLIN & MADGWICK 1968, LEWANDOWSKA & al. 1977, LEVERENZ & JARVIS 1980a, 1980b, GREF & TENOW 1987, ELLSWORTH & REICH 1993). In general, leaves grown at higher photon flux are thicker, have higher leaf mass per unit area, higher stomatal conductances, and higher photosynthetic capacity per unit leaf area (BOARDMAN 1977, BJÖRKMAN 1981, TROENG & LINDER 1982, SIMS & PEARCY 1994). On the other hand, shade leaves have lower structural carbon investments and lower respiration rates per unit leaf area than sun leaves (BJÖRKMAN 1981, GIVNISH 1988, HERRICK & THOMAS 1999). Adaptation to shaded conditions is a matter of carbon economics, in which gains are maximized through investments in the harvesting of photons while losses are minimized through reduced respiration (BJÖRKMAN 1981). To our knowledge only few studies investigated the effect of light on non-structural carbohydrates of trees (KÖRNER & ARNONE 1992, MELETIOU-CHRISTOU & al. 1994, HARLEY & al. 1996, WÜRTH & al. 1998, HERRICK & THOMAS 1999), and the full spatial variability within a single tree has not yet been examined, as far as a literature survey revealed. Here we explore such potential variabilities of TNC concentrations in isolated trees on a S- and a N-slope, at the treeline in the Swiss Central Alps.

We hypothesize (1) that S-exposed trees should have higher TNC concentrations than N-exposed trees, (2) that sun-exposed parts of the crown should contain more TNC than shade exposed ones, and (3) that TNC concentrations are higher in the top than at the base of a tree's crown. The rationale behind these three hypotheses is, that TNC concentrations are related to source activity (more light, more TNC) and the variability within a tree reflects the tissue exposure and position. Hence, our sampling was designed to capture TNC variation across these three spatial dimensions, in order to examine the probability of three scenarios: (a) should trees be carbon saturated, spatial variability should be low (pools are full anyways), (b) *moderate carbon shortage should maximize* variability (strong source dependence), (c) extreme C-shortage, again should reduce variability in TNC (supplies are too short anyways, no leeway for variability in reserves).

Material and Methods

Study sites

The study was conducted within the natural climatic treeline ecotone at Mont Noble (46°12′N″, 7°30′E), Canton Valais, Swiss Central Alps. Test trees (*Pinus cembra* L.) grew at about 2300 m a.s.l. on a ca. 35° S-slope (called the S-site) and 2340 m on a ca. 30° N-slope (called the N-site). The root zone temperature at 10 cm depth averages at about 7 °C during the growing period. Soils belong to the acid rendzina type on calcareous bedrock, with a ground cover dominated by *Arctostaphylos uva-ursi* (L.) SPRENGEL, *Calluna vulgaris* (L.) HULL., *Festuca* spp., *Poa* spp. at the S-site, and *Vac-*

cinium myrtillus L., *Empetrum hermaphroditum* (LANGE) HAGERUP, *Arctostaphylos alpina* (L.) SPRENGEL, *Loiseleuria procumbens* (L.) DESV., *Cladonia* spp., *Cetraria islandica* at the N-site.

Since these were natural, open sites with scattered trees, it was simple to find six solitary study trees of similar size (three on each slope). Each test tree was fully isolated and we used only healthy and undamaged specimen. Sampled trees were about 70–90 years old, 330–420 cm tall and had a stem diameter of 9–12 cm at breast-height. Crown length and width ranged from 270 to 400, and from 170 to 350 cm, respectively.

Sampling

The main stem and the crown of each tree were divided into three equal segments on upper, middle and lower section. All samples were collected in the middle of each of these segments. The first set of samples was taken on 26 May 2000, about 3 weeks before budbreak. The second and third sampling date were 26 July and 28 September 2000, i.e. during the peak of shoot growth and at the end of the growing season. Buds (terminal buds) and 1-year-old needles of leading branches were sampled on the E-, S-, W- and N-side of tree crowns. 2- to 5-year-old needles (current year needles in July and September only) and branch wood (xylem only, 5-, 10- and 15-year-old segments, in May and September only) of leading branches, and stem xylem (using a ∅ 5 mm corer; samples excluding phloem and bark), were collected on the S- and N-side of each tree. All samples were immediately stored in a cool box and killed in a microwave oven (30 seconds at 600 W) within 7 hours after collection. Thereafter, samples were dried to a constant weight at 75–80 °C and were ground to fine powder.

