

Caloric value of Norway spruce organs and its seasonal dynamics

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The caloric value (i.e. caloric content of plants' unit mass) of different types of needles, shoot bark and shoot wood, stem bark and stem wood, seeds, vegetative buds and resin of Norway spruce *Picea abies* (L.) Karst. has been estimated with a microbomb calorimeter. As a result of detailed tree calorimetric analyses it has been revealed that the caloric value as a highly variable parameter explains the calorificity of tissue and can be used as a characteristic of the biochemical status of organs. Changes are due to a number of regularities related first of all to the intensity of physiological and growth processes and the effect of ecological factors. The calorificity of organs depends on their chemical composition, i.e. dominant structure (cellulose and lignin) and reserves (carbohydrates, protein, lipids). Seasonal dynamics of the caloric value is related to the proportion between low- and high-energy components in tissue.

Key words: caloric value, calorificity, Norway spruce

Introduction

The energy and caloric content of plants' unit mass has generated greater interest in connection with the studies of biological production in the framework of the International Biological Program (Runge, 1973). Data on the energy content, collected in the 1960s, are mainly based on a considerably larger amount of material owing to the use of calorimeters that needed no less than 2...3 grams of dry matter per analysis. By applying this method the following aspects of the caloric value changes have been determined: seasonal aspect (Madgwick, 1964, Hughes, 1971), age aspect (Ovington, 1961), ecological aspect (Steubing et al. 1979), taxonomical aspect (Runge, 1973), topographic aspect (Kononenko, 1976, Oszlany, 1982). Over the last years, only a small number of papers are published on this field (Singh and Kostecky, 1986, Fuwape, 1989; Nurmi, 1993) but lately the ecologists are interested in the measuring of caloric value.

The present article presents a summary of the estimates of the caloric content of Norway spruce *Picea abies* (L.) Karst. with a microbomb calorimeter. The reduction of the amount of the analysed material down to few milligrams has enabled to observe more exactly the variation in the caloric value of plant tissues and reach conclusions concerning the allocation of photosynthates, accumulation of reserves (carbohydrates, proteins and lipids) and synthesis of structurals with

high energy content (lignin). The caloric value of different types of needles, shoot bark and shoot wood, stem bark and stem wood, seeds, vegetative buds and resin has been determined considering mainly the age and topographic aspects as causes of variations in the caloric value, as well as ecological variability problems. Possible energy relations between different organs have also been taken into account.

Materials and methods

The materials were collected on the sample areas of the Vooremaa Forest Ecology Station. The description of the climate, relief, soil and vegetation of the areas was published by Frey (1977). Needle samples for establishing changes of caloric value within a shoot were collected from a dominant tree (age 80 years, height 38 m), separate samples from light and shadow shoots. Light and shadow needles were determined on the basis of needles' morphological parameters: the ratio of thickness to width ratio of light needles 1.0...1.3 and of shadow needles 1.8...2.8 (Frey and Ivask, 1983). To establish caloric value changes as depending on age and season, needles (one by one) from each examined shoot (age c - a current year needle, and c+1 - a last-year needle), as well as 4 bark and wood samples and vegetative buds of the shoots grown last year from different trees were analysed. Needle samples were taken during the following periods: from May 1978 to May

1979 with an interval of 2 weeks (N = 1300); from April 1984 to June 1985, with an average interval of 1...2 weeks (N = 492); from May to July 1981, with an interval of 2...3 days (N = 640).

Eight increment bore samples at stem height of 1.3 m from 4 trees (aged 45, 70, 72, 82 years) were taken in March and June 1979 for analysing the caloric content of stem wood. A total of 80 annual layers, early and late wood separately (at random, within the whole stem basal area) were analysed. Stem bark samples were taken from the increment bore samples of the 70-year-old Norway spruce, at heights of 0.3; 1.3; 9 and 23 m (totalling 10 samples).

Root samples have been excavated at random points of the sample area, washed well with water and separated into fractions: growth roots (N = 18), woody roots with a diameter <5 mm (N = 28), woody roots with a diameter 10...25 mm (N = 25). The samples were collected during the period from April to November 1983, on average with one-week interval. The caloric value of seeds was determined in 61 seeds chosen at random from the cones of one tree in March 1986. Resin samples (N = 8) were collected from a 45-year-old tree in June 1981.

