

# Responses of species-specific sap flux, transpiration and water use efficiency of pine, spruce and birch trees to temporarily moderate dry periods in mixed forests at a dry and wet forest site in the hemi-boreal zone

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## Abstract

Predicted climate changings can affect hemi-boreal forests especially for soil conditions with low water-holding capacity and susceptibility to soil water deficits. In our study, species-specific sap flux, transpiration and water use efficiency of growth (WUE) were investigated at a mixed hemi-boreal forest ecosystems, especially during temporary moderate dry periods in the main growing season. Therefore, two representative forest sites with different drought susceptibility were selected in Northwest-Lithuania. The aim of our investigations was to identify the responsible factors influencing transpiration and WUE from Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* L. H. Karst.) and birch (silver birch: *Betula pendula* Roth. and downy birch: *B. pubescens* Ehrh.) during temporary drought incidents at a water-limited, oligitrophic sand dominated forest site and at a water saturated, mesoeutrophic organic peat forest site for the whole vegetation period and two moderate short-term drought incidents in 2016. During the dry periods Norway spruce trees exhibited lowest sap flux compared to Scot pine and birch while similarly showing highest WUE. Up-scaled to a virtual pure stand none of the species were differing in species specific transpiration. Thus, we found no evidence for extended drought sensitivity of Norway spruce at the water limited site during the first investigation year. Sap flux of Scots pine trees was more or less constantly high during the main growing season and the dry periods at both plots, while WUE was quite low during the “dry periods”. Thus, we assume that Scots pine trees are less affected by temporarily drought events than Norway spruce. Birch trees exhibited significantly highest sap flux during dry periods at the water limited site whereas quite low WUE was not differing between sites. Thus, birch may compete with Scots pine trees at the study sites in terms of water consumption and growth in future.

**Key words:** Mixed pine-spruce-birch forests, Short-term drought, Species specific transpiration, Water use efficiency, Xylem sap flow

## 1. Introduction

The response of tree transpiration, carbon assimilation and subsequently growth to drought incidents is an important aspect for the future forest functioning. Tree specific composition and age distribution has large influence on stand water budget (Cienciala *et al.*, 1994). The response of mixed forests to the effects of a changing climate is more diverse than that in monospecific forests (Larson, 1992; Pretzsch *et al.*, 2015) and knowledge on growth and dynamics especially of the slow growing and long-lived mixed boreal forest ecosystems is limited (Ge *et al.*, 2011). Higher frequency of climatic extremes is a widely recognised result of climate change (Karl *et al.*, 1995; Bonan, 2008; IPCC, 2013). There is rising evidence that

even without severe climatic incidents, extremes in rainfall distribution during the growing season are becoming more uneven with specific regional differentiations (Cienciala *et al.*, 1997; Bonan, 2008; Sellin *et al.*, 2014). In boreal and northern temperate regions of Europe rising air temperature and precipitation is predicted (Lindner *et al.*, 2010; Kont *et al.*, 2003). Long-term analysis of meteorological data for a gradient from the coastal to eastern inner Lithuania revealed an increase in annual air temperature and precipitation and rising variation in monthly patterns during the period 1981–2010 compared to 1950–1980 (Augustaitis *et al.*, 2007, 2014). In Lithuania, at the end of the 20th century air temperatures during winter months increased as well as the incidence of drought events in spring and late summer (Bukantis *et al.*, 2001; Vitas and Erlickyte, 2008; Vitas and Žeimavičius, 2006).

Changes in the atmosphere-canopy-soil system e.g. elevated air temperature and decreased soil water availability in spring or summer, or short term increases of air temperatures within cold winters can strongly affect forest growth (Bonan, 2008; Ge *et al.*,

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2011). Different growth response to the amount of precipitation in spring months for Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) H.Karst) particularly in mature canopies (Oberhuber *et al.*, 2015; Schuster and Oberhuber, 2013; Swidrak *et al.*, 2013, 2014) is reported, i.e. growth of Scots pine was favoured by April-May precipitation while Norway spruce growth rather depended on May-June precipitation.

The widely distributed pioneer species Scots pine is known as being tolerant to moderate drought effect (Boratynski, 1991; Cregg, 1993; Cregg and Zhang, 2001; Irvine *et al.*, 1998; Matias and Jump, 2012; Lebourgeois *et al.*, 2012; Eilmann and Rigling, 2012). Its drought sensitivity is depending on site related factors especially on relief, topography and soil characteristics such as rooting and water holding capacity of soils (Rigling *et al.*, 2002; Weber *et al.*, 2007; Lévesque *et al.*, 2014a).

Norway spruce is an intermediately shade tolerant species widely spread in Europe sensitive to drought episodes (e.g. Lebourgeois *et al.*, 2010; Lévesque *et al.*, 2013; van der Maaten-Theunissen *et al.*, 2013), while concurrently its vulnerability is increasing in monocultures in synergy with subsequent biotic attacks (Allen *et al.*, 2010; Hart *et al.*, 2014; O'Connor *et al.*, 2015). Recent research of Lévesque *et al.* (2014a) confirmed highly sensitive growth reactions of Norway spruce to drought events and mentioned that these effects are mediated strongly by soil water recharge in winter and thus water availability at the beginning of the growing season as well as by nutrient availability (Lévesque *et al.*, 2014b, 2016). Severe spruce mortality recently has been documented in Eastern Europe, in the Baltic region and the European part of Russia (Ukraine, Belarus) (Arkhipova, 2013; Vasiliauskas, 2013; Sazonov *et al.*, 2013; Usitsky, 2013; Kharuk *et al.*, 2015). Kharuk *et al.* (2015) found that Norway spruce mortality in Belarus was mainly caused by increased air temperature and drought always in combination with pests which was explained as a result of low adaptation, thus, the authors postulated the necessity of Norway spruce replacement. In terms of a changing climate, simulation models suggest a reduced suitability of Norway spruce by the end of this century in Europe (Feltona *et al.*, 2010).

