

Linking Phenological Data to Ecophysiology of European Beech

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Abstract

Phenological observations and ecophysiological measurements were conducted in a 45-year-old European beech stand in the Dražanská vrchovina (the Czech Republic). Ecophysiological studies included sap flow measurements on stem using trunk heat balance method, transmittance of photosynthetically active radiation (PAR) and stem volume changes. Sap flow was tightly connected to the phenological stage of the tree and to other ecophysiological measurements. Utilization of instrumental techniques better specified tree physiological status and phenophase than pure observations and qualified guess. Onset of spring phenological stages (i.e., leaf area development) was easily identifiable from sap flow measurements, dendrometer readings and PAR transmittance. Given longer duration of autumn development and higher variability in external factors, autumn phenological stages were not as easy to identify as spring stages, however, they were still projected into the long term ecophysiology. We conclude that ecophysiological measurements provide additional value in objectification of phenological studies, and phenological observations can help to interpret ecophysiological measurements and thus to help to underlying physiological processes.

INTRODUCTION

At scales from organs to ecosystems, many processes, particularly those related to the cycling of carbon (productivity and growth), water (evapotranspiration and runoff), and nutrients (decomposition and mineralization), are directly mediated by phenology, and the seasonality of these processes is implicitly phenological (Gu et al., 2003). The good knowledge of all phenological interactions to environment might lead to better understanding of ecosystem functioning in short term as well as long term point of view. European beech forms mono-specific or mixed stands under a broad range of soil chemical, hydrological and climatic conditions, from highly acidic to basic soils, from low to high rainfall regimes and from low to high altitudinal zones. Therefore, this species provide reliable study field of phenology. Seasonal cycle of leaves development determines many crucial aspects of forest canopy functioning, such as photosynthetic uptake, radiation extinction, rainfall interception and evapotranspiration. Rapid increase in LAI is generally recorded from early May to mid-July in European beech (Bequet et al., 2011; Gond et al., 1999; Mussche et al., 2001; Saigusa et al., 2002).

Sap flow rate and leaf area development are in good correlation in deciduous trees. Simultaneously with leaves development, transpiration has to progress (Střelcová et al., 2006) to participate on forming the leaves and follow-up tree radial growth. Radial growth is initiated after budburst for diffuse-porous species (such as European beech). In conditions of sufficient soil water availability and, based on potential evapotranspiration, the maximal transpiration rates occur when tree is in full foliage (Meier and Leuschner, 2008). But beech exhibits a number of physiological and morphological traits that characterize it as comparatively drought-sensitive (Backes and Leuschner, 2000; Granier et al., 2007). Leaf area reduction is a common response to soil water shortage thereby reducing the transpiring surface area and avoiding severe decreases in cell water potential

and turgor (Hinckley et al., 1981; Kozłowski and Pallardy, 1997). Our objective was to link the phenological data in *Fagus sylvatica* in a context of environmental factors to tree ecophysiology.

MATERIALS AND METHODS

Research Site

The research plot was situated in a forest stand named 512D2 at a research plot of the Institute of Forest Ecology, Mendel University in Brno (49°26'29.946"N; 16°42'6.237"E, altitude 600 m). Long term mean air temperature and annual precipitation are 6.6°C and 683 mm. Annual precipitation in 2012 was 518 mm and mean air temperature was 7.9°C. Soil type was cambisol oligotrophic. This 45-year-old single species forest stand was composed entirely of European beech (*Fagus sylvatica*). The total stem basal area was 38 m² ha⁻¹. Ten sample trees were selected for the phenological observations. Six of them, chosen among the dominant and co-dominant trees (excluding suppressed ones), with breast height diameter (DBH) from 16 to 26 cm were chosen for detailed instrumental measurements of sap flow and stem diameter increment.