All samples (except resin samples) were dried at +75°C during 24 hours. The caloric value was determined with microbomb calorimeter MBK-2 (Löhmus et al. 1984), into which whole samples (M=1...40 mg) were placed without being milled. The ash content was measured in calorimeter KL-5 (Poland), humidity content of samples was measured by weighing the samples dried at +105° C. The caloric value was calculated in ash-free absolute dry mass or absolute dry mass (seeds and resin).

All biochemical data used in the discussion are quoted from the literature.

Results

The seasonal dynamics of shoot caloric value was studied in shoot grown current year (c) and last-year (c+1), separately in needles, bark and wood (Fig. 1) as well as in the vegetative buds of a shoot of the current year (Fig. 2). Both the caloric value and variation decreased as follows: bark>needle> wood. The average caloric value of light needles grown last year exceeds that of shadow needles by 9,5% (20.79 and 18.81 kJ × g⁻¹).

Table 1 gives the average caloric value of needles of different ages (c ... c+4) during the vegetation period, separately for light and shadow needles. In all age groups the caloric value of light needles exceeds that

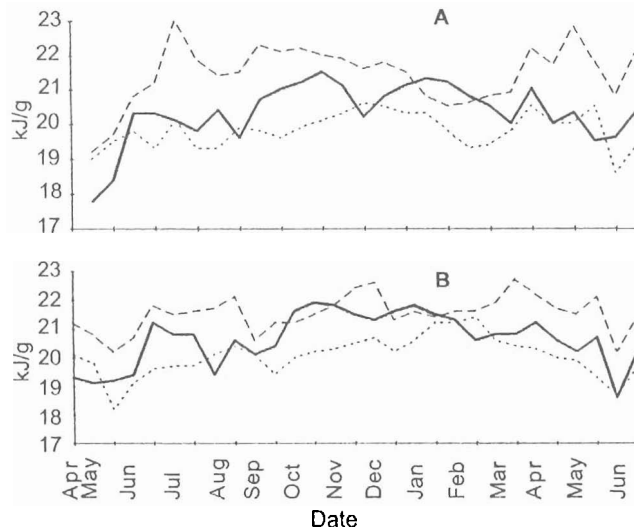


Figure 1. Seasonal dynamics of caloric value (kJ × g⁻¹) of current-year (A) and last-year (B) light shoots of an 80-year old Norway spruce (— needles, --- bark, ... wood). Data are the means of 364 shoots, sampled at 1...2-week intervals.

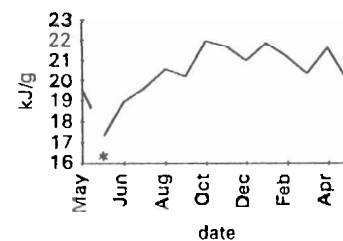
of shadow needles; the caloric value of light needles increases slightly with age, while no such trend was discovered in the case of shadow needles. The average caloric value of shoot wood in 1...5-year-old shoots (Table 1) was 20.32±0.22 kJ·g⁻¹, the average caloric value of shoot bark was 21.84±0.27 kJ·g⁻¹.

Table 1. The caloric value of Norway spruce shoot's during the vegetation period in 1981 (as average ± SE, kJ·g⁻¹) per absolute dry ashfree weight

Shoot age\N	Matter			
	Needles		Light shoots	
	Light 14	Shady 5	Bark 7	Wood 7
C+0	20,49±0,26	19,10±0,46	21,67±0,25	19,52±0,20
C+1	20,79±0,29	18,81±0,38	22,15±0,38	20,39±0,26
C+2	21,19±0,23	18,51±0,28	21,29±0,27	20,70±0,08
C+3	21,29±0,32	19,91±0,18	21,52±0,32	20,81±0,28
C+4	21,46±0,31	18,95±0,35	22,03±0,41	20,69±0,23
Average	21,04±0,18	19,06±0,23	21,84±0,27	20,32±0,22

The seasonal variation in the caloric value of vegetative buds is minimal in the first weeks of bud formation (17.2 kJ·g⁻¹), which reaches its maximum in late autumn (22.6 kJ·g⁻¹) (Fig. 2).