A widespread early successional pioneer species in the temperate and boreal forests of Europe is birch, which is generally known to be fast growing and exceptionally tolerant to spring frost, low air temperatures and nutrient deficiency, growing at both the wet and the dry limit of forest distribution (Ellenberg, 2009; Hynynen *et al.*, 2010). Birch genotypes are known to differ in plasticity and in their adaptation to drought (Aspelmaier and Leuschner, 2004). Two commercially important birch species occur naturally in Europe: silver birch and downy birch (*Betula pendula* Roth. and *B. pubescens* Ehrh.). Silver birch prefers moderate fertile to fertile rather dry sandy and silty till soils and fine sandy soils and is generally not favoured by flooding whereas downy birch has intermediate site requirements ranging from compact clay or silt soils to poorly aerated wet peatlands (Sutinen *et al.*, 2002). Most of the birch resources in the Baltic and Nordic countries are growing at moderate fertile or fertile forest sites in mixed stands as birch prefers similar sites to Scots pine in Northern Europe (Sutinen *et al.*, 2002; Ge *et al.*, 2011) and thus, a typical species composition is a birch

admixture in stands dominated by Scots pine or Norway spruce (Johansson, 2003; Hynynen *et al.*, 2010).

Predicted climate changings can impair these forests especially for soil conditions with low water-holding capacity and susceptibility to soil water deficit (Kellomäki *et al.*, 2008). Ge *et al.* (2011) found a different species response to water depletion in mixed spruce-pine-birch and monoculture forests in Finland and emphasised the importance of appropriate species mixtures and thinning adapted to site conditions. Reduced precipitation and elevated temperatures had only small effects on Scots pine and birch species but large impact on Norway spruce in boreal forest in Finland (Briceño-Elizondo *et al.*, 2006).

Water-use efficiency (WUE) is a key plant response mechanism to moderate to severe soil water deficits. Generally WUE refers to the ratio of fixed carbon to transpired water in plants. WUE was originally defined as CO<sub>2</sub>-uptake per transpiration rate or photosynthetic rate per transpiration rate (von Willert *et al.*, 1995; Tang *et al.*, 2006), but WUE can also refer to the ratio of produced biomass to the rate of transpiration. Thus, WUE can be used as a stress indicator for mature trees and it was found that WUE of trees is increasing with the extent of stress. Long-term investigations of intrinsic water use efficiency for fir and Norway spruce indicate an increase which is explained not only by enhanced CO<sub>2</sub> concentrations (Keenan *et al.*, 2013; Penuelas *et al.*, 2011; Wullschleger *et al.*, 1995), but mainly by enhanced adaptive capacity of species to face stressors by augmenting WUE (Beer *et al.*, 2009; Sanders *et al.*, 2016).

The aim of this study was to detect the whole tree xylem sap flow and species-specific traits regarding transpiration of mature trees of Scots pine, Norway spruce and silver and downy birch grown in soils with different water conditions. Regarding tree transpiratory traits, we hypothesize that Norway spruce was more sensitive to moderate short-term drought at a water-limited site, but birch was more sensitive at a water-saturated site, whereas Scots pine was insensitive at both sites.

To test the hypothesis, we attempted to assess the species-specific responses of xylem sap flow, canopy conductance for water vapour ( $G_c$ ), and WUE of growth to the intra-annual differing climatic conditions throughout the growth season, and identify the responsible factors influencing species-specific transpiratory responses in mature trees of Scots pine, Norway spruce, and birch grown in two typical edaphically differing forest sites with water-limited and water-saturated soils in the hemi-boreal forests of Lithuania.

## 2. Material and methods

### 2.1 Study sites and stand conditions

Investigations were conducted in the strict reserve area in the Northwest part of the Aukštaitija National Park (682 m a.s.l.) located in eastern Lithuania (for details see: Augustaitis *et al.*, 2007, 2008, 2010, 2018). Two hemi-boreal natural to semi-natural mixed conifer-deciduous forest sites (*Pinus sylvestris* L. *Picea abies* L. H. Karst., *Betula pendula* Roth., *Betula pubescens* Ehrh.) growing on different soil types differing in water availability and groundwater connection (Table 1) representing the area were selected.

Temporary water-limited, oligotrophic mineral soil forest site:

at the integrated monitoring station IMS (monitoring station plot, MS plot), an intensively monitored site established in 1993 and a part of the ICP-forest network, located on a side glacio-aquatic accumulation with sand, gravel and stones transferring into fluvio-glacial terrace delta plain with decreasing fine sand typical for mixed coniferous forest in this region. Soil type is a deep (>120 cm) haplic arenosol, with a high proportion of sand (~90%) within the rooting zone of ~80 cm soil depth, moderately acid with a saturated water content of ~20% in the rooting zone, groundwater connection is at about 300 cm (Table 1). Dry and wet bulk density amount to ~1.5 g cm<sup>3</sup> and ~1.6 g cm<sup>3</sup> soil in the main rooting zone (Table 1). Effective field capacity (FC<sub>eff</sub>) for the main rooting zone is 145 mm.