Analysis of TNC

Starch, sucrose, glucose and fructose, for simplicity termed total non-structural carbohydrate, TNC, were analyzed using an enzymatic digest technique with subsequent spectrophotometric glucose tests (KÖRNER & al. 1995). From detailed gas chromatographic analysis we know that mobile carbon fractions included <1 % of dry matter (d.m.) of raffinose and <3 % of pinitol, not accounted for in our data (in essence restricted to needles; G. HOCH, unpublished data). After boiling powdered samples for 20 minutes in distilled water, the soluble fraction was treated with invertase and isomerase and analyzed for glucose using a Hexosekinase reaction kit (Sigma Diagnostics St. Louis, Mo., USA). In a second step, the insoluble material (including starch) was incubated for 20 h at 40 °C with the dialyzed crude enzyme Clarase (a fungal α-amylase from *Aspergillus oryzae*; Miles Laboratory Inc., Elkhart, Ind., USA). Starch and sugar standards as well as a laboratory standard of plant powder were used as controls for all analyses. Carbohydrates other than starch, sucrose, fructose and glucose are not covered by this assay. All sugar, starch and TNC concentrations (%) were calculated on a dry matter basis.

Data analysis

A single factor ANOVA and Tukey's test were used to determine differences in TNC concentrations and its components (starch and soluble sugars) per organ per sampling date between S- and N-site ($n = 3$ trees per site), and between different orientations/positions within a single tree ($n = 6$). Since we are interested in the responses at discrete developmental stages, a time series analysis would not be appropriate. Except for Tab. 1 we present only TNC, which in essence reflects variation in starch, whereas the sugar concentration is relatively constant over time.

Results

Exposure effects

TNC concentrations did not differ between trees growing on the S- and N-slope at any time of the growing season, except for a 15% higher concentrations ($p < 0.05$) in needles sampled on the S-slope in May, which seems to reflect a slightly advanced development due to the higher temperature in the early growing season (Fig. 1). Surprisingly, there was also no difference in TNC concentration between different compass directions within the tree canopy at any time of the season in both upper, middle and lower sections (Fig. 2). Similarly, there were no differences in TNC concentration in buds and 1 year old needles between E-, S-, W- and N-side of the crown surface (data not shown).

Vertical position effects

As with exposure effects, there were no differences in TNC concentration in any tissue between the upper, middle and lower sections in any orientation of tree crowns and at each sampling date (Fig. 3).

Depth of crown and age

The only consistent and significant position effect was in branch wood and in needles of different age-classes. Tissue TNC concentrations

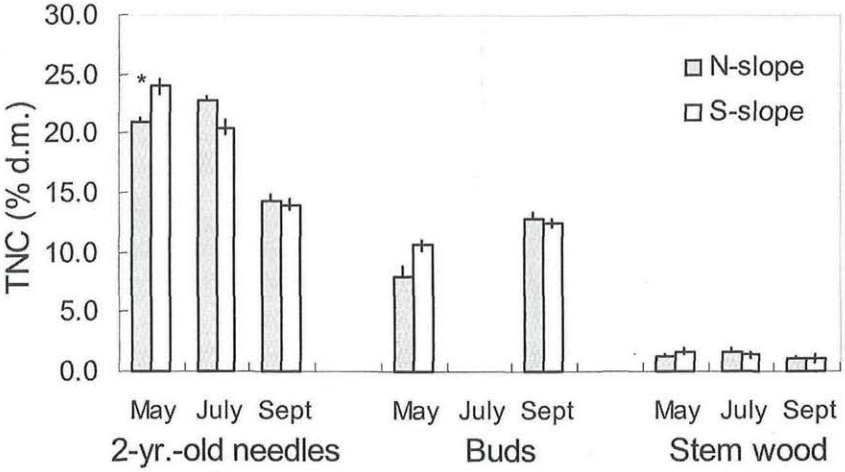

Fig. 1. Tissue TNC concentration in % of dry matter (d.m., mean values (± SE) of trees on a S- and N-slope. Mean values for all branch orientations and crown sections. For the sake of clearness, we omitted data for 1 and 3–5 years old needles, since these were very similar to those for the 2-year-old needles. There are buds available in July. * $p < 0.05$.

