

Daily and seasonal variation of stem radius in oak

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Abstract – Seasonal and diurnal variation of stem radius and sap flow in large pedunculate oaks (*Quercus robur* L.) as dependent on environmental factors was studied in the floodplain forest in southern Moravia from April to October several years after cessation of regular natural floods. Two main processes as driving variables of stem radius were considered separately: growth of plant tissues and their hydration (i.e. shrinking and swelling). Different types of diurnal dynamics of stem radius occurred including growth with and without shrinkage, growth at night and shrinkage during daytime and vice versa. A simple physiological model was applied to describe the dynamics of stem radius. Data on sap flow, global radiation and air temperature were used as model input. Net growth was simulated by means of photosynthesis and respiration, calculated for real meteorological conditions and tissue hydration was derived from the difference between potential and real transpiration (sap flow). Simulation showed good approximation of seasonal dynamics of stem radius by the model under mild weather conditions and mostly non-limiting soil moisture. © 1999 Éditions scientifiques et médicales Elsevier SAS.

Quercus robur / radial growth / sap flow / simulation modelling / floodplain forest

Résumé – **Variation journalière et saisonnière du rayon du tronc du chêne pédonculé.** La variation journalière et saisonnière du rayon du tronc du chêne pédonculé (*Quercus robur* L.) a été étudiée en dépendance des facteurs environnementaux dans une forêt marécageuse en Moravie du sud d'avril à octobre, plusieurs années après le fin des inondations naturelles régulières. Les deux principaux processus généraux qui contrôlent le rayon du tronc ont été étudiés séparément : la croissance des tissus de l'arbre et leur hydratation (contraction et gonflement). Différents types de dynamique journalière de variation de dimension du rayon du tronc ont été obtenus, y compris la croissance avec et sans contraction, la croissance nocturne et la contraction diurne et vice versa. Un modèle physiologique simple a été utilisé pour décrire la dynamique du rayon du tronc. Des données concernant le flux transpiratoire, le rayonnement global et la température de l'air ont été utilisées comme données d'entrée. La croissance a été simulée à partir de la photosynthèse et de la respiration calculées pour les conditions météorologiques réelles et l'hydratation des tissus a été déduite de la différence entre la transpiration potentielle et réelle (flux transpiratoire). La simulation à partir du modèle a démontré une bonne approximation de la dynamique saisonnière de variation dimensionnelle du tronc en conditions climatiques modérées et humidité non limitante. © 1999 Éditions scientifiques et médicales Elsevier SAS.

chêne pédonculé / croissance radiale / flux transpiratoire / modélisation / forêt alluviale

1. Introduction

Diurnal and seasonal variation in stem radii in trees in connection with other processes, environmental conditions and tree parameters represents an important

characteristic of tree physiology and was studied by different authors ([1, 15, 17, 25, 30, 35, 38] among others).

Variation of stem radius (dr) involves two components: variation caused by growth of stem tissues and

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variation caused by changes in stem tissue water content. Growth means a division and enlargement of cells, in which the seasonal course can usually be distinguished. In contrast, variation caused by changes in tissue water content of stem tissues has a pronounced diurnal pattern. Usually shrinkage occurs during the daytime when high transpiration rate exceeds the water supply capacity of the root systems and causes dehydration of the tissues. Swelling occurs mostly over night as a result of rehydration of stem tissues under low transpiration rates [9, 12].

This study focused on modelling of both the diurnal and seasonal variation in stem radius in large oaks in the floodplain forest growing in the plateau of the Dyje river in southern Moravia. In this site, different aspects of tree physiology [6, 7], biometry [42] and many fields of ecology were investigated in the framework of extensive ecosystem studies [28, 29]. A simple simulation model based on meteorological data and sap flow measurements as input parameters based on previous experience on modelling photosynthesis and trees [24, 37] was applied to explain the stem growth. Data characterize the period shortly after cessation of regular floods in the region when the diurnal course of growth was measured for the first time together with other processes [7, 33] in the course of long-term studies of forest ecosystems. Besides modelling, the practical aim of the study was to characterize the behaviour of trees under favourable water supply, i.e. in conditions typical for original, regularly flooded floodplain forests. General features of tree behaviour were compared elsewhere with the situation in these forests over the years after cessation of floods in the region and over 20 years later, when flooding was again renewed artificially [2, 34].

2. Materials and methods

2.1. Field study

2.1.1. Site characteristics

The study site is located in the floodplain forest on the alluvium of the Dyje River on an elevation of 161–162 m. The site is in the forest district Horní les, no. 523 (latitude 48°48'22", longitude 16°46'32"). Phytocoenologically it is an Ulmeto-Fraxinetum carpineum according to the Zlatník [44] classification or a moist ash floodplain forest according to the classification of the National Forest Management Institute [32]. The fully developed mixed stand with prevailing oak (*Quercus robur* L.) and admixture of ash (*Fraxinus excelsior* L. and *F. angustifolia* Vahl.) and lime (*Tilia cordata* Mill.) was planted around 1880, and has at present a mean upper height of 27 m.

The stocking density was 90 %. The soil profile was created by a heavy alluvial sediment layer and is classified as semigley [27] or Fluvi-eutic gleysols (FAO 1970). Climatically, the region is relatively warm (mean annual temperature 9.0 °C) and dry (mean precipitation 500 mm·year⁻¹) with moderate winters.