Water-saturated, mesoeutrophic organic peatland forest site, with groundwater level at about 50 cm soil depth (groundwater plot, GW plot). Soil type is a deep (>80 cm) terric histosol consisting mostly of low moor deep eutrophic peat soil (Table 1). Dry and wet bulk density is differing (0.19 and 0.87 g cm<sup>3</sup> soil), and as the major organic material is connected to the groundwater table the poorly drained site is mostly water saturated (Table 1). The rooting zone reaches down to 40 cm soil depth with a water content of ~400–500% (Gulbinas and Samuila, 2002). FC<sub>eff</sub> for the main rooting zone is determined to 155 mm, the distance of rooting zone to water table is ~10 cm. The concept of field capacity, as usually applied for mineral soils, is not very useful for peat soils as the groundwater table is relatively near to the soil surface and the matric suction corresponding to equilibrium is lower than usually measured for mineral soils (Paavilainen and Päivänen, 1995). For a near vicinity of rooting zone and groundwater table a capillary rise of soil water of 3–5 mm per day even during drought in the upper soil part can be assumed, thus, limitation of water supply is expected only for extreme drought incidents at this plot (Deutsche Bodenkundliche Kartieranleitung, 2005).

Both flatland forest sites are situated in the vicinity of the villages Rugsteliskis and Mincia in the basin of the Versminis river (Basin area 102 ha; 160–189 m a.s.l.; longitude – 26°03'20" – 26°04'50", latitude – 55°26'00" – 55°26'53") and

are in a distance of about 4.5 km to each other.

The hemi-boreal sites are both stocked with over-mature (>120 years), multi-aged and multi-layered mixed conifer-deciduous forest dominated by pine accompanied with Norway spruce and birch belonging to the *Pinetum vaccinio-myrtilosum* forest type (Augustaitis *et al.*, 2008). Main dendrometric characteristics of the considered mixed-forest sites are described in detail in Augustaitis *et al.* 2018.

In order to provide comparable results within the natural, different aged mixed forest sites, at each investigation plot (MS, GW) three subplots were selected (for tree parameters see Table 2). The classification of the social position of the tree in the forest stand was conducted according to Kraft (1884). At both plots each subplot was sized of about 300–500 m<sup>2</sup> and comprised pre-dominant (KRAFTclass 1) and similar sample trees (concerning different tree parameters, Table 3) of each species, which were growing in a group with other species. According to their different niches silver birch was available at the MS plot and downy birch at the GW plot was chosen for the examination (in the following: at MS silver birch, at GW downy birch).

In order to determine temporary dry periods, we used meteorological, soil water and plant related parameters (see 3.4.4)

## 2.2 Meteorological data

Meteorological data were monitored continuously in hourly time resolution at the Aukstaitija IMS more than 20 years (for details: Augustaitis *et al.*, 2008, 2010). Meteorological data are assumed to be valid for both investigation plots (MS, GW).

The long-term (20 years) average annual air temperature is  $6.9 \pm 0.8^\circ\text{C}$ , the average annual precipitation is  $680 \pm 100$  mm and  $13.2 \pm 0.6^\circ\text{C}$  and  $420 \pm 94$  mm for the growing season of 189 days in average. Such meteorological conditions are typical to a cold continental climate with high humidity and abundant precipitation as well as high air temperatures especially during the summer months (June–August; mean monthly precipitation ~80 mm, temperature  $16.4^\circ\text{C}$  per month) and low precipitation and air temperature in the winter months (December–March; mean monthly precipitation ~40 mm, air temperature  $-3.5^\circ\text{C}$ ).

**Table 1.** Soil characteristics at the monitoring station plot and groundwater plot at the examination site in Aukstaitija National Park.

Soil horizon	Monitoring station plot				Groundwater plot			
	O	AB	B	C	O	H1	H2	H3
Depth (cm)	0–8	9–24	25–120	>120	0–9	10–45	46–80	>80
Saturated water content (%)		21.6	20.7					
Water content (%)		5.6	5.7			369	522	
Dry bulk density (g cm <sup>-3</sup> )		1.4	1.5			0.19	0.17	
Wet bulk density (g cm <sup>-3</sup> )		1.5	1.6			0.87	1.03	
Sand (%)		90	92					
Silt (%)		6	5					
Clay (%)		4	3					
pH <sub>KCl</sub>		4.4	4.9			6.7	6.7	
Soil type	Haplic arenosol,				Terric histosol			
Rooting zone (cm)	~ 80				~ 40			
Water table (m)	~ 3				~ 0.5			
Effective field capacity (mm)	145				155			

### 2.3 Canopy tree parameters

Tree and growth parameters (DBH, basal area, tree height, volume/stem radial increment, basal area per hectare, tree age) were monitored annually on permanent observation plots at both investigation plots (MS, GW), since more than 20 years and embedded in the ICP-forest monitoring network (Augustaitis *et al.*, 2008; Vuorenmaa *et al.*, 2017).

Sample tree parameters at the selected subplots were monitored for pre-dominant (Norway spruce also dominant) trees per species for each site ( $n=7-17$  trees, including sample trees, Table 2) and for the selected sample trees within the subplots (Table 3).