Ecophysiological Measurements and Phenological Observations

Measurements and observations were conducted from 28 March until 3 November 2012. Data were obtained every minute and 10-minute averages were stored in a memory of datalogger (ModuLog, EMS Brno, Czech Republic). Sap flow was measured on the stems of six sample trees using the trunk heat balance technique (Čermák et al., 2004; Kučera et al., 1977), (Fig. 1a). We used EMS51 heat balance system (EMS Brno, Czech Republic). Temperature difference between heated and reference part of the stem was fixed to 2 K. Measuring points were installed from the north and covered with the reflective radiation shield. Upscaling of sap flow from individual trees to the forest stand was based on the regression between tree diameter and corresponding sap flow (Čermák et al., 2004). Reference evapotranspiration for the grass surface (PET) was calculated from available meteorological data according to FAO approach (Allen et al., 1998).

Stem diameter changes were measured in a breast height of the six sample trees using the automatic band dendrometers (DRL26, EMS Brno, Czech Republic; Fig. 1). Difference between thermal expansion of the tree and dendrometer estimated before the leaf flush was between 1.9 and 2.3 μm K for individual trees. Altogether thirteen PAR sensors (EMS12, EMS Brno, Czech Republic) were placed in a regular web under the canopy, 60 cm above the soil surface. Ambient PAR was obtained from the PAR sensor (EMS 12, EMS Brno, Czech Republic) at the meteorological station. PAR transmittance was calculated as a ratio of the mean understory PAR to ambient PAR.

Phenological observations were carried out according to methods of the ČHMU (1987)/Czech Hydro-meteorological Institute. Phenology was observed on the same six trees, which were selected for sap flow measurements. Following phenological stages were observed: bud break from 10%, foliation beginning from 10%, foliation beginning from 50%, foliation beginning from 100% and full foliation (100% unfolded leaf area), leaf colouring 10%, leaf colouring 50%, leaf colouring 100%, leaf fall 10%, leaf fall 50%, leaf fall 100%. Exact day of the onset of phenological phase was calculated as mean of all sample trees.

Minikin thermometer with radiation shelters, global radiation and photosynthetically active radiation (PAR) sensors and precipitation gauge (EMS Brno, Czech Republic) were situated 300 m from the experimental plot. Soil water potential (SWP) was measured in three replications at depth 20 cm using gypsum blocks (Delmhorst Inc., USA; datalogger SP1, EMS Brno, Czech Republic).

RESULTS AND DISCUSSION

Phenology

Beginning of the bud break was observed on the 116th day of the year 2012 (DOY), which was eleven days later than is a long term (1991-2012) average. The later growth started, the faster was subsequent development. Duration of all spring phenological stages was only 14 days in 2012, which was 11 days shorter than long term average 25 days. Autumn phenological stages were in accordance with the long term average (Table 1).

PAR Transmittance

PAR transmittance was between 1.5% of ambient illumination when the foliage was fully developed and 33% before bud break (Fig. 2). In five spring days the transmittance dropped from 33 to 9%, which corresponds to leaf area 33% of the full area. In three more days transmittance decreased to 3%. Subsequent development of the leaf area was slower but by the end of May transmittance reached stable value of 1.5%. Strong correlation was observed between PAR transmittance and sap flow in the spring while different (and weaker) relationship was found in the autumn (Fig. 1b).

Stem Growth Increment and Stem Volume Changes

In the context of this study we use stem circumference changes as a proxy for two different issues. The first one is connected to the cambial activity and actual stem growth. Second approach means indirect estimation of tree water potential. Initial increase of the growth in the beginning of May was more rapid in dominant than in codominant trees (Fig. 2b). First almost negligible stem shrinkage was visible between 26 and 27 April and also the next night. Sharp stem shrinkage on the 28 April indicated steep decrease in the stem water potential. Smallest stem diameter was measured on 29 April and it was increasing from 30 April. Therefore we may be reasonably sure that the vascular cambium was active at latest on 30 April. Exact beginning of the cambial activity is, however, impossible to estimate from the dendrometrical measurements as the stem enlargement resulting from the cell division and their elongation is mutually contradicted by stem shrinkage originating in withdrawal of water from elastic tissues. The end of cambium activity in the end of June is linked to the decrease in the sap flow rate and to summer colouring of leaves (Fig. 3b).