2.1.2. Experimental material

Seasonal and diurnal variation in stem radius (dr), sap flow rate (Q_{wt}) and environmental parameters were measured in the large oak tree (*Quercus robur* L.). The set of 17 trees (in some of them the sap flow rate was also under study) was measured with simple band dendrometers for several years. However, on the single tree the continually recording radial dendrometer was applied – only these data were considered in the present study. The height of the experimental tree was 33 m and diameter at breast height (with bark) (DBH) was 61.8 cm (the initial stem xylem radius, equal to 292 mm measured in early spring was taken as zero for dr measurements). Areas characterizing tree crown were almost equal: projected area of tree crown ($S_p = 86.9$ m²), part of stand area ($S_{stand} = 10\,000$ m²) occupied by the tree ($S_{tree} = 87.4$ m²) which was proportional to the ratio of tree basal area ($S_{bas,tree}$) and stand basal area ($S_{bas,stand}$), i.e. very close to S_p , which is natural for the closed stand canopy under consideration.

$$S_{tree} = S_{stand} \cdot \frac{S_{bas,tree}}{S_{bas,stand}} \quad (1)$$

S_{tree} was applied to calculate the relative transpiration (T_{rel}) from daily totals of sap flow rate (Q_{wt}) and potential evapotranspiration (E_{pot})

$$T_{rel} = \frac{Q_{wt}}{E_{pot} \cdot S_{tree}} \quad (2)$$

The experimental data applied in the present study cover the entire growing season, when potential evapotranspiration was still equal to the actual one for most days of the growing season under moderate climatic conditions [43]. Already measured data (from April to October 1979) were applied in the model in order to characterize the situation a short time after cessation of regular seasonal floods in the region. Two sets of data were used in the study. 1) Daily totals of sap flow rate (Q_{wt}), global radiation balance (I_0) and stem radius (dr) recorded every 12 h (at 06:00 and 18:00 hours) were available for most of the growing season. Daily means of air temperature and air humidity and daily precipitation were obtained from the nearest meteorological station

(Mendeleum) about 2 km aerial distance from the experimental site. 2) Diurnal courses of Q_{wt} and dr , recorded every hour were available for 33 days; air temperature (T_a), soil temperature (T_{soil}) and net radiation (I_n) were also recorded hourly for 23 of these days (after 6 July). The effective temperatures (degree-days) were calculated from daily means of $T_a > 5$ °C. In addition, already published data of soil water content in layers over depths of 0–12, 12–30 and 30–50 (100) cm [33] measured weekly over the whole year in three measuring points were considered when evaluating physiological data.

The sap flow rate was measured with the tree trunk heat balance technique (THB) applying internal (direct electric) heating of tissues and sensing of temperature [6, 16]. Two measuring points were installed on the opposite sides (north–south) at breast height on the sample tree, each representing a stem section 8 cm wide. The four channel sap flow meter with constant power made at the institute (Kucera, 1976) was applied for the field work. The sap flow in the whole tree, Q_{wt} was estimated by multiplying the average of two measuring points by stem xylem circumference (the very high correlation between two measuring points, $r^2 = 0.95$, made this calculation easy).

Changes in stem radius were measured by the electronic dendrometer based on the induction sensor made in our institute (Holec, 1978) working with precision of 0.005 mm. The device was fastened onto the smooth bark surface at a height of 1.3 m using three small screws and insulated by the polyurethane foam and reflective shielding; its needle contacted the plain reference head of the long screw, freely penetrating through the 25 mm deep sapwood and fixed in the heartwood 5–10 cm beneath the cambium.

The two possible impacts of temperature on the result of radius measurements were considered: that of the dendrometer and that of the stem. The thermal extension coefficient of the metal from which dendrometer was made, was about $1.0 \cdot 10^{-5} \cdot K^{-1}$. Temperature variation of the dendrometer was small (maximum diurnal range 2–3 °C) since the device was attached at the stem surface, for which variation was much lower compared to the variation of air temperature. That is why the impact of temperature (up to 0.003 mm) was lower than the error of measurement. The radial expansion of xylem water was estimated for 2 cm xylem width with 50 % water content (as measured on the cores) and 1 h time shift between the air and xylem temperature [11]. The correction terms were subtracted from the observed stem radius values in order to obtain the net shrinkage/swelling dynamics.

After measurements, the cores were taken from the wood from four cardinal points around the stem (one of

them from below the dendrometer needle), the width of the annual ring was estimated and mean width (dr_{mean}) was calculated. The continually recorded data from the dendrometer which represented one point (dr_{point}) were corrected accordingly in order to obtain data representing the entire tree trunk $dr = dr_{measured} \cdot dr_{mean} / dr_{point}$.

Only the dr data were used in further calculations. We distinguished between the changes of dr caused by growth and those caused by hydration processes in the following way. The net growth (dr_+) was estimated as the maximum change in stem radius obtained before the given day. The stem shrinkage dr_s was taken as the difference between maximal obtained and the actual radius (figure 1). For the days with continual records of dr data, dr_+ and dr_s were taken in 1 h intervals.

Air temperature (T_a) was measured by the ventilated platinum thermometer, global radiation balance (I_0) by the pyranometer Schenk (Austria). All sensors were located about 5 m above the canopy. All the data were recorded by six channel point tape recorders (Metra Blansko, Czechoslovakia) and were averaged with a time step of 1 h. From the above primary meteorological data the daily totals of standard crop potential transpiration (E_{pot}) were calculated according to Penman [26]. In order to characterize the environmental conditions from such data (under mostly stable soil water conditions), the soil water balance (W_b) was evaluated over the growing season as follows:

$$W_b(t) = \int_{t_0}^{t_1} \left(W_p(\tau) - E_{pot}(\tau) - \frac{d}{d\tau} \left[\int_0^{120} W_s(h, \tau) / 100 \cdot dh \right] \right) d\tau \quad (3)$$

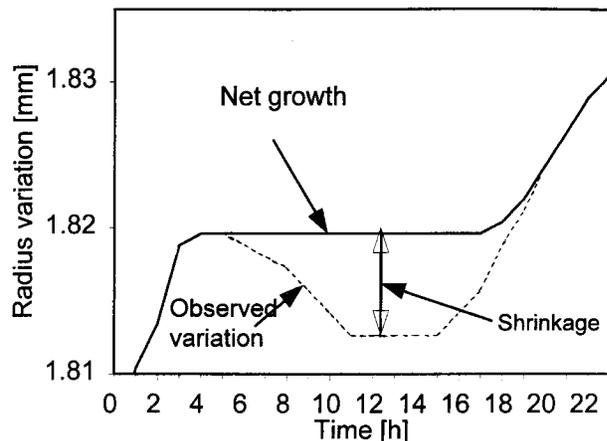


Figure 1. Illustration of the method applied for the separation of stem radius variation of pedunculate oak in the floodplain forest into net growth and shrinkage.

