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Sap Flow in Xylem of Mature Norway Spruce: a Case Study in Northwestern Latvia During the Season of 2014–2015

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Abstract

Sap flow velocity (SFV) in sapwood of a mature Norway spruce (*Picea abies* (L.) Karst.) was monitored in the northwestern part of Latvia by the heat ratio method during 2014–2015. The effect of temperature and soil water potential was assessed by a bootstrapped Pearson correlation analysis. Seasonal and daily variation of SFV was observed. The highest SFV was observed in late April and during summer months whilst the lowest SFV occurred in winter months. During most of the studied period, SFV correlated with temperature. A negative effect of temperature was observed in summer suggesting occurrence of water and/or heat stress. The effect of soil water potential also has been significant in summer supporting the occurrence of water deficit conditions. During the dormant period, SFV was low, but still it reacted to temperature, suggesting that tree has been physiologically active. Nevertheless, sap flow differed between the inner and outer part of sapwood likely due to the differences in area of foliage of different age.

Key words: circulation of sap, *Picea abies*, dormancy, heat ratio method.

Introduction

Climatic conditions affect physiological processes in trees thus altering their vigour (Dobbertin 2005) and hence their survival and growth (Bergh et al. 1998). Under changing climate, detailed information about the effect of weather conditions on functioning of trees is necessary for a better understanding and prediction of possible changes in growth in future (Sykes and Prentice 1996). For mature trees, the information about the significant climatic factors has been mainly assessed by the analysis of variation of increment (Fritts 2001) or by the analysis of biochemical proxies (Lichtenthaler et al. 2007). The response of trees to stresses has been also studied experimentally by the subjection of saplings to altered conditions (Helenius et al. 2002), but the reaction of mature trees may differ notably (Delzon and Loustau 2005). Still, these studies do not provide detailed information about the physiological activity of trees throughout the year, as they have been mainly focusing on the vegetation season, although significant relationships between increment and conditions during the dormant period have been observed (Mäkinen et al. 2000).

The movement of sap in xylem is one of the characteristics that represent physiological activity (Wullschleger et al. 1998) of woody plants, which varies throughout the year (Pallardy 2008). During the vegetation period, the amount of water transport reflects the extent of transpiration and hence it might be referred to the intensity of assimilation (Wullschleger et al. 1998). In spring, sap flow is deployed for transport of nutrients and growth hormones, thus initiating growth (Dambrine et al. 1995); in autumn, assimilates are transported to the storage allocations, i.e. roots (Lipavska et al. 2000, Gall et al. 2002). During the cold hardening and the dormant period, sap flow can occur as the concentrations of anti-freeze compounds are dynamically altered (dehydration of cells) to decrease the damage caused by low temperature (Essiamah and Eschrich 1985, Wisniewski et al. 2003). For evergreen species, an ascent of sap during the dormant period is needed to countervail the transpiration and to avoid winter desiccation (Sowell et al. 1996).

The aim of this study was to assess the intra-annual dynamics of xylem sap flow of a mature Norway spruce (*Picea abies* (L.) Karst.) tree and to evaluate the effect of environmental conditions on it. We hypothesized that a sap flow of different intensity has been occurring throughout the year. We also assumed that the effect of environmental factors on the sap flow has been shifting as the seasons advanced.

Material and Methods

Study area and measurements

Study area was located in the northwestern part of Latvia near Mazirbe (57°40'14" N, 22°19'26" E). The relief is a complex of ridges and depressions (ancient dunes) oriented parallel to the coastline that has been formed during the development of the Baltic Sea. The elevation of ridges and depressions varies from 2.5 to 10 and from 0.5 to 2 MASL, respectively. Tops of the ridges are mainly covered by dry nutrient poor pine forests while the depressions are over moist and covered by bog vegetation. Soil on the ridges is sandy, but the depressions are covered by a peat layer. The site was covered by a naturally regenerated forest with a low intensity management.

The climate is mild as determined by the dominant western winds, which bring cool and moist air masses from the Atlantic Ocean and the Baltic Sea. Mean annual temperature is ~ +6.7 °C and mean monthly temperature ranges from -3.7 to 17.8 °C in February and August, respectively. The vegetation period, when mean diurnal temperature exceeds +5 °C, usually extends from late April to late October. Annual precipitation is about 670 mm, but most of the precipitation falls in summer months in the form of showers, usually resulting in a positive water balance (Krams and Ziverts 1993).