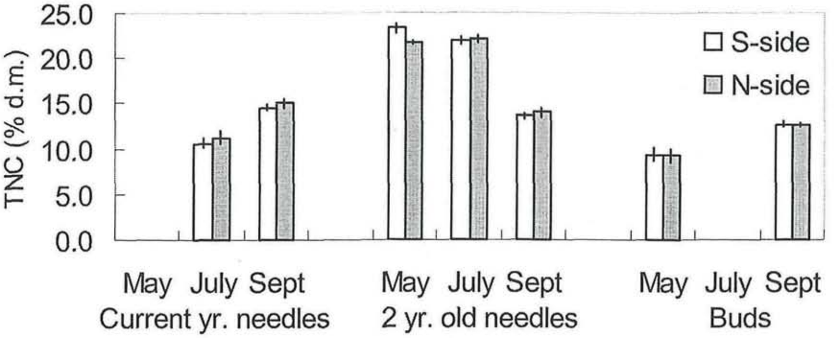

Fig. 2. The variation of TNC concentrations in % of dry matter (d.m.) in needles and buds with the compass direction of the branch sampled (mean values (± SE for all vertical crown positions as given in Fig. 3). There are no current-year needles available in May and no buds in July.

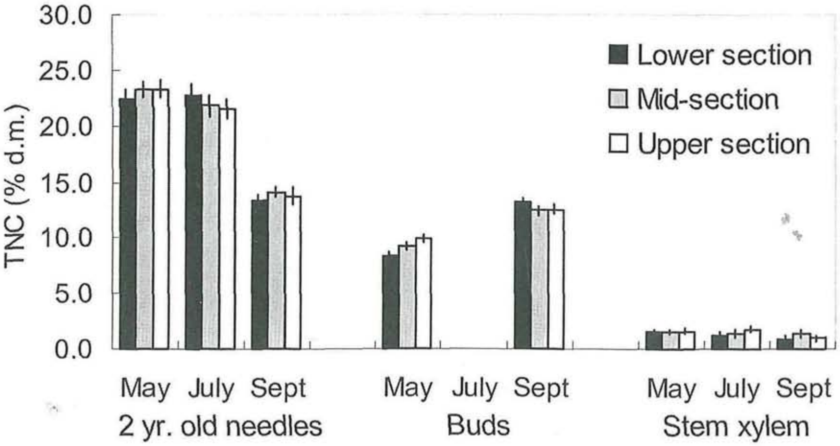

Fig. 3. The vertical variation of TNC concentrations in % of dry matter (d.m.) in trees. Means (± SE) for all branch directions (cf. Fig. 2). There are no buds in July.

decreased from the surface to the inner part of the green crown, irrespective of orientation and vertical position (Tab. 1, Fig. 4). Except for the end of the season, older needles had significantly lower TNC concentration than younger needles (Tab. 1). TNC in branch xylem also diminishes from younger to older parts (Fig. 4; data for September only, as an example). There was a remarkable seasonal change in the sugar versus starch contribution to needle TNC (Tab. 1), with a markedly small sugar component in May and July and nearly a 1:1 relationship in September. This trend is similar in all except the youngest needle age class. Hence, the change in