Figure 2. Seasonal dynamics of caloric value (kJ × g⁻¹) of vegetative buds (N=120). * - the opening time of buds; the caloric values are given for buds before the opening and for new forming buds after opening time.



The average caloric value of stem wood is $20.54 \pm 0.09 \text{ kJ} \cdot \text{g}^{-1}$. The caloric value is uniform within the annual layer. The analyses of the caloric value of early and late wood of 80 annual layers in four trees has shown that the energy content of anatomically different parts of an annual layer has no statistically significant difference. The variation in the caloric value of annual layers in the same tree comprises 10%. The average caloric value of the stem bark is $21.78 \pm 0.30 \text{ kJ} \cdot \text{g}^{-1}$.

In Table 2, the average root caloric values during the vegetation period are presented. The seasonal dynamics of root caloric value is shown in Figure 3. The caloric value of growth roots during the vegetation period correlates with the time of taking samples and with soil temperature at the depth of 30 cm (Ivask, 1987). The caloric value of all fractions of woody roots rises, reaches the maximum in the second half of summer and decreases by the end of the period. The caloric value of thin woody roots ($\bar{x} < 5 \text{ mm}$) is higher than that of thick roots but the difference is statistically not significant.

Table 2. The average caloric content of Norway spruce roots during the vegetation period \pm SE, $\text{kJ} \cdot \text{g}^{-1}$

Matter	N	Caloric content	
		Absolute dry weight	Absolute dry ashfree weight
Growth roots	18	$18,50 \pm 0,79$	
Woody roots " $< 5 \text{ mm}$,			
bark	28	$20,55 \pm 0,67$	$21,87 \pm 0,75$
wood	26	$22,17 \pm 0,54$	$22,97 \pm 0,61$
Woody roots " $> 10 \text{ mm}$,			
bark	25	$21,35 \pm 0,10$	$22,37 \pm 0,36$
wood	25	$22,28 \pm 0,40$	$22,81 \pm 0,44$

The data on the caloric value of Norway spruce seeds are given in Table 3. Within each group the variation in the weight and caloric value is negligible, the differences between groups being statistically significant ($P = 99.9\%$).

The average caloric value of resin samples of Norway spruce is $40.10 \pm 0.62 \text{ kJ} \cdot \text{g}^{-1}$.

Discussion

The assimilating organs of conifers are characterized by a comparatively high caloric content because of the high content of lignin and lipids (39% and 13,3...17,7%, respectively) (Runge, 1973). The variation in the caloric value of needles within a shoot is low and despite a great morphological variety, the caloric value does not depend on a position of a needle on the shoot. Consequently, the shoot can be considered an energetic

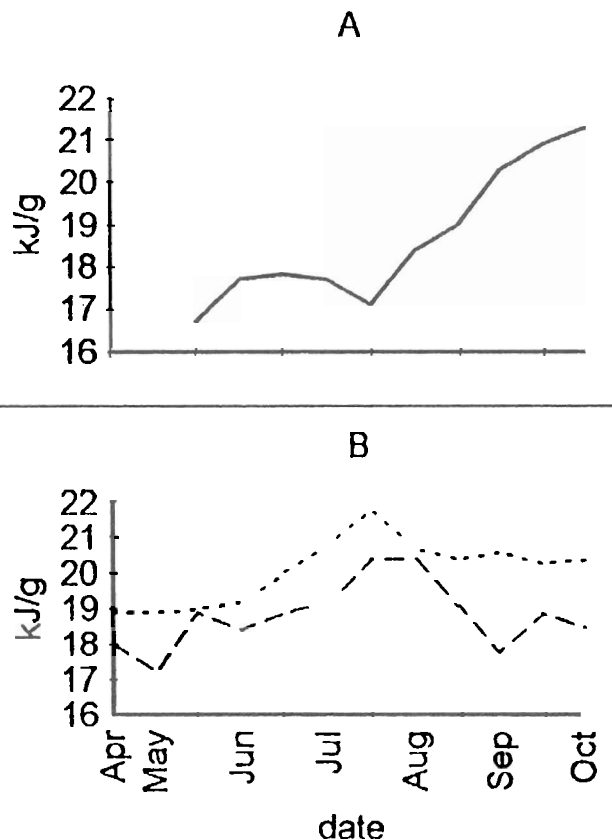


Figure 3. Seasonal dynamics of caloric value ($\text{kJ} \times \text{g}^{-1}$) of growth roots (A) ($N=18$) and woody roots (B) ($N=104$) (--- bark, - - - wood).