Stem radial increment growth was measured weekly using mechanical manual band dendrometers. Additionally, since April 2016, stem increment was continuously monitored with high-resolution electronical logging band dendrometers (DRL26, EMS Brno, Czech Republic). In September, the prolongation in stem circumference of the monitored trees was detected. Based on this, stem increment in tree diameter/radius was computed. Tree volume was calculated as function of tree basal area, stem factor and height. Based on this methodological approach, tree volume increment was determined by multiplying increment in stem basal area with tree height and stem factor, which indicated the shape of the tree. The latter was estimated in response of tree height and diameter made for Scots pine trees to about 0.45, for Norway spruce trees about 0.51 and birch trees about 0.43 (for details see Augustaitis *et al.*, 2018).

In order to up-scale species specific transpiration from the xylem sap flow measurement of the sample trees to the canopy scale of “virtual” pure stands, mean basal area is estimated assuming that there would be pure stands of each Scots pine, Norway spruce and birch for the MS and the GW plots.

### 2.4 Soil moisture

Soil moisture tension (SMT) was determined weekly at 10 cm, 20 cm and 40 cm soil depth at both sites for each forest site ( $n=4-6$ ; WATERMARK, Eijkelkamp Soil and Water).

In order to recheck SMT measurements at the MS plot and to get continuous information about soil water supply at the plots, we used a model to estimate plant available soil water (PAW). PAW is characterised as the soil water that can be used by plant roots. PAW was modelled by a simplified regression approach based on meteorological data and BROOK90-modelled evapotranspiration data sets (Bender *et al.*, 2015). The regression model was established, calibrated and validated with data sets of various mature deciduous and coniferous trees. Meteorological data and the  $FC_{eff}$  for the respective soil type are necessary to run the model and generate PAW on a daily or hourly basis (data not shown; Baumgarten M., for details see Bender *et al.*, 2015; for BROOK90 see Federer 1995; Federer *et al.*, 1996; Hammel and Kennel, 2001; Raspe, 2012). As not suitable for soil conditions with groundwater connection, the PAW model was not applied to the GW plot.

**Table 2.** Tree and growth parameters at the subplots selected at the monitoring station (MS) plot and groundwater (GW) plot at the examination site in Aukstaitija National Park. Mean values  $\pm$  standard deviation. Basal area “pure stand”: assuming pure stand conditions for each species and plot based on species composition and tree parameters at subplots.

	DBH (cm)	Basal area (cm <sup>2</sup> )	Tree height (m)	Tree volume 2016 (m <sup>3</sup> )	Increment volume 2016 (dm <sup>3</sup> )	20-year average stem radial increment (mm)	Basal area of “pure stand” (m <sup>2</sup> ha <sup>-1</sup> )	Mean tree age (years)
MS plot								
Pine (n=17)	33.9 $\pm$ 4.8	926 $\pm$ 292	29 $\pm$ 2	1.2 $\pm$ 0.4	23 $\pm$ 7	1.6 $\pm$ 0.2	34	100
Spruce (n=7)	26.1 $\pm$ 6.4	560 $\pm$ 275	23 $\pm$ 4	0.7 $\pm$ 0.5	21 $\pm$ 9	3.4 $\pm$ 0.2	26	50
Birch (n=17)	29.6 $\pm$ 5.1	709 $\pm$ 346	29 $\pm$ 3	0.9 $\pm$ 0.4	15 $\pm$ 8	1.7 $\pm$ 0.4	35	60
GW plot								
Pine (n=10)	38.7 $\pm$ 4.7	1193 $\pm$ 312	28 $\pm$ 3	1.5 $\pm$ 0.5	14 $\pm$ 5	0.7 $\pm$ 0.1	41	140
Spruce (n=16)	37.6 $\pm$ 9.6	1192 $\pm$ 597	28 $\pm$ 4	1.6 $\pm$ 0.9	27 $\pm$ 19	2.7 $\pm$ 0.5	32	70
Birch (n=13)	32.2 $\pm$ 5.8	844 $\pm$ 313	27 $\pm$ 3	1.0 $\pm$ 0.5	16 $\pm$ 14	1.3 $\pm$ 0.3	41	80

**Table 3.** Sample tree parameters at the monitoring station (MS) plot and groundwater (GW) plot at the examination site in Aukstaitija National Park. Sapwood area was determined according to site specific equations.

	DBH (cm)	Basal area (cm <sup>2</sup> )	Tree height (m)	Tree volume 2016 (m <sup>3</sup> )	Increment volume 2016 (dm <sup>3</sup> )	Bark thickness (cm)	Crown projection (m <sup>2</sup> )	Sapwood depth (cm)	Sapwood area (cm <sup>2</sup> )
MS plot									
Pine (n=7)	33.0 $\pm$ 3.6	864 $\pm$ 180	28.5 $\pm$ 2.1	1.06 $\pm$ 0.24	19.7 $\pm$ 3.1	2.1 $\pm$ 0.1	11 $\pm$ 1	5.6 $\pm$ 0.4	421 $\pm$ 92
Spruce (n=5)	26.6 $\pm$ 7.5	599 $\pm$ 370	22.7 $\pm$ 4.6	0.71 $\pm$ 0.52	23.2 $\pm$ 9.2	1.0 $\pm$ 0.0	12 $\pm$ 4	3.6 $\pm$ 0.9	258 $\pm$ 160
Birch (n=7)	31.2 $\pm$ 6.2	794 $\pm$ 290	20.2 $\pm$ 6.2	1.00 $\pm$ 0.42	17.4 $\pm$ 6.9	2.4 $\pm$ 0.6	14 $\pm$ 5	7.6 $\pm$ 1.4	464 $\pm$ 171
GW plot									
Pine (n=4)	39.1 $\pm$ 5.2	1220 $\pm$ 340	28.3 $\pm$ 2.4	1.50 $\pm$ 0.53	12.4 $\pm$ 4.8	2.4 $\pm$ 0.4	10 $\pm$ 3	6.8 $\pm$ 0.9	596 $\pm$ 166
Spruce (n=5)	40.4 $\pm$ 6.9	1320 $\pm$ 402	28.0 $\pm$ 2.4	1.74 $\pm$ 0.56	43.7 $\pm$ 19.8	1.0 $\pm$ 0.0	16 $\pm$ 4	5.3 $\pm$ 0.8	568 $\pm$ 173
Birch (n=5)	36.7 $\pm$ 4.5	1071 $\pm$ 252	25.6 $\pm$ 1.8	1.34 $\pm$ 0.36	24.7 $\pm$ 17.2	2.3 $\pm$ 0.6	15 $\pm$ 5	9.4 $\pm$ 1.2	680 $\pm$ 155