Weather during the study period (March 2014 to March 2015) was anomalously warm (particularly in winter); mean annual temperature was 7.8 °C and mean monthly temperature ranged from 0.3 to 19.0 in December 2015 and July 2014, respectively. Nevertheless, a few short cold periods (up to four days), when mean daily temperature dropped below -5 °C, occurred in December and January. The total amount of precipitation that fell during the studied period was 681 mm and the monthly precipitation sums ranged from 10 to 186 mm in November and August, respectively. Soil water potential generally showed a decrease during the vegetation season from -15 to -147 hPa at the beginning of measurements and in mid-October 2014, respectively. Mean value of the recorded water potential was -65 hPa (Figure 1 B).

In this study, sap flow velocity (SFV) was monitored for a 70-year old dominant Norway spruce (diameter at breast height = 32 cm and height = 25 m) from March 24, 2014 to March 23, 2015. The spruce was growing in the depression ~ 0.6 m above its bottom level on a mound of mineral soil. The local density of stand was ~ 450 trees/ha. One sap flow measurement device SFM1 (ICT International, Armidale, NSW) using heat ratio method (Burgess et al. 2001) was installed at 1.3 m height on the north-facing side of the stem (perpendicular to the slope). The system consists of two thermo-sensors with two measuring point and a heat pulse generator. The sensors were installed so that the measurement points were located in sapwood at 0.5 (outer) and 2 cm (inner) depth below the floem (Burgess and Downey 2014). A heat impulse of 20 and 40 J was used during the vegetation and the dormant period, respectively. Sap flow intensity was measured every 10 minutes. Ambient temperature was recorded hourly by a Davis Vantage Pro2 meteorological station located at ~ 20 m distance from the tree. Soil water potential (water content) at 0.3 m depth directly besides the tree was measured hourly by a T8 tensiometer (UMS, Munich, Germany) from May 31 to October 22 in 2014.

Data analysis

All measured time series were averaged for days. Time series of SFV of the inner and outer measurement points were not pooled and were used separately. The differences in SFV between the measurement points were compared by the t-test. The relationships between SFV and temperature were assessed by bootstrapped Pearson correlation analysis conducted for the entire periods covered by the datasets and for the moving 30-day intervals within them. The intervals of 30 days were applied to capture the temporal changes in relationships between the daily variation of SFV and the environmental factors. The analysis was conducted using DendroClim2002 software that has been developed for the time-series analysis (Biondi and Waikul 2004). The program has been written to facilitate the assessment of environmental signals and their shifts in time series of different response parameters of trees.

Results

During the studied period, SFV expressed both seasonal and daily variation (Figure 1 A). At the beginning of studied period, SFV rapidly increased reaching its maximum around the 20th of April 2014, thus suggesting the initiation of vegetation season, and afterwards a gradual decrease until November followed. Upon this trend, explicit daily variation was observed throughout the season. During the period from mid-November to early March, SFV was considerably lower than observed during the period from mid-March to October. Nevertheless, complete cessation of sap flow was not detected as the minimum SFV values differed from zero (Table 1). Additionally, descending sap flow, as suggested by the negative SFV, was observed in several days during the dormant period (Figure 1 A). The increase of SFV in mid-March 2015, apparently, indicated the beginning of the next vegetation season.

Sap flow in sapwood was heterogeneous as SFV was significantly higher in the inner part of sapwood during most of the analysed period (Table 1). Still SFV in the outer part of sapwood was higher during several days in the dormant period and in March 2015 (Figure. 1 A). The time-series of the inner and outer SFV showed similar trends as suggested by the tight correlation (r = 0.87) calculated for the entire period (Table 1). Still, the similarity of high-frequency (daily) variation of SFV in the inner and outer sapwood shifted throughout the season. During the March–November period, the inner and outer SFV had nearly identical high-frequency variation as shown by the values of correlation coefficients calculated for the 30-day intervals that ranged from 0.83 to 0.99 (Figure 1 D). However, during the December–February period, the patterns of high-frequency variation of SFV in the inner and outer part of sapwood rapidly diverged, as correlations became mainly non-significant or even significant and negative (at the end of February).