Table 3. The average dry weight ($M \pm \text{SE}$, mg) and caloric content ($Q \pm \text{SE}$, $\text{kJ} \cdot \text{g}^{-1}$) of Norway spruce seeds on absolute dry weight.

Matter	N	M	Q
Normally developed seeds	41	$6,57 \pm 0,13$	$28,24 \pm 0,21$
Abnormally developed seeds	5	$4,64 \pm 0,24$	$21,23 \pm 0,21$
Empty seeds	15	$2,41 \pm 0,09$	$18,96 \pm 0,29$

and metabolic whole: the number of needles that allow us to characterise a shoot is 5 ... 8 ($P = 99\%$) (Frey and Ivask 1983). The amount of reserves (low-energy carbohydrates, proteins, and high-energy lipids) in needles increases with age while metabolic activity decreases. In the course of time physiological changes take place in a needle (e.g. lignin biosynthesis, accumulation of minerals). On the other hand, metabolic process in needles is influenced by climatic factors in the crown and their seasonal changes. The caloric value of shadow needles does not increase with age. Evidently, the most important factor affecting a certain shoot in the shade

of a crown is the limiting light conditions. The essential difference of the caloric values of different needle types results from the difference in the chemical composition of their tissues (Runge 1973): light needles contain considerably more high-energy lignin (caloric value $Q = 26.36 \text{ kJ}\cdot\text{g}^{-1}$) and lipids ($Q = 36,8 \text{ kJ}\cdot\text{g}^{-1}$), shadow needles contain comparatively more cellulose ($Q = 17.0 \text{ kJ}\cdot\text{g}^{-1}$) and proteins ($Q = 23.01 \text{ kJ}\cdot\text{g}^{-1}$). Consequently we can make a conclusion that the morphological and metabolic difference of light and shadow needles is accompanied also by a difference in the caloricity.

The variation of the caloric value of wood and bark of the shoot decreases with the age of shoots but a clearly evident age trend has not been found. The maximum difference of shoot wood in the 1...5- year-old shoots during the vegetation period constitutes 10.7%, whilst the maximum difference of shoot bark 14.6%.

The caloric value of the vegetative bud is formed first of all by the caloric value of bud scales that account for a very large part of the whole bud mass. The caloric value of bud can be compared to the caloric value of needle but it has an essentially lower variability (15% and 28% accordingly). Although bud caloric value does not depend on bud weight, the apical bud of a shoot has always a greater weight and caloric value than the other buds of the same shoot. The seasonal variation in the caloric value of buds is rather significant; it rises during the vegetation period and reaches its maximum in late autumn. The high caloric value persists through the winter rest period, decreasing slightly before the opening of buds in spring (Fig. 2).

Stem wood contains 41%...51.5% of cellulose and 27%...28% of lignin, which constitutes 72% of the wood caloric content (Runge 1973). Considering wood extractives, the caloric value is affected essentially only by resin whose caloric value ($Q = 40.2 \text{ kJ}\cdot\text{g}^{-1}$) is significantly higher than that of all other wood components. Early wood layers and late wood layers differ considerably only by their anatomical parameters and to a smaller extent by their chemical composition. In accordance with the data obtained by Fergus et al. (1969) early wood contains 1.5%...2% more lignin than late wood. Possible differences in the caloric value resulting from the chemical composition remain still evidently within the measurement error. From the calorimetric analyses of early and late layers we can conclude that anatomical differences are not related to energy differences.

The assimilating organs of trees and stemwood react differently to various ecological conditions in different years. The chemical composition of wood as a

supporting and conductive tissue is comparatively stable (Uprichard and Lloyd 1980) despite marked differences in the width of annual layers. The maximum difference in the caloric value of annual wood layers is essentially smaller than the differences in the average caloric value of needles of different years. A weak correlation occurs between the width and the caloric value of annual layers: the wider the annual layer, the higher is the caloric content ($r = 0.44 \dots 0.74$; $P = 95\% \dots 99.9\%$) (Ivask 1984).