where W_p is the precipitation and $W_s(h)$ is the soil water content at the depth h from [33] expressed as percentage of volume. The daily and actual tree transpiration deficit (WD_t) expressed as the difference between corresponding values of sap flow and transpiration calculated according to the Penman-Monteith equation [26] was also estimated. The canopy conductance used for the Penman-Monteith equation was taken as the stomatal conductance multiplied by LAI (taking into consideration the development of leaf area in spring). The stomatal conductance was approximated by parabolic regression on radiation according to the data of Reiter and Kazda [36].

The stepwise variable selection was applied to the dependence of seasonal variation of stem radial growth rate (dr/dt) and then the analysis of variance was applied to estimate the impact of each selected factor on dr/dt .

2.2. Simulation modelling

A simple physiological, process-based model was proposed to explain relationships between variation of the stem radius and other measured physiological and environmental variables. Two versions of the model were applied: one for seasonal growth and another for diurnal variation of stem radius with a time step of 1 day and 1 h, respectively. The diurnal version of the model was applied only for the mid-summer period because diurnal meteorological data were not available before 6 July.

2.2.1. Main hypotheses, applied for modelling

The following main hypotheses were applied for the construction of the model.

1) The stem growth begins before the budburst in spring using the assimilates from the storage originated in the course of previous year. The use of new assimilates is simulated as increasing proportionally to the increment of leaf area and simultaneously with leaf development; use of old assimilates from the storage was taken as decreasing at the same time.

2) Leaf development begins at the time when the annual total of effective temperature (degree-days) reached a certain value and was taken as dependent initially on the use of old assimilates from the storage, and later on the use of the new assimilates originated during current photosynthesis.

3) Distribution of new assimilates between different organs was taken as determined this way. The leaf and fruit development was taken as strictly determined by corresponding values of degree-days (fixed dependencies on annual total of effective temperatures), so that the cur-

rent assimilates are used first for the leaf and fruit growth and then the rest is used for skeleton growth (including stem, branches and roots).

4) The rate of usage of the old assimilates for radial growth is dependent on their amount available in storage and on cambium temperature. The cambium temperature was derived from air temperature according to Herrington [11]. The calculated time shift used for the diurnal version of the model was 1 h. For the seasonal version the time shift between the cambium and air temperatures was neglected.

5) Decrease in the radial growth rate down to complete cessation is driven by the internal control, approximated by the empirical dependence of the fraction of assimilates used for the skeleton growth on degree-days. This hypothesis is based on the known fact that the cessation of cambial activity is driven by the decreasing export of auxines from the growing shoots after the cessation of their growth (see, for example, [19] or [22]).

6) Root and branch growth was supposed to be proportional to the stem growth (in terms of usage of assimilates); fruit growth was approximated by the empirical function.

7) Stem respiration was taken as dependent on temperature of tissues [11] and rate of allocation of assimilates from leaves along the stem down to the roots [40].

2.2.2. Description of the model

The equation describing the seasonal and diurnal radial growth of stem was the following:

$$\frac{dr_+}{dt} = \frac{\left[(A_s + P - P_1 - P_f) \cdot a_{ws} \cdot a_s - R_s \right] \cdot k_{cv}}{S_s} \quad (4)$$

where A_s is the rate of use of the old assimilates from the previous year for skeleton growth, P is net photosynthesis of the entire crown, P_1 and P_f are the rates of use of assimilates for the leaf and fruit development, respectively, a_{ws} is the part of stem dry mass in the total skeleton dry mass (including roots and branches), a_s is the part of assimilates used for skeleton growth, R_s is the stem respiration, k_{cv} is the coefficient converting the mass of the assimilated CO_2 into growth of stem radius and S_s is the stem surface.

When the leaf area is fully developed (over the period from July to early October) $A_s = P_1 = P_f = 0$ and equation (4) can be simplified:

$$\frac{dr_+}{dt} = \frac{(P \cdot a_{ws} \cdot a_s - R_s) \cdot k_{cv}}{S_s} \quad (5)$$

The relation of net photosynthesis of the entire crown (P) was obtained by approximating the data, presented for the same species in Malkina [20] and Tselniker [40] using the equation:

$$P(h,t) = P_{\max}(D_y) \cdot \left[1 - \exp \left\{ -b \cdot I_n(h,t) - c \right\} \right] \cdot L(h) \quad (6)$$

$$\text{where } P_{\max}(D_y) = a_1 \cdot \exp \left[-b_1 \cdot (D_y - c_1)^2 \right] \quad (7.1)$$

when $D_y < D_1$

$$\text{or } a_2 - D_y \cdot b_2, \text{ when } D_y \geq D_1 \quad (7.2)$$

where D_1 is a day of year (corresponding to the value of 530 degree-days) and

$$L(h) = \text{LAI}(h) S_p L_{\text{rel}}(D_y) \quad (8)$$

is the leaf area of the entire tree crown. I_n was calculated from the irradiation measured above the canopy (I_0) according to the light penetration pattern described in the same stand by Vasicek [41] and Cermak [3]. LAI height distribution, $\text{LAI}(h)$, was taken from the same publications. S_p , the crown projected area, was estimated according to equation (1). The function L_{rel} was taken as 1 during the summer period after the leaf development was completed. L_{rel} was approximated by the sigmoidal relation growing from 0 to 1 in the spring using the data for oak from Tselniker et al. [40] and Moisl [23], and by the reversed sigmoidal relation (declining from 1 to 0) in the fall. Terms b , c , a_1 , b_1 , c_1 , a_2 , b_2 and D_1 are empirical constants (0.008, 7.3, 0.6021, 0.0196, 137.58, 0.62, 0.001 and 142, respectively, for I_n in $\text{W} \cdot \text{m}^{-2}$ and P in $\text{mg CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$).