Sap Flow

Tree sap flow begun on 28 April and ceased with leaf fall by the end of October (Fig. 3). Amount of transpired water was highest in the June and July. It reflected high soil water availability and evapotranspirative demands in those months. At the end of July transpiration levels decreased (mutually with onset of summer leaf colouring) and have not recovered even after rain events in August. Possible explanation, alongside with loss of the leaf area may include cavitation-based loss of xylem hydraulic conductivity (Leuschner et al., 2001; Ogasa et al., 2010; Whitehead, 1998).

Causal Connections between Phenology and Ecophysiology

The following chapter will discuss unification of phenology, as a rather subjective tool to study externally the tree life processes, with information from the instrumental ecophysiological measurements bringing more insight to the tree behaviour. Spring is the time period of most rapid changes in the deciduous species. Trees that shed their leaves and put themselves into the dormancy have to activate metabolic processes, build (and fix) water conducting pathways and to develop photosynthetically active surfaces. Buds burst on 26 April according to phenological observations. This process was not visible on PAR measurements and possible water flow was beyond the resolution of the sap flow sensors. Very small stem shrinkage (about 0.02 mm from the total tree circumference in a breast height) was visible in trees on the band dendrometers in the night between 26 and

27 April and also the next night. This fact confirmed dendrometers as very sensitive indicators of stem water potential in a transition period between the root pressure induced sap flow and the flow from foliage-developed negative force. First statistically significant change of the canopy transmittance appeared with the 50% foliation beginning on 28 April. This day, in the afternoon, appeared the first measurable sap flow (Fig. 2c). Leaf area amounted to 20% of the full cover (Table 1). Also sharp stem shrinkage without refilling in the night (partly due to the high night vapour pressure deficit and resulting night transpiration) indicated decrease in the stem water potential as a result of the transpiration. Smallest stem diameter was measured on 29 April and from 30 April stem diameter increased. Relation between PAR transmittance and sap flow was exponential and very tight ($R^2=0.99$) in the early stages of leaf development (Fig. 1b). Sap flow was rising until the 2 May when the foliage area was developed from about 40% and then maintained almost stable levels depending only on the atmosphere evapotranspiration demands. Further increase of the foliage area by 60% until the full foliation (10 May) had no proportional effect on the transpiration. Very slight increase in the transpiration between beginning and end of May more correlated with decrease in the light transmittance thus expressing high effect of sunlit leaf area on the water vaporization.

First hint of the onset of autumn phenological stages – summer colouring – appeared on 30 July. It was associated with short episode of soil drought, with cessation of radial stem growth and with decrease in sap flow rate. Sap flow then did not recover even after soil water had recharged in the beginning of August. Autumn phenological stages lasted longer than spring stages. Therefore, transpiration was only weakly linked to autumn phenology, given considerable decrease (and variability) in a quantity of external factors driving water vaporization and variation in the soil moisture over this long time period. However, longer continuous trends of cessation of transpiration with the loss of leaf area were clearly visible, even though correlation was much weaker than during spring phenophases (Fig. 1b). Loss of the sap flow in the late autumn (i.e., beginning of October, Fig. 3a) was more connected with the degree of leaf yellowing than to the actual shedding of the leaves. The explanation may include formation of the suberin layer between the twigs and foliage resulting in a loss of branch to petiole hydraulic conductance. End of the vegetation season was reflected also in the stem volume changes. After the growth cessation, stem size volume changes followed the development water potential (i.e., shrinkage as the result of transpiration and swelling to some level due to the water refilling, Fig. 3b). During October, however, stems of all studied trees continuously increased their diameters. This ‘growth’ was a result of refilling of stem elastic tissues with water associated with the degree of loss of leaf area.

CONCLUSIONS

1. Phenology is tightly connected to the ecophysiological processes of the deciduous tree species. Measurements of PAR transmittance, stem volume changes and sap flow provided valuable additional information specifying the tree development during both spring and autumn phenological stages.
2. Spring and autumn phenological stages are different in their dynamic as well as in the light transmittance, sap flow and stem volume changes. It is a result of different external driving factors (i.e., sun elevation angle).
3. Bud break occurred on 26 April and consequent decrease in stem water potential was almost immediately sensed by dendrometers. Sap flow became measurable two days later.
4. Summer leaf colouring at the end of July was linked to end of stem growth increment and to decrease in the sap flow rate.