## 2.5 Xylem sap flow

Xylem sap flow measurements were conducted by applying the heat ratio method (Burgess *et al.*, 2001) using sap flow meter (SFM1) from ICT International (Australia). Sap flow was measured at 5–7 sample trees for each Scots pine, Norway spruce and birch to determine tree crown and species specific stand transpiration at the water-limited MS plot and the water saturated GW plot (Table 3).

For sap flow measurements pre-dominant sample trees (KRAFT class 1) of each species within the subplots were selected at the MS and the GW plot (see 2.1). The selected trees exhibited similar DBH, basal area, tree height, crown projection, volume and sapwood area (Table 3) and the mean tree size was in the range of the monitored canopy tree size (see Table 2). As availability of Norway spruce in vicinity was limited at the subplots at the MS plot, also sample trees of KRAFT class 2 (dominant) were selected, therefore, mean size of selected Norway spruce trees was lower compared to other species and to the GW plot (Table 3).

Sap flow sensors were installed at approximately 120 cm stem height in N-exposition and sheltered with aluminium foil caps. Bark thickness was measured for each sample tree by using a bark depth gauge, sensor needles measuring at two different depths were inserted into the sapwood with a bark depth of 10 mm (bark removed or spacer set). Sapwood cores were taken with a conventional coring tool at breast height from 10 trees per species and plot to determine wood properties (fresh, dry weight; thermal diffusivity) and to measure sapwood thickness by dye indication or microscopic analysis (acc. to SFM1 manual, ICT international). Sap flow monitoring has started in the mid of April of 2016 using a 15 min measuring interval. 15 min measuring intervals were summarized to hourly values as basis for all further calculations.

Sapwood area for the sample trees was determined by equations for each species, derived by correlation of the basal area and the sapwood depth of the analysed trees. Additionally, the results were related and counter-checked to results from literary sources. Sap flux for the entire cross-sectional area was calculated linearly assuming zero sap flux at the sapwood-heartwood boundary (Fig. 4).

The SFM sensors store data as raw temperature measurements. For conversion to sap velocity, sap flow and total plant water use these data were computed using ICT International Sap Flow Tool Software (Sap Flow Tool software for HFD and HRMI, ICT international).

For each sample tree xylem sap flux was calculated as flow rate per unit basal area and is presented in mean values of sap flux for each species and considered site (ml per cm<sup>2</sup> basal area per time span).

Crown transpiration is determined by multiplying the mean daily sap flux per basal area per sample tree. Species-specific stand transpiration (in l m<sup>-2</sup> ground surface area) is calculated from mean values of crown transpiration for each species, the number of days and the stand basal area per hectare assuming pure stand conditions for each species and plot for different time intervals (Baumgarten *et al.*, 2014, Table 2).

## 2.6 Canopy conductance

For calculating  $G_c$ , the sap flow-derived crown transpiration rate of trees was related to the respective foliage area (Matyssek *et al.*, 2009; Kühn *et al.*, 2015), yielding unit foliage area basis for canopy transpiration ( $E_c$ ). Foliage area was calculated according to Sidabras and Augustaitis (2015) whose evaluations for Scots pine, Norway spruce and birch were in concordance with other relations of different tree parameters in the literature (e.g., for pine: Delzon *et al.*, 2004; Mencuccini and Grace, 1994; for spruce: Burger, 1950; Köstner *et al.*, 1998; Patzner, 2004; for birch: Repola *et al.*, 2007). Sap flux calculations referred to foliage area are based on projected leaf area for birch and on whole foliage area for coniferous species according to Niinemets *et al.* (2001). Finally,  $G_c$  was calculated from  $E_c$  versus leaf-air mole fraction difference of water vapor ( $\Delta w$ ) as  $G_c = E_c / \Delta w$ , where  $\Delta w$  is derived by  $\Delta w =$  water vapour pressure deficit (VPD) / air pressure  $p$ , presuming leaf temperature equals to air temperature (Tang *et al.*, 2006) as an approximation at the crown level. Time lags between the onset of transpiration in the canopy and xylem sap flow at breast height were compensated for by mathematically synchronizing both time courses through matching at the instant of sunrise, when  $E_c$  became initiated (Matyssek *et al.*, 2004, 2008). The onset of  $E_c$  was deduced from the onset of global radiation in combination with  $\Delta w > 0$ .