The equations (5), (6), (7.1) and (7.2) were applied for each hour for the diurnal version of the model. In the seasonal version the photosynthesis daily totals were obtained by the integration of function (equation (6)) in time and according to the tree height, as described above.

The total rate of use of assimilates for the leaf growth, P_1 was calculated by the equation:

$$P_1 + A_1 = k_1 \cdot \frac{dL}{dt}, \quad (9)$$

where k_1 is the amount of carbon needed for the growth of 1 m^2 of leaf area. It was supposed that the new assimilates are used first for the leaf growth, so if $P > k_1 dL/dt$ then $A_1 = 0$ otherwise $P_1 = P$.

Part of the assimilates, used for the skeleton growth, a_s was approximated by the declining sigmoidal relation with parameters, estimated by our simulation experiments. The part of the stem skeleton dry mass, a_{ws} was taken as a constant, calculated by the regression equations from the data published by Vyskot [42]. The rate of use of old assimilates for skeleton growth, A_s was described by the equation:

$$A_s = \frac{dA}{dt} - A_1, \quad (10)$$

where total rate of use of assimilates was

$$\frac{dA}{dt} = -k_A \cdot A \cdot \exp \left[b_R \cdot (T_a - 10) \right] \quad (11)$$

where A is the storage of old assimilates, $k_A = 0.04 \text{ day}^{-1}$ is the empirical coefficient; the parameter characterizing the temperature dependence of respiration $b_R = \ln(2.2) / 10 = 0.078846$ [40] and the rate of use of old assimilates for leaf growth, A_1 is calculated using equation (9) as described above. The rate of use of assimilates for fruit growth, P_f was approximated by the empirical relation (polynom of 2nd order) from D_y . The evaluation of the storage of old assimilates $A = 0.23 [\text{kg} \cdot \text{m}^{-2}] \cdot S_s$ was obtained according to our data of mean earlywood width in oak at the same stand (T. Krejzar, 1996, pers. comm.) supposing that all earlywood was produced using the above-mentioned storage.

In the diurnal version of the model the stem respiration (R_s , in $\text{g of CO}_2 \cdot \text{m}^{-2} \cdot \text{h}^{-1}$) was calculated as linearly dependent on temperature, but by applying different relations for different months [39]. For the seasonal version of the model these equations were not precise enough to approximate fast changes in growth rate at the beginning of the growing season. That is why we used another equation, taking into account the rate of stem growth (R_s in $\text{gCO}_2 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$):

$$R_s = R_0 + a_R \cdot (A_s + P - P_1) \cdot \exp \left[b_R \cdot (T_a - 10) \right] \quad (12)$$

where b_R is the same as in equation (11) and $R_0 = 12 \text{ g (CO}_2 \cdot \text{m}^{-2} \cdot \text{day}^{-1})$, respiration ratio, $a_R = 0.00229$ (dimensionless), i.e. constants, approximated in simulation experiments using previous data [39, 40] and our experimental data on stem growth.

Stem shrinkage was simulated only for the diurnal version of the model from the difference between the courses of transpiration by the Penman-Monteith equation, E_T , considered as the actual transpiration rate, and the measured sap flow Q_{wt} , considered as the rate of water supply by roots (both in $\text{mm} \cdot \text{h}^{-1}$).

$$dr_s = k \cdot \int (E_T - Q_{wt}) dt = -k \cdot \int WD_t(t) dt \quad (13)$$

where $k = 0.00022$ [$\text{mm}_{\text{dr}}/\text{mm}_{\text{H}_2\text{O}}$] is the empirical coefficient. Thus, the stem radius at the moment t will be:

$$r = \int_{t_0}^{t_c} (dr_+ / dt) dt - dr_s \quad (14)$$

Sensitivity analysis of the model for main parameters, approximated in simulation experiments, was performed by the estimation of the change in final growth of radius at the end of growing season under the 10 % variation of a parameter at the direction of increasing or decreasing (for parameters having the mean of the day of the year the variation was ± 5 days).

3. Results and discussion

3.1. Seasonal courses of tree processes and meteorological parameters

The seasonal course of soil water balance W_b during the whole growing period characterizes typical arid climate of the region (figure 2a, b, about 100 km east from this site is situated the single Central European sand desert). W_b decreased dramatically in May; it decreased more slowly from mid June to September and no changes occurred in October. The soil water content was rather high from May to mid August (from 55 to 40 % vol., from 50 to 40 % vol. and from 45 to 35 % vol. in upper, medium and lower soil horizons, respectively, which corresponds to values from 0 to 0.106 MPa, from 0 to 0.050 MPa and from 0.008 to 0.173 MPa of water potential) and supplied sufficient water for evapotranspiration. However, a certain lack of soil water became significant in the fall [33]. During the whole growing season 164 mm of potential evapotranspiration were compensated by soil moisture depletion from the upper 120 cm of soil. A certain water deficit remained at the end of the season (figure 2b) can be explained by capillary ascent of water from the ground water level and by the fact that the standard crop potential transpiration (E_{pot}) applied for the calculation of balance partially overestimated the actual stand transpiration.