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Tables

Table 1. Terms of phenological stages. DOY = day of year.

		DOY	Leaf area [%]
Budbreak 10%	26.4.2012	116	0
Foliation begining 10%	27.4.2012	117	5
Foliation begining 50%	28.4.2012	118	15
Foliation begining 64%	29.4.2012	119	25
Foliation begining 85%	30.4.2012	120	30
Foliation begining 100%	1.5.2012	121	33
Full foliation 100%	10.5.2012	130	100
Bud formation	9.6.2012	160	
Shoot lignification	12.6.2012	163	
Summer colouring	30.7.2012	211	
Leaf colouring 10%	13.9.2012	256	
Leaf fall 5%	1.10.2012	274	
Leaf fall 10%	13.10.2012	286	
Leaf fall 25%	15.10.2012	288	
Leaf colouring 60%	15.10.2012	288	
Leaf colouring 100%	20.10.2012	293	
Leaf fall 50%	4.11.2012	308	
Leaf fall 100%	10.11.2012	314	

Figures

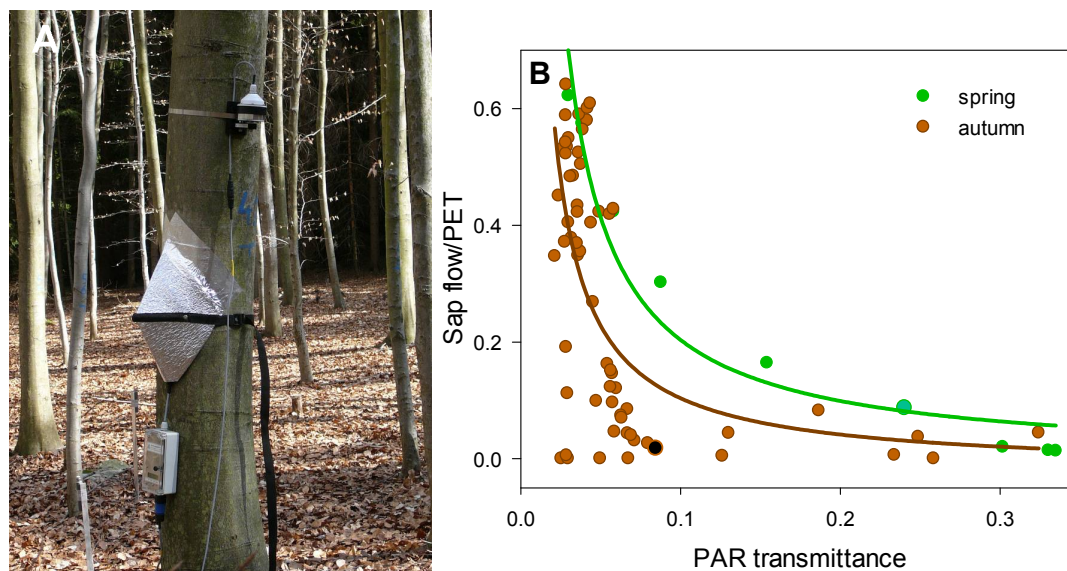


Fig. 1. A: Sample tree equipped with sap flow sensor (under the radiation shield) and automatic band dendrometer. B: Relationship between PAR transmittance and sap flow in spring (green) and autumn (brown). Regression equations are $y=1.08^{-11.4x}$, $R^2=0.99$ and $y=1.05^{-24.6x}$, $R^2=0.39$ in spring and autumn, respectively.