## 2.7 Water use efficiency of growth

In our study, we used the WUE of growth, defined as the ratio of biomass production to the transpired water (Cienciala *et al.*, 1994, Forrester *et al.*, 2015). Thus, WUE of growth was calculated for each sample tree as daily cm<sup>2</sup> stem radial increment divided by the tree transpiration for different time intervals (monthly, dry periods, growing season; WUE, cm<sup>2</sup> stem radial increment per liter of transpired water per tree per time interval).

## 2.8 Statistical analysis

R, a free available language and environment for statistical computing, was used for statistical analysis (R Core Team, 2014; Rstudio Team, 2015). In advance to all statistic tests we used Barlett- and Filigner-Killeen test of homogeneity of variances. Shapiro-Wilk normality test was used to test residuals. ANOVA was applied to analyse for variances of different factors. Modell interactions between various factors were tested for sap flux (plot, species, time period, species:time period). Tukey Post Hoc test was applied to determine significancies.

## 3. Results

### 3.1 Meteorological conditions

Meteorology at the investigation site (Aukstaitija IMS) was monitored intensively since 1980. Augustaitis *et al.* (2018) presented a long-term data set establishing temporal changes in meteorology, which were confirming a statistically significant increase in mean annual air temperature and a significant trend of decreasing precipitation most evident during September and December.

2016 was a year without meteorological extremes, however, it has to be considered that the previous year 2015 was

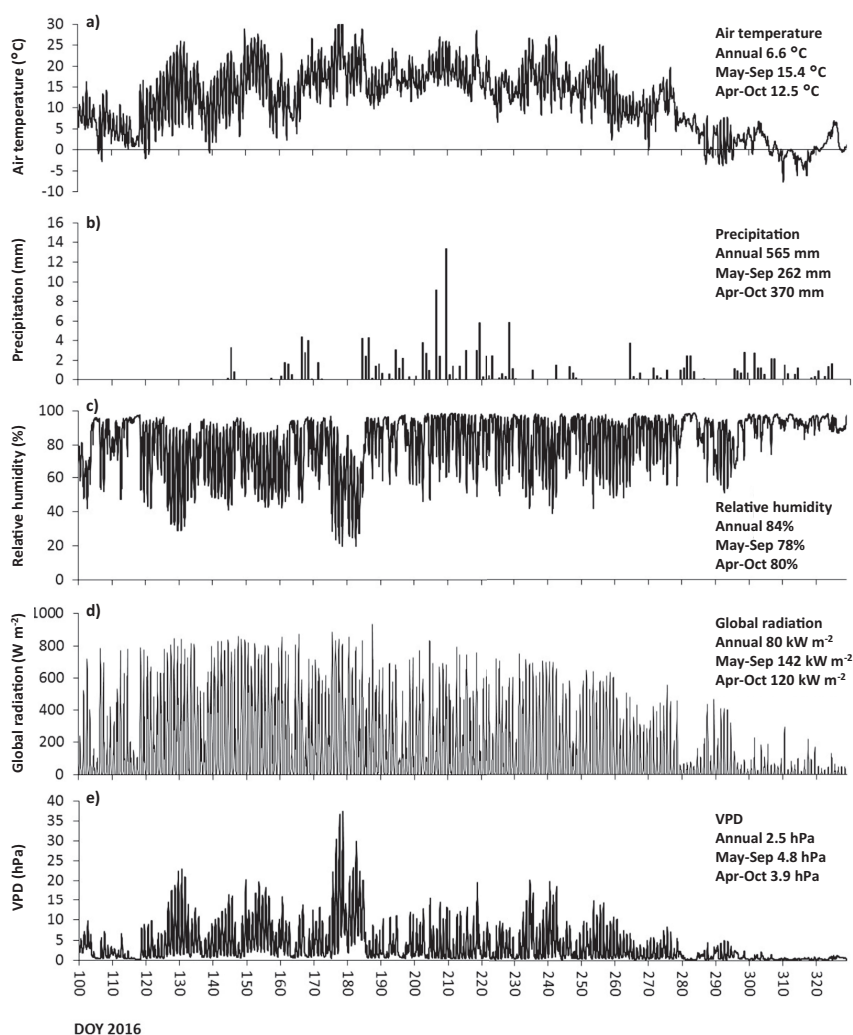
characterized by extremely low yearly precipitation sums, especially during the autumn and winter month (Augustaitis *et al.*, 2010, 2018). Low precipitation and air temperatures were characteristic for January to March 2016 (data not shown), quite high air temperatures and precipitation occurred from June to August 2016 (Fig. 1). Seasonal (April-September) and annual means were slightly differing from the long-term means (20 years), seasonal air temperatures were 15% higher and seasonal and annual precipitation was 20% and 17% lower compared to the 20-years long term means (data not shown, Augustaitis *et al.*, 2018). The lowest mean air temperatures were recorded in January, and slightly higher air temperatures were recorded for February and March 2016 compared to the long term means. Precipitation was extremely low from February to May 2016 (February: 9.5 mm, March: 0.3 mm, April: 0 mm, May: 6.7 mm), followed by rather high and continuously occurring precipitation from July (121 mm) until the mid of August (79 mm) with quite high air temperatures (Fig. 1). From mid of August until the early October 2016 precipitation amounted to only 25 mm (Fig. 1).