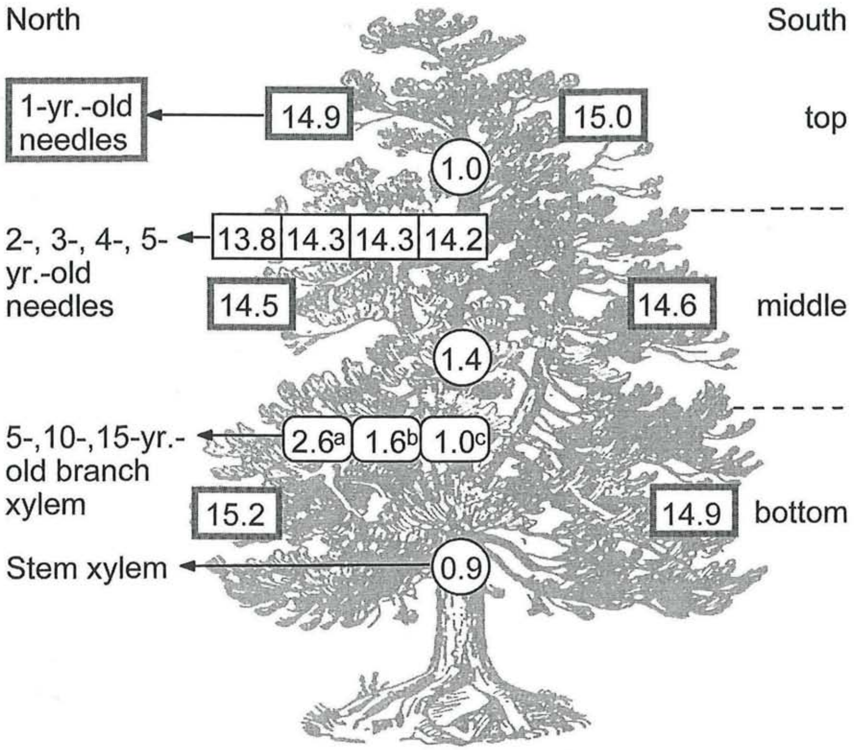

Fig. 4. The spatial variability of TNC concentrations in % of dry matter (d.m.) in whole tree crown at the end of September. Since TNC concentrations in needles and branch wood did not differ statistically with compass direction and crown position, we show the means across all directions and all sections for 2- to 5-year-old needles and 5-, 10-, 15-year-old branch segments only. Different letters indicate statistically significant ($p < 0.05$) differences within each tissue type.

TNC concentration is largely due to changes in starch concentration, with the sugar fraction varying little. The other tissues exhibited similar seasonal changes of starch and sugars (data not shown).

Discussion

Our study revealed hardly any spatial variation in the tissue specific TNC concentrations of treeline trees. Neither slope exposure nor sun exposure within the crown had a significant influence on tissue TNC of treeline trees, and this consistency within one type of tissue (of the same age) persisted throughout the season, hence all three hypothesis are falsified. Given that most studies on sun versus shade crown photosynthesis arrived a significantly higher net photosynthesis in sunlit parts (e.g. Harley & al. 1996, Herrick & Thomas 1999), this uniformity in TNC con-

Table 1.

Sugar, starch and TNC concentrations (% of dry matter, mean value ± SE) of needles of different age-classes*

	May			July			September		
	Sugars	Starch	TNC	Sugars	Starch	TNC	Sugars	Starch	TNC
Current-yr. needles	no needle	no needle	no needle	3.8 ± 0.3^{a}	7.2 ± 0.2^{a}	11.0 ± 0.5^{a}	9.1 ± 0.4^{a}	5.7 ± 0.3^{a}	14.8 ± 0.4
1-year-old needles	7.3 ± 0.2^{a}	16.4 ± 0.5^{ab}	23.7 ± 0.3^{a}	5.9 ± 0.3^{b}	17.5 ± 0.5^{b}	23.4 ± 0.4^{b}	8.7 ± 0.5^{a}	6.7 ± 0.3^{ab}	15.4 ± 0.3
2-year-old needles	6.7 ± 0.3^{ab}	16.3 ± 0.5^{ab}	23.0 ± 0.4^{a}	5.5 ± 0.2^{bd}	16.5 ± 0.3^{b}	22.0 ± 0.5^{c}	7.3 ± 0.4^{b}	6.5 ± 0.4^{ab}	13.8 ± 0.3
3-year-old needles	6.7 ± 0.4^{ab}	16.5 ± 0.3^{a}	23.2 ± 0.4^{a}	5.0 ± 0.2^{cd}	16.3 ± 0.4^{b}	21.3 ± 0.4^{c}	7.0 ± 0.2^{b}	7.6 ± 0.6^{b}	14.6 ± 0.7
4-year-old needles	5.8 ± 0.3^{b}	15.5 ± 0.4^{ab}	21.3 ± 0.5^{b}	4.7 ± 0.2^{c}	16.2 ± 0.4^{b}	20.9 ± 0.4^{c}	6.3 ± 0.3^{b}	8.3 ± 0.4^{b}	14.6 ± 0.6
5-year-old needles	6.0 ± 0.3^{b}	14.6 ± 0.3^{b}	20.6 ± 0.2^{b}	4.8 ± 0.2^{c}	16.5 ± 0.3^{b}	21.3 ± 0.4^{c}	6.8 ± 0.3^{b}	7.4 ± 0.3^{ab}	14.2 ± 0.3