The seasonal course of radial stem growth, dr , became visible in late spring (April), i.e. before the budburst (which started on approximately 25 April). The sap flow started with about a 10 day long delay (approximately from 4 May, significant values from 10 May). Onsets of both the above-mentioned processes correspond to the value of degree-days of $T_{\text{ef}} = 186$ and 321 °C, respective-

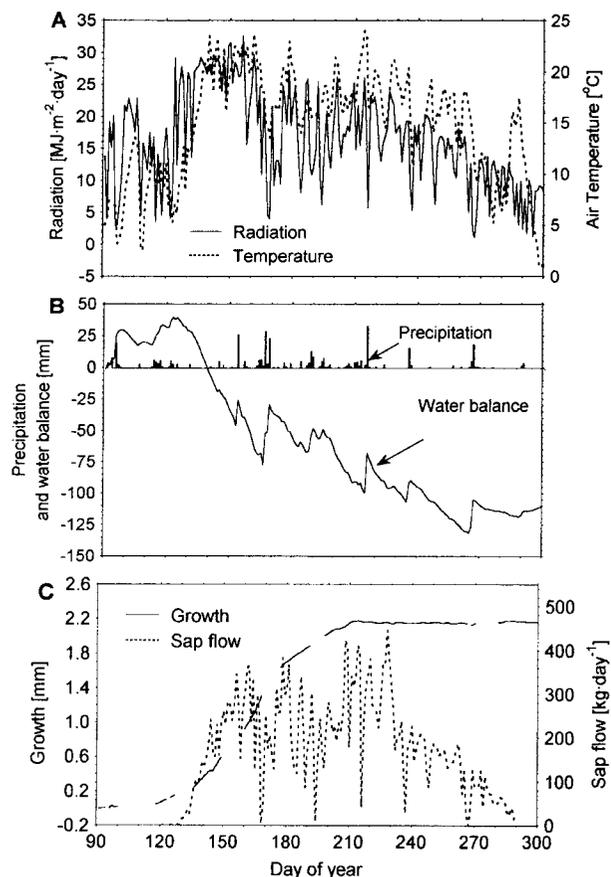


Figure 2. A) Seasonal course of global radiation balance and air temperature in the floodplain forest, southern Moravia six years after cessation of regular floods in the region (1979). B) Seasonal course of precipitation and cumulative soil water balance W_b in the floodplain forest. C) Seasonal course of stem radial growth and sap flow rate in the experimental pedunculate oak in the floodplain forest.

ly. Maximum rate of stem growth occurred in mid June, i.e. it followed the development of foliage with a delay of about 25 days. During the early period of growth (i.e. up to about 40 % of the final dr), the low density early-wood containing mostly large vessels was created (up to $T_{\text{ef}} = 888$). The growth then gradually slowed down in July, when more and more high density latewood with only very small vessels was created under a relatively slow growth rate and completely ceased in the early August (when $T_{\text{ef}} = 1837$); figures 2c and 3.

In general, the onset of radial growth of tree stems is determined genetically [21]. Specifically for oaks it is known that because most of the conducting vessels are

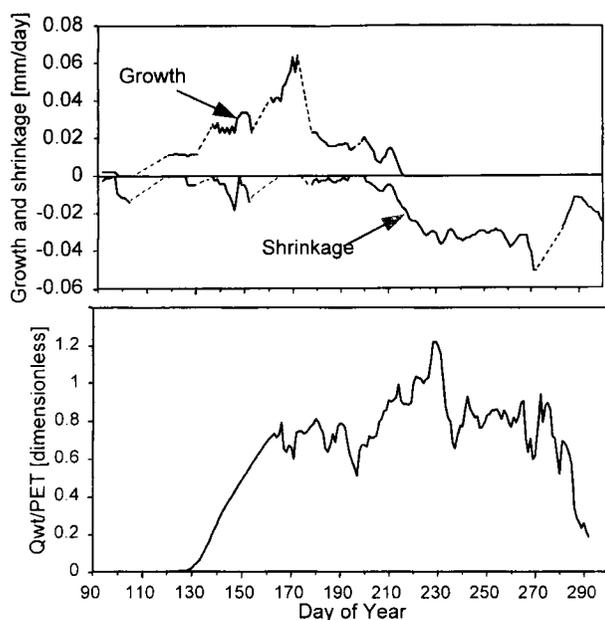


Figure 3. A) Seasonal course of maximum daily stem shrinkage (r_s) and rate of growth (dr/dt) in the experimental pedunculate oak in the floodplain forest. B) Seasonal course of relative transpiration (Q_{wl}/E_{pot}) in the experimental pedunculate oak in the floodplain forest.

embolized and closed by tylls over the course of previous years and the current winter, the new large xylem vessels have first to be created every spring in order to supply enough water for transpiration [1, 13, 45]. A tree uses the assimilates from the previous year's storage for that purpose [18].

Cessation of stem radial growth during late summer was rather closely related to some environmental factors (figure 2), including the beginning of a constant decrease in daily totals of radiation and the acceleration of the climatic water deficit (after strong rain on 4 August there were no significant rains for next 20 days). At the same period the soil water content decreased down to a level which began to have a significant impact on the water availability for the trees. This was true for the upper soil horizons in mid August and for the deeper soil horizons from about 10 September (see [33]).

During the whole period of growth (April–July) under conditions of non-limiting soil water supply the stem shrinkage was usually rather small (0–0.02 mm) or absent during the daytime compared to later periods and fully compensated by swelling during the night. When the growth ceased in August, the shrinkage increased (0.01–0.05 mm) owing to a continuous loss of water

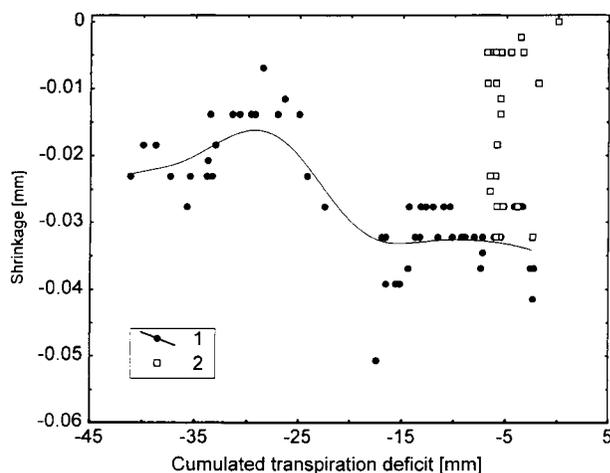


Figure 4. Stem shrinkage on cumulative transpiration deficit of the experimental pedunculate oak in the floodplain forest ($WD_{t,cum}$) for two spans of water content in soil layer 0–12 cm ($W_{s,12}, \% vol$): (1) – $W_{s,12} < 40$, (2) – $W_{s,12} > 40$.

from stem tissues because the supply of water from the drier soil was not sufficient to supply the relatively high transpiration at this time (figure 3). This figure shows that the relative transpiration (Q_{wl}/E_T) was the highest between approximately 1 August and 25 August, just in the period of permanent shrinkage.