### 3.2 Soil water conditions

$FC_{eff}$  of the main rooting zone at the MS plot was already reduced at the beginning of the vegetation period because of the low precipitation during the winter month 2015/2016 and the complete lack of rainfall from April until the end of May (Fig. 3), whereas we assume no soil water limitation at the GW plot.

SMT at the MS plot was rather high ( $\sim 10 - 40$  kPa) in the upper soil horizons (10 cm, 20 cm) of the haplic arenosol until the end of August and was then declining down to about 140 kPa until October (Fig. 3). At 40 cm soil depth, SMT continuously decreased after the start of the vegetation period down to  $\sim 100$  kPa in June and declined to about 120 kPa after a short dry period at the beginning of July. Due to permanent precipitation until mid of August SMT was rising slightly but declined to  $\sim 160$  kPa during a further dry period in September. From October with the onset of rain and low temperatures, and thus the limitation of tree transpiration SMT was increasing at all soil depths to high values (near field capacity) again (Fig. 3).

In summary, soil moisture tension at 40 cm soil depth declined to low values indicating limited water supply in the deep sandy arenosol during the main growing period, but water supply in



**Fig. 1.** Meteorological parameters monitored at the meteorological station on the monitoring station plot assumed to be valid for the examination area. All the values are in hourly time resolution. a) air temperature, b) precipitation, c) relative humidity, d) global radiation and e) water vapour pressure deficit (VPD).

the upper soil horizons was limited only at the end of the main growing season in September.

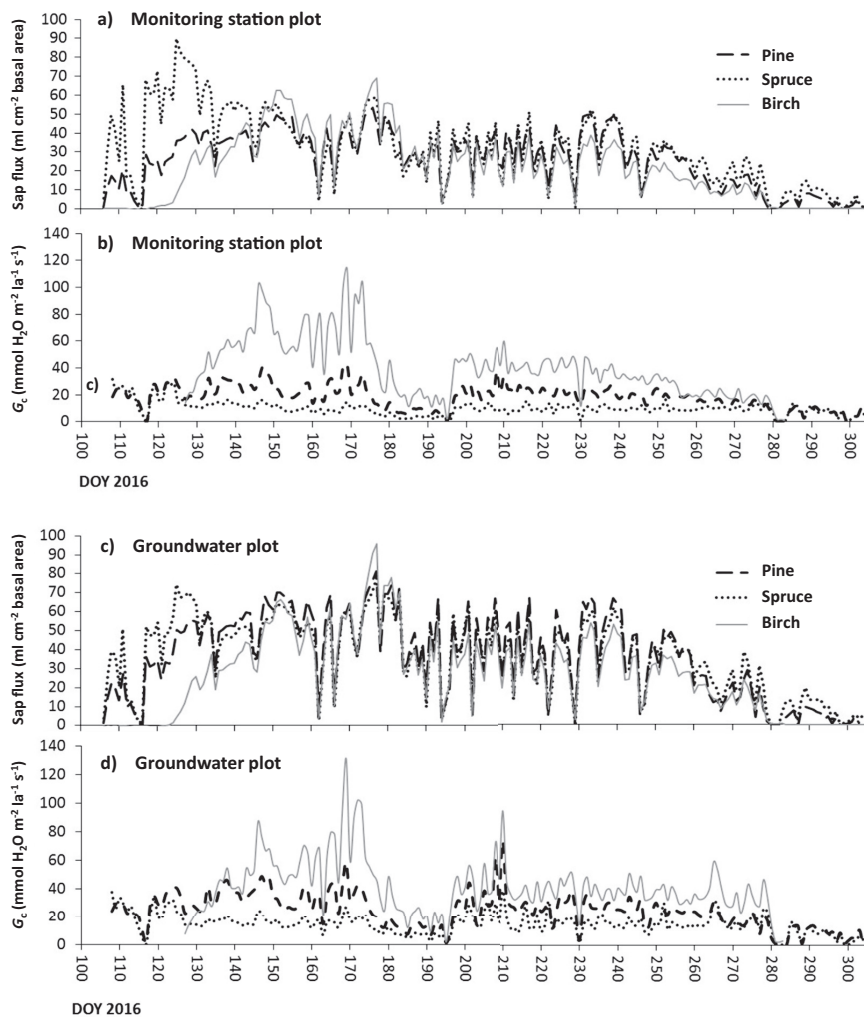
Weekly assessed SMT measurements were consistent with PAW modelled on a daily time resolution with a simplified regression model approach (described in Bender *et al.*, 2015), resulting in a quite high regression coefficient  $R^2$  of 0.72 for the considered MS plot (Fig. 3).

At the GW plot the soil moisture tension was quite high at all sample depths (~1.5 – max. 18 kPa), indicating saturated water conditions during the entire season. Whereas SMT was decreasing slightly to still lower values of 10–18 kPa at the soil depth of 10 cm and 20 cm during the dry period in September, at 40 cm soil depth SMT was persistently high during the entire season (Fig. 3). This seasonal course measured for the GW plot is in consistency with the soil parameters measured for the terric histosol, indicating that no water limitation is assumed for the deep low moor peat soil with a main rooting zone of ~40 cm soil depth and groundwater connection is at ~ 50 cm soil depth. A capillary rise of soil water of 3–5 mm per day into the main rooting zone will provide sufficient water supply even during drought in the upper soil part (Deutsche Bodenkundliche Kartieranleitung, 2005).