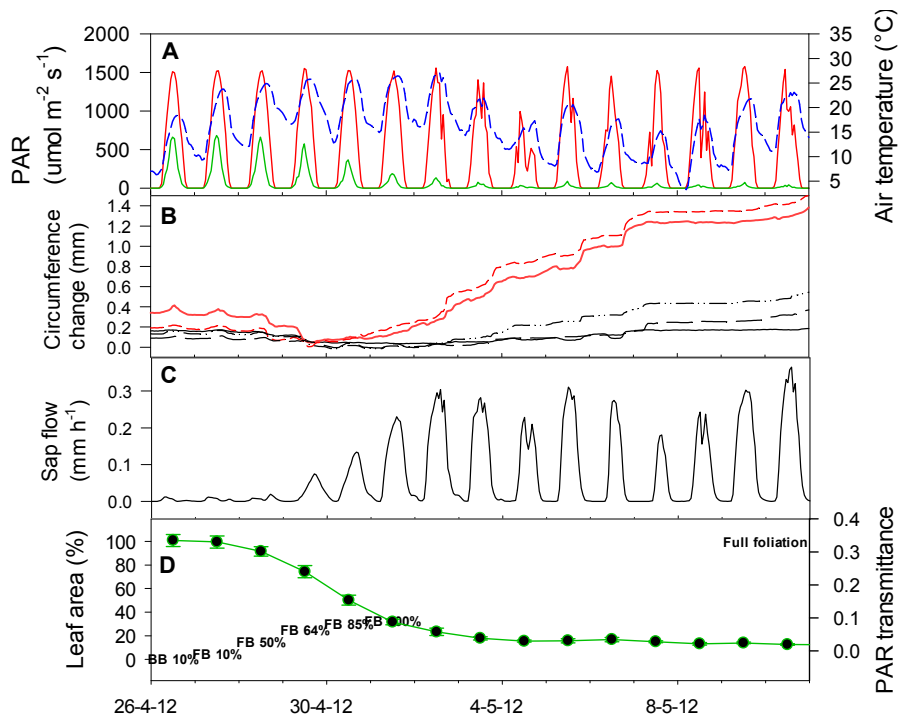


Fig. 2. Weather conditions and development of tree and stand characteristics in spring. A: ambient (red) and understorey PAR (green), ambient air temperature (blue). B: stem circumference fluctuation of the sample trees (red – dominant, black – codominant). C: stand sap flow. D: phenological stages with respect to the stand foliage development and PAR transmittance. Abbreviations: BB – bud break, FB – foliation beginning.

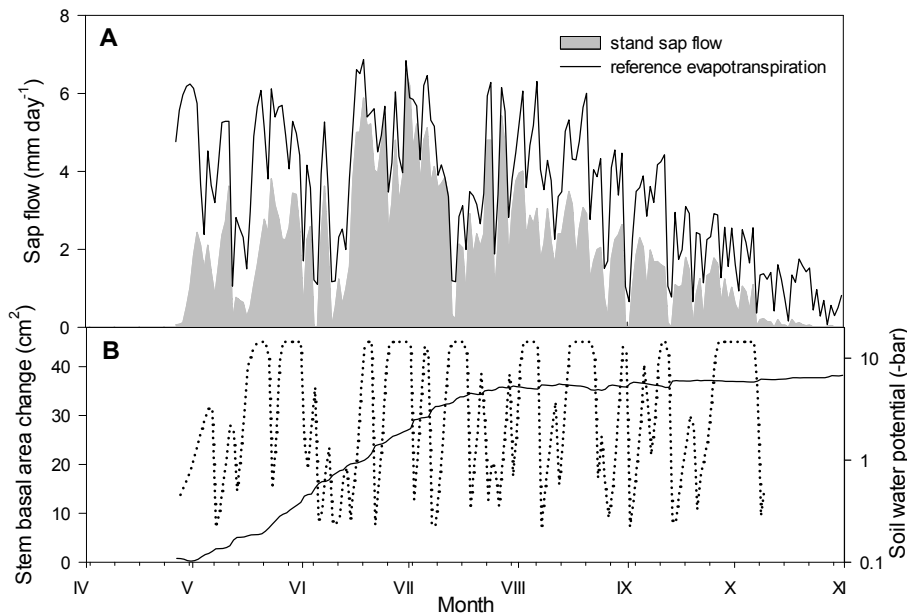


Fig. 3. A: daily sums of sap flow from the forest stand compared with reference evapotranspiration (A). B: changes in stem basal area (mean of all measured trees, full line), soil water potential (dotted line).