The relation between stem shrinkage and cumulative transpiration deficit of tree ($WD_{t,cum}$) occurred at the end of the growing season, when the net growth was low or none. This allowed a clear distinction between growth and shrinkage. A certain plateau of shrinkage was reached at the level of approximately 0.035 mm, which corresponds to 1.03 dm³ of stem volume; figure 4. Decreasing shrinkage after the period of high values of transpiration deficit occurred in October, when the leaf-fall began and actual transpiration became significantly lower than potential evapotranspiration.

The daily tree transpiration deficit (WD_t) reached a minimum in mid May ($-3.2 \text{ mm}\cdot\text{day}^{-1}$) when the xylem vessels were not yet developed enough to provide water for transpiration of still developing foliage (i.e. still low LAI) under clear and hot weather conditions (figures 2 and 5b). The absolute maximum of WD_t (+2.2 mm) occurred in mid August and was related to short-term dramatic changes of water in the upper horizon of soil. Such phenomena can probably be explained as follows: high amounts of fine roots could be expected in the upper horizon which would be able to enhance rapidly the water uptake under favourable soil water conditions.

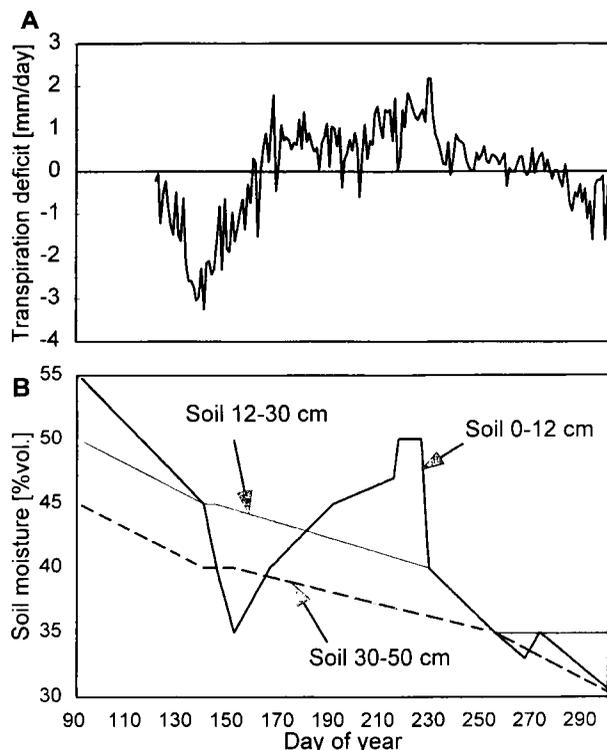


Figure 5. A) Seasonal course of daily transpiration deficit of the experimental oak tree (WD_t). B) Seasonal course of soil water content in three layers of depth (data from Prax, 1980).

The upper soil horizon was overwettered after the strong rain ($38.8 \text{ mm}\cdot\text{day}^{-1}$) on 4 August (according to Prax [33] the soil moisture was over 50 % vol., i.e. the soil was saturated with water). The subsequent hypoxia should limit root respiration and water uptake [5], which may explain the very low water uptake (WD_t about 0 mm) which we observed for several subsequent days. Then water uptake increased rapidly following a decrease in soil water content down to a certain value, evidently assuring sufficient aeration of roots. Maximum sap flow persists for only 2 days (16–17 August), then the water uptake decreased rapidly for 1 day. This high transpiration rapidly used up most of the easily available water from the shallow upper horizon, where its content decreased from 50 to 40 % vol., while in deeper horizons it did not change significantly [33].

3.2. Analysis of variance of stem radial variation

The analysis of variance showed that the environmental factors explained 75 % of seasonal variation of stem

radius dr/dt . Most closely dr/dt was related to degree-days T_{ef} , amounting to 93.0 % of explained variance. Less important were the soil water potential in the upper soil layer (0–12 cm) and the cumulated total of transpiration, Q_{wt} (5.1 and 1.9 % of variance, respectively). Maximum daily shrinkage $dr_{s,max}$ (where 83 % of variance was explained by environmental factors) was most closely related to the cumulated total of Q_{wt} and to T_{ef} (73.3 and 18.1 % of explained variance, respectively). Less important was the daily total of potential evapotranspiration (4.8 %), and the daily means of the soil water potential in upper and medium layers (0–12 cm and 30–50 cm – both 2.6 % of variance) and of air humidity (1.2 %). Interestingly, the integrated variables characterizing the whole season (cumulative totals of Q_{wt} and degree-days) showed the most significant impact on both differential parameters of tree growth under consideration (dr/dt and $dr_{s,max}$). In contrast, the dependence of both above-mentioned differential variables on independent differential variables characterizing individual days of the growing season was low or insignificant.

3.3. Diurnal variation of stem radius

It was possible to distinguish several different types of relationships between stem shrinkage and swelling, which are visible on the diurnal courses of stem radius during the growing season (figure 6).