*different letters indicate statistically significant ($p < 0.05$) difference within the group per date. Note, current year needles were not yet mature in July, hence data should not be compared with other age classes in absolute terms centration is surprising. However, what we observed at the cold end of tree distribution, seems to hold for tropical lowland forests as well. A study in 17 tropical forest species by WÜRTH & al. 1998 revealed no difference in TNC concentrations between sun and shade leaves in both the wet and dry season. In a study with four Mediterranean evergreen sclerophyll species, MELETIOU-CHRISTOU & al. 1994 found, that sun leaves of 2 species contained significantly more and those of other 2 species significantly less starch than shade leaves, but the soluble sugar content was also not affected by radiation in all four of these species.

In general, adult Pinus trees are only moderately shade-tolerant, and individuals of *Pinus cembra* in the alpine treeline ecotone are often found isolated from their neighbors. They show a stunted morphology with a wide green-crown, somewhat reducing the effective spatial variability in light dose on the crown surface. The frequent fog or cloudiness enhances diffuse, i. e. non-directional radiation in the alpine zone, further diminishing potential exposure differences.

In contrast, we noticed very large differences in TNC concentration between the various tissue types (needles, buds, branch and stem xylem), which relates to a tissue specific TNC and may reflect differences in the number of living cells within the specific tissue types. However, significant differences in TNC concentrations in the same tissue (needles or branch segments) from different age-classes may relate to their light capture and tissue activity, and may to a large extent also be explained by the volume density of the respective tissue. In other words, the dry matter reference itself varies and structural carbohydrates (cellulose, lignin) are 'diluting' TNC. It is known that needles get heavier (more scleromorphic) as they age (PERTERER & KÖRNER 1990). Except for newly formed (current year) needles in the early part of the season, younger needles and branch segments contained more TNC than older ones. Such age-effects were also observed by OLEKSYN & al. (2000; *Pinus sylvestris*) and by NIINEMETS (1997; *Picea abies*). OLEKSYN & al. reported that soluble carbohydrate concentrations increased during the life span of the needles from 3-6% of dry matter in current year needles to 6–14% in 1- and 2-year-old needles ($p < 0.01$). NIINEMETS found that TNC concentrations were 11.6, 13.8 and 16.3% (of d.m.) in current-, 1- and 2-year-old needles, respectively. At equal 'per cell' activity, soft, low density organs contain less cellulose and concentrations of any non-structural component including TNC and mineral nutrients will show a greater value on a dry matter basis, as compared to a volume basis (PERTERER & KÖRNER 1990). Hence, here we can not separate the light dependency of needle TNC from age and toughness. In the case of branch wood the smaller TNC concentration in older branch segments may indicate a loss of tissue specific activity towards the center of the crown.

Conclusion

The differences in bioclimates between a sun-exposed and shaded slope, and around a tree canopy do not appear to induce substantial differences in TNC concentration of tissues in the studied treeline trees. The low TNC variability at comparatively high concentrations may reflect our scenario (a), i.e. little carbon limitation in the treeline trees. According to the analysis presented here, a broad screening for potential C-limitation of treeline trees using TNC can rely on a relatively low spatial replication within a tree crown, but needs to adhere to a strict age specific tissue selection.

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