In general, the variation of SFV has been positively affected by both temperature and precipitation as suggested by the correlation analysis conducted for the entire periods covered by the measurement time series (Table 1). The effect of soil water potential was similar for SFV in the inner and outer part of sapwood (r ~ 0.53), but the effect of temperature was notably weaker for SFV in the outer than in the inner part of sapwood (r was 0.20 and 0.53, respectively). Nevertheless, during the analysed periods, the effect of the tested factors on high-frequency variation of SFV has shifted several times as shown by the correlation analysis conducted for moving intervals (Figures 1 E, F). At the first part of the vegetation period (until July), temperature had positive effect while soil water potential had negative effect on sap flow. A rapid diametrical shift in the effect of both factors occurred in July-August period, when the highest temperature was observed (Figure 1 B). Then, a shift to positive effect of temperature and negative effect of soil water potential was again observed for ~20 moving intervals ending before September. After that, for the next 20 moving intervals, a negative effect of temperature was observed, but the effect of soil water potential was non-significant. Sequentially, for ~20 moving intervals ending before the third decade of October, when soil moisture reached its minimum and temperature was still high (Figure 1 B), SFV was positively affected by soil water potential, but not by temperature (Figures 1 E, F).

Table 1. Statistics of time series of mean daily sap flow velocity (SFV) in sapwood of Norway spruce recorded in inner and outer measurement points (0.5 and 2 cm under the floem, respectively).
P-value of difference of mean SFV of inner and outer measurement point was estimated by *t*-test. Pearson correlation coefficients were calculated between the time series SFV and between SFV and tested environmental factors (temperature and soil water potential). Note that the length of period covered by soil water potential measurements is shorter. Asterisks indicate the significance of correlations at α = 0.05

	Inner	Outer
Min., cm/h	0.03	0.01
Max, cm/h	10.43	6.50
Mean, cm/h	2.33	1.27
St. dev.	2.42	1.37
Coefficient of variation	1.04	1.08
Difference of means, *p*-value	< 0.001	
Pearson correlation coefficient between entire time series of SFV	0.87*	
Pearson correlations coefficients between entire series of SFV and environmental parameters		
Temperature	0.51*	0.20*
Soil water potential	0.54*	0.53*

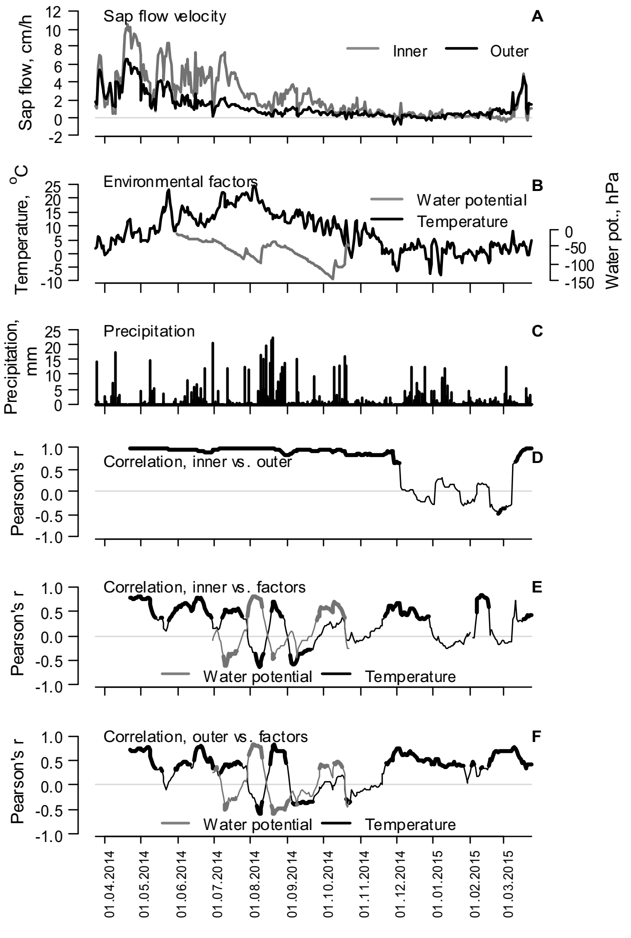

Figure 1. Daily mean sap flow velocity (SFV) in sapwood of Norway spruce recorded in the inner and outer measurement points (0.5 and 2 cm under the floem, respectively) (A); mean daily values of temperature, soil water potential (B) and precipitation (C), and Pearson correlation coefficient values calculated for 30 day moving intervals between SFV in the inner and outer measurement points (D) and between environmental parameters and SFV in the inner (E) and outer (F) measurement point. The significant correlations at α = 0.05 are shown by the thick line. In A, negative values indicate descent of sap. For the moving correlations (D, E and F), dates corresponds to the last day of moving interval

Although SFV during the dormant period was considerably lower compared to the vegetation period (Figure 1 A), sap flow had a pronounced reaction to temperature as suggested by the correlation analysis (Figures 1 E, F). Nevertheless, the reaction to temperature differed between the inner and outer parts of sapwood. Sap flow velocity in the outer part of sapwood correlated with temperature during most of the dormant period with a short phase of unresponsiveness in January. Periods when SFV of inner sapwood was unresponsive to temperature were longer as a significant effect of temperature was observed in scattered intervals around November, February and March.