- 1) No shrinkage occurred at the beginning of growing period (6 May) under low transpiration and rather intensive growth of earlywood.
- 2) Shrinkage was much lower and insignificant compared to the growth. The variation in stem radius (i.e. growth minus shrinkage) is positive during the whole day and night over the seasonal maximum of photoperiod (17 June, figure 6a) under conditions of good water supply (16–18 June were rainy days).
- 3) Shrinkage took place during the daytime only and the growth occurred during the night during a part of the growing period after worsening of the soil water supply conditions (6 July, figure 6b, similar situation was around 17 May).
- 4) The stem growth took place only during the daytime while shrinkage occurred during the night at the time of low growth with sufficient water supply (7 August, figure 6c, after a strong rain on 4 August).
- 5) Swelling during the daytime and shrinkage at night, exactly following the sap flow and temperature dynamics occurred close to the end of growing period (31 August–1 September, figure 6d). This situation was typical for the fall: for 18 days of hourly measurements from

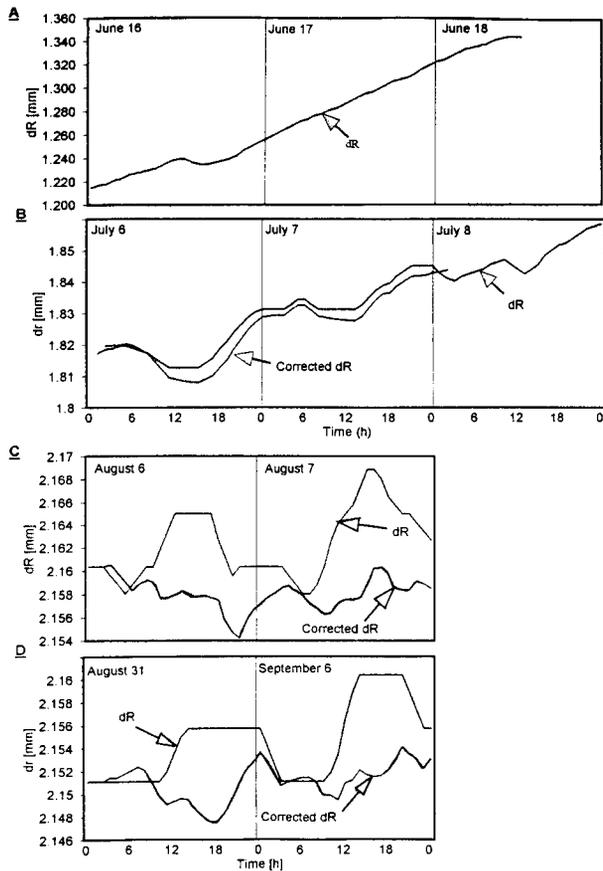


Figure 6. Diurnal courses of stem radius variation (observed and after the temperature correction) of the experimental oak tree during selected days of the growing season.

13 August to 24 October the minimum value of stem radius was obtained between 04:30 and 08:00 hours (mean term 06:00 hours) and the maximum value between 12:30 and 18:30 (mean term 15:00 hours). The phenomenon can be explained by the thermal expansion of xylem water. After taking this process into consideration we obtain the variation of diurnal radius as the result of three processes with different tendencies. The first is net growth, which is a monotone increasing function or a constant. Two others are periodical processes with approximately opposite extremes: the shrinkage/swelling process usually has a minimum during the daytime (shrinkage) and a maximum at night (swelling), whereas the changes of xylem water volume caused by temperature oscillated in the opposite way. During the period of active growth this correction did not change the pattern of the water-driven dynamics of stem radius, only slight-

ly increased its amplitude. However, after the cessation of growth subtraction of heat-driven variation of radius the water-driven dynamics showed almost no impact on stem radius (see *figure 6d*).

The cross-correlation analysis of diurnal courses of sap flow and radiation showed the time shift between these variables to be about 1 h or less for different periods. The daily mean stem capacitance (daily amount of water transpired from the stem storage estimated as the maximum of cumulated difference between the values of sap flow at the given moment and 1 h ago), was about $0.3 \pm 0.14 \text{ mm}\cdot\text{day}^{-1}$, which corresponds to our previous results [6].

3.4. Limits of precision of the model

The most difficult problem of plant growth modelling deals with the mechanism of allocation of assimilates. Some models based on the optimization of distribution of assimilates aimed at the maximum growth were proposed (see, for example [10]). We did not apply such principles because we did not have enough data about branch, root and fruit growth. A hypothesis of the pipe-model (allometric relations as proportional to sapwood cross-section area and leaf area, see [31]) was also not applied here because of the short period of modelling, allowing significant time shifts between different growth processes (for example, between growth of leaves and sapwood area). It is known that different parts of the same tree may slightly differ in their growing periods [18]. That is why we applied the determined distribution of assimilates according to existing data on stem and leaf growth. Taking into account the use of assimilates for flower development in May slightly improved the seasonal curve of dr .

The main source of error in the diurnal version of the model is probably the transpiration rate (E_T), approximated by the Penman-Monteith equation and applied for derivation of the shrinkage and the transpiration deficit. Meteorological data obtained at the meteorological station in the open may differ from those in the closed floodplain forest which might somewhat disturb the estimated value of transpiration. The difference between Q_{wt} and E_T is usually low compared to absolute values of both these variables which could have a significant impact on the derived value of transpiration deficit and shrinkage (equation (14)).

3.5. Simulation experiments

Sensitivity analysis of the model considering its main parameters, approximated in simulation experiments, showed that the parameter R_0 , corresponding to the maintenance respiration (see equation (12)), had the most significant impact on the simulated radial growth (table I). In contrast, the parameters corresponding to the use of old assimilates (A_0 and k_A) had very small influence on the final growth (see table I), but were principally important for simulating the growth of the stem before leaf development. Within the time parameters the term of the leaf development was the most significant. In general, in the seasonal version of the model the correlation between experimental and simulated values was 0.6655 for the growth rate (dr/dt) and 0.9987 for the growth (dr).