The caloric value of growth roots is essentially lower than that of woody roots and depends mainly on the time of sample collecting, which is obviously related to the amount of synthesized high-energy components (lignin, resin) in cell walls during the vegetation period (Kramer and Kozlowski 1979). The caloric value of woody roots is high, which can be explained by the peculiarities of the chemical composition: according to the literature data found in the root wood contains more resin than stem and branch wood (Runge 1973). Root bark has a lower caloric value than root wood, while this difference also results from differences in the chemical composition.

The caloric value of seeds is determined by reserves. In accordance with the data found in the literature (Grodzinski and Sawicka-Kapusta 1970) lipids form 35.1% of Norway spruce seeds dry mass; the percentage of proteins in conifer seeds is 30% ...40% (Kramer and Kozlowski 1979). The high caloric value is characteristic of normally developed seeds, while the caloric value of empty seeds equals practically to the energy content of seed shell. The mass of a seed and its caloric value are in a strong positive correlation ($r=0.91$; $P = 99.9\%$), hence an increase in the mass of a seed takes place at the expense of lipids.

The seasonal dynamics of caloric value of organs is based on the corresponding metabolic changes. The caloric value of above-ground organs is lowest during the elongation of the shoot, i.e. in May-June. A considerable rise in the caloric value follows achieving the maximum at the end of summer. Further, several periods characterised by a relatively high caloric value are observed from the end of November to December and in March-April. The seasonal dynamics of the caloric value is related to the proportion between low- (carbohydrates) and high- (protein, lipids and resin, lignin) energy components in tissues, their accumulation and location. Caloric value changes can be explained, on the one hand, by the inflow of assimilates and the dynamics of carbohydrates (reserve sugar); on the other hand, one

has to consider the changes in the lipid content which occur in vegetative organs. Maximum values of the calorificity of crown organs at the end of summer, at the beginning of winter and early spring indicate the synthesis of compounds with storage and protective functions due to adaptation to winter conditions (Glerum and Balatincez 1980) or preparation for growth processes (Glerum 1980). The caloric value of below-ground parts and its dynamics during the vegetation period has one maximum in the second half of summer. The maximum caloric value of below-ground organs falls on a period when the inflow of photosynthates into roots is maximum and growth processes are practically finished.

As a result of detailed tree calorimetric analyses it has been revealed that:

1. The caloric value is a highly variable parameter; changes are due to a number of regularities related first of all to the intensity of physiological and growth processes and the effect of ecological factors (different ecological conditions in the crown, seasonal changes in climatic conditions).

2. The seasonal dynamics of the caloric value is related to the proportion between low- (carbohydrates) and high- (protein, lipids and resin, lignin) energy components in tissues, their accumulation and location. Maximum values of the calorificity of crown organs at the end of summer, at the beginning of winter and early spring indicate the synthesis of compounds with storage and protective functions due to adaptation to winter conditions or preparation for growth processes. The maximum caloric value of below-ground organs falls on a period when the inflow of photosynthates into roots is maximum and growth processes are practically finished.

3. Considering the wide range of calorificity, it is evident that a random estimate of the caloric value yields very little information. Making reliable conclusions on the energetic status of organs' systems is feasible only basing on knowledge of the organs' stage of development and climatic conditions at that time.

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КАЛОРИЙНОСТЬ ОРГАНОВ ЕЛИ ЕВРОПЕЙСКОЙ И ЕЕ СЕЗОННАЯ ДИНАМИКА

М. Иваск

Резюме

Изучена калорийность световых и теневых хвонпок, коры и древесины побегов, коры и древесины ствола, семян, вегетативных почек, корней и смолы ели европейской при помощи микробомбового калориметра. Установлена переменность калорийности, которая выражает свойства анализируемой ткани и связана с ее химическим составом, в основном с содержанием структурных и резервных веществ. На формирование калорийности влияют интенсивности физиологических и ростовых процессов, а также экологические факторы. Сезонная динамика калорийности органа зависит от соотношения доли низко- и высококалорийных веществ и тканей.

Ключевые слова: калорийность, энергосодержание, ель европейская.