Discussion

The variation of SFV (Figure 1 A) portrayed the intra-annual differences in physiological activity of the studied Norway spruce. In the spring of 2014, cessation of dormancy, apparently, has occurred before the measurements of sap flow were started as shown by the intermediate values of SFV. The highest SFV was observed before the bud break in April that might be explained by the transport of stored nutrients from roots to facilitate the early growth of shoots (Dambrine et al. 1995). High rates of sap flow were also observed at the beginning of summer, when assimilation is the most intense (Lundmark et al. 1998). After mid-July when temperature reached its maximum, SFV became slower that might be explained by the decreased stomatal conductivity caused by water deficiency (Lu et al. 1995) as suggested by the decreasing soil water potential (Figure 1 B). Although soil water potential re-established around the 15th of August, the increase of SFV occurred only after about two weeks, suggesting delayed response to watering. During the September-October period, SFV gradually decreased (Figure 1 A) marking the cessation of vegetation period. Apparently, in the season of 2014–2015, the dormant period of studied Norway spruce extended from mid-November to early March, as shown by low SFV. Still, daily variation in SFV was observed as a minimal ascent of sap is needed to compensate winter desiccation (Sakai 1970) and sap movement is necessary to regulate the concentration of antifreeze compounds (Essiamah and Eschrich 1995, Gupta and Deswal 2014).

During the studied period, most of the sap was conducted by the inner part of sapwood (Table 1) that might be related to the hydraulic architecture of tree (Tyree and Ewers 1991). On a mature spruce, higher proportion of needles occur on the older shoots, which are receiving water by the older (inner) part of sapwood (Tyree and Ewers 1991, Sellin 1994). The older needles also might transpire more water due to longer period of open stomata (Sellin 2001) explaining higher SFV. Although the seasonal trends in SFV was similar between the inner and outer parts of sapwood (Table 1), the moving correlation analysis (Figure 1 D) suggested that functioning of the inner and outer sapwood might differ, particularly during the dormant period, when non-significant correlation was observed between them. In addition, a down-going sap flow, observed in the inner and outer part of sapwood for a few days during the dormant period (Figure 1 A), suggested that a circulation of sap might be maintained in xylem, likely by the deployment of different parts of the stem, probably due to burdened transpiration (Jarvis and McNaughton 1986).

Temperature mainly had positive effect on SFV (Table 1) as expected for trees growing in the hemiboreal conditions, where the available warmth affects growth. A positive effect of soil water potential was also observed (Table 1) as the availability of water influences transpiration and hence the ascent of sap (Jarvis and McNaughton 1986, Lu et al. 1995), though water potential did not drop below 60 % (-147 hPa) of the field capacity (Saxton and Rawls 2006). Apparently, the effect of availability of water becomes considerable even at much lesser decrease of the water potential. A negative effect of temperature on daily variation of SFV was observed during the vegetation period (Figures 1 E, F) that might be explained by an increased transpiration and closure of stomata to prevent water deficit (Jarvis and McNaughton 1986) or by the burdening of assimilation by high temperature (Salvucci and Crafts-Brandner 2004). The negative effect of soil water potential (Figures 1 E, F) at that time is more difficult to explain. Since the soil water potential expressed low daily variation (Figure 1 B), the negative correlations also might be coincidental. The positive correlations between SFV and temperature during the dormant period (Figures 1 E, F) might be explained by the winter transpiration (Sakai 1970, Baig and Tranquillini 1980). Sap flow in the inner part of sapwood showed longer periods of unresponsiveness, suggesting that the outer sapwood is more involved in sap transport in winter. Nevertheless, the observed relationships might not be completely representative for the entire tree as SFV may differ across the radial profile of stem (Fiora and Cescatti 2008), but the measurements were done only at one radius.

Conclusions

Sap flow of different intensity in the sapwood of the studied Norway spruce was observed throughout the year and it has been mainly driven by temperature, although the effect of soil water potential also had been pertinent. The daily variation of sap flow intensity was mainly positively affected by temperature. Nevertheless, during the warmest period in summer, the negative effect temperature suggested heat-induced stomatal closure and hence burdening of assimilation. Low intensity sap flow was detected also during the winter months; still SFV showed a clear reaction to temperature, suggesting that the spruce has been responsive and hence physiologically active throughout the dormant period. In addition, a sap circulation in sapwood during the dormant period has been suggested by the descending flow.

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