Two main differences between simulated and experimental data of seasonal stem growth occurred (figure 7). 1) The plateau on the simulated curve appeared at the beginning of the growing season. The simulated growth began by using the old assimilates and then it stopped in late April and early May, respectively, because of the very high growth rate of leaves and the depletion of old assimilates during this period. A very fast increase in radial growth was possible when the leaves reached a certain area and started to export the assimilates. The real curve was smooth, without steps, which means that probably some more complex mechanisms of assimilate allocation took place. 2) Highest growth rate occurred in mid June, i.e. approximately 3 weeks after completion of leaf development, while the modelled growth was highest just at the end of leaf development (mid May). This means that the applied simple model underestimates the buffering capacity of the system or it neglects the use of assimilates for other purposes.

4. Conclusions

1) The seasonal course of stem radial growth in oak (*Quercus robur* L.) took place from early April (before

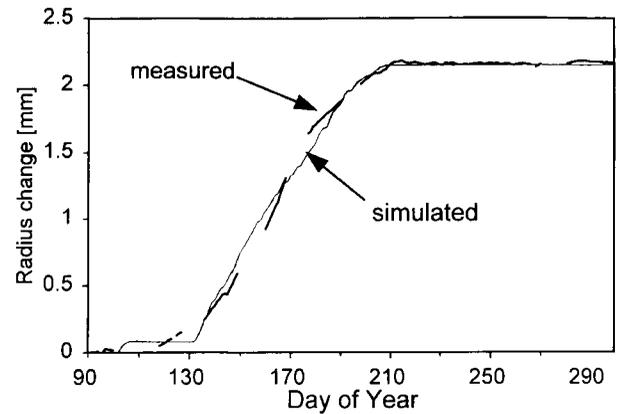


Figure 7. Measured and predicted seasonal variation of stem radius in the experimental pedunculate oak in the floodplain forest.

flushing of leaves) to early August in floodplain forest several years after cessation of regular natural floods.

2) Significant diurnal stem shrinkage began in August, when the drought stress occurred during the given growing season.

3) Different types of diurnal variation of stem radius occurred, including growth without shrinkage, growth at night and shrinkage at daytime and vice versa. This behaviour is dependent on the time of year and tree water supply.

4) Data of sap flow, global radiation and air temperature applied to the model, based on simulation of photosynthesis, stem respiration and dynamics of stem water content, were found sufficient for simulating the seasonal and diurnal variation of stem radius in large oak in the floodplain forest.

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Table I. Change of simulated final stem radial growth (in %) under 10 % increasing and decreasing of model parameters.

Parameters	Value	+10%	-10%
Maintenance respiration, R_0	12	-14.4	+13.4
Respiration ratio, a_R	0.00229	-7.19	+7.16
Initial assimilates storage, A_0 (kg C/m ² of stem surface)	0.1	+1.0	-0.9
Rate of old assimilates use, k_A	0.12	+0.5	-0.4
Day of leaf development to 1/2 of max. area (variation ± 5 days)	May 8	-9.2	+5.0
Day of a_s decrease down to 1/2 (variation ± 5 days)	July 31	+6.0	-7.0
First day of use of old assimilate storage (variation ± 5 days)	April 12	+0.25	-0.16

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List of symbols

A_0 – initial storage of assimilates from previous year (kg C·tree⁻¹)

A_s – use of assimilates from the previous year for skeleton growth (g C·day⁻¹·tree⁻¹)

A_l – use of assimilates from the previous year for leaf growth (g C·day⁻¹·tree⁻¹)

a_s – the part of assimilates, used for skeleton growth (relative units)

a_{ws} – the proportion of stem dry mass in total skeleton dry mass (relative units)

dr_{mean} – mean width of annual ring of 1979 (mm).

dr_{point} – width of annual ring of 1979 in the measuring point of stem (mm)

dr_+/dt – radial growth (without shrinkage) (mm·h⁻¹) or (mm·day⁻¹)

dr_s – shrinkage (mm)

D_y – day of the year

E_T – actual transpiration (mm·h⁻¹)

E_{pot} – potential evapotranspiration (mm·h⁻¹) or (mm·day⁻¹)

h – height above ground (m)

$I_n(h)$ – radiation balance at height h (W·m⁻²)

I_0 – global radiation balance above the canopy (W·m⁻²)

k_{cv} – coefficient converting the mass of CO₂ assimilated (mg) to skeleton volume growth (dm³)

L – leaf area (m²)

SLAI – solar equivalent leaf area index (relative units)

P – net photosynthesis of crown (mg CO₂·h⁻¹·tree⁻¹) or (mg CO₂·day⁻¹·tree⁻¹)

P_f – the use of assimilates for fruit development (g C·day⁻¹·tree⁻¹)

P_1 – the use of new photosynthetic products for leaf development (g C·day⁻¹·tree⁻¹)

Q_{wt} – sap flow rate (kg·h⁻¹·tree⁻¹) or (kg·day⁻¹·tree⁻¹)

R_s – the stem respiration (mg CO₂·dm⁻²·h⁻¹)

R_0 – the stem respiration of maintenance (mg CO₂·dm⁻²·h⁻¹)

r – stem radius at 1.3 m (mm)

$S_{\text{bas. stand}}$ – stand basal area (dm²)

$S_{\text{bas. tree}}$ – tree basal area (dm²)

S^p – crown projected area (m²)

S_s – stem surface (dm²)

$S_{\text{stand}} = 10\,000\text{ m}^2$ – unit of stand area of part stand area occupied by the tree

S_{tree} – part of stand area occupied by the tree (m²)

t – time (h) or (day)

T_a – air temperature (°C)

T_{ef} – sum of effective temperatures (degree-days)

WD_t – tree transpiration deficit (mm·day⁻¹)

W_b – cumulative soil water balance (mm)

W_p – precipitation (mm·day⁻¹)

W_s – soil moisture (% vol.)

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