### 3.3 Tree parameters

Mean DBH, tree basal area, tree volume and stand basal area were higher for each species at the subplots at GW compared to MS (Table 2). Norway spruce was varying in ages and thus, in DBH, showing lower increment volume at the MS plot compared to the GW plot. Norway spruce trees at the MS plot exhibited the lowest DBH, tree/stand basal area and tree height, the lowest volume but quite high stem increment compared to Scots pine and birch, indicating heterogeneous stand structure with a proportion of lower age classes. At the GW plot, DBH, tree basal area and tree height were similar for Scots pine and Norway spruce, but lower for birch (Table 2). The long-term (20 years) average stem radial increment is higher at the MS plot than at the GW plot for all tree species, with Norway spruce exhibiting the highest increment at both plots. Tree parameters of the selected sample trees (Table 3) indicate their pre-dominant/dominant position compared to the tree ensembles at the subplots.

Main stem radial increment for Scots pine and Norway spruce each occurred between the end of May (23rd May) until the end of August (22nd), for birch increment growth started about one week later (31st May) and finished earlier around the beginning



**Fig. 2.** Mean daily xylem sap flux and canopy conductance  $G_c$  at the monitoring station plot (a, b) and the groundwater plot (c, d) for Scots pine, Norway spruce and birch sample trees. All the values are calculated in hourly time resolution. la: leaf area (coniferous species: whole foliage area, birch: projected leaf area).

of August (data not shown), indicating the main growing season. The start of the vegetation period was determined by the beginning of constant daily sap flux, namely for Scots pine and Norway spruce from the start of the measurements in April until the beginning of November, for birch from the 2nd of May until the 6th of October (Fig. 2).

### 3.4 Determination of sapwood area

Sapwood area was determined from the measured sapwood depths at DBH and correlated to the corresponding basal area for each tree species at the MS and the GW plots (Fig. 4). As shown in higher correlations, both plots were quite similar for each tree species and one overall linear equation was developed for each species to calculate the sapwood area for the sample trees (Fig. 3). The resulting equations were in consistency with literature

values, e.g. for Scots pine similar equations are described from Zimmermann *et al.* (2000) ( $y = 0.50x$ ), from Delzon *et al.* (2004) ( $y = 0.53x$ ) and from Poyatos *et al.* (2005) for young Scots pine ( $y = 0.6x$ ), for Norway spruce similar equations are described from Köstner *et al.* (1998) for old stands ( $y = 0.41x$ ) and for young Norway spruce from Alsheimer *et al.* (1998) ( $y = 0.56x$ ), and for birch similar equations are described from Herbst *et al.* (2008) ( $y = 0.8x$ ) and for yellow birch from Tang *et al.* (2006) ( $y = 0.6x$ ).

### 3.5 Seasonal sap flux and canopy conductance

Mean daily sap flux during the whole season tended to differ between the two plots, with constantly higher fluxes at the GW plot compared to the MS plot (Fig. 2). Norway spruce tended to higher sap fluxes in April and slightly higher sap flux during September-October compared to Scots pine at both considered

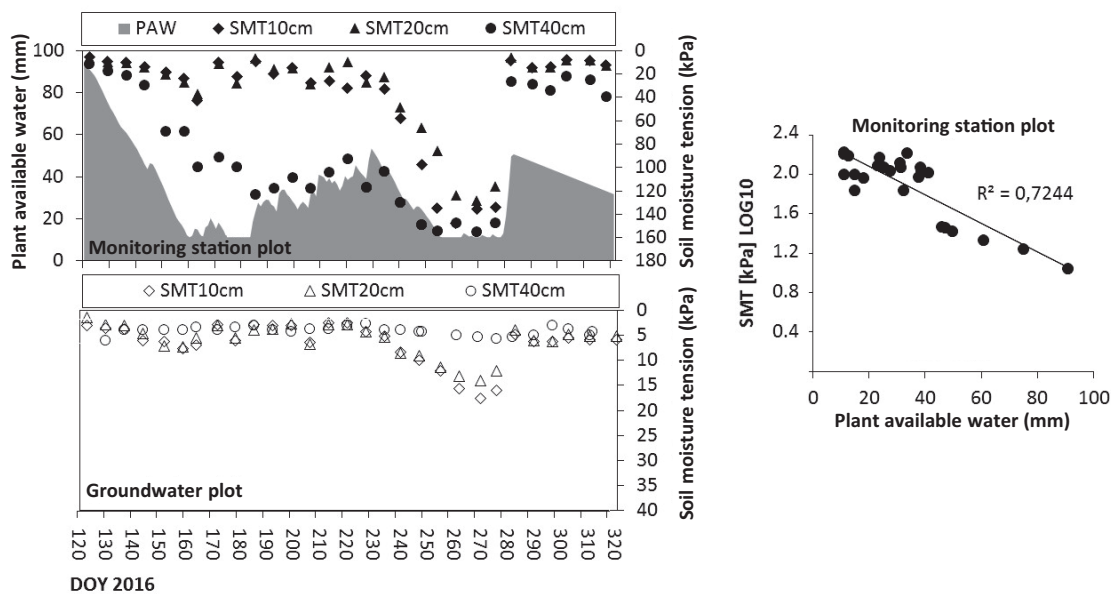


Fig. 3. Measured soil moisture tension (SMT) at different soil depths and modelled plant available water (PAW) for the whole rooting zone at the monitoring station plot in Aukstaitija National Park in 2016 (above); SMT in different soil depths at the groundwater plot in Aukstaitija National Park in 2016 (below); correlation of measured SMT (40 cm soil depth) and modelled PAW at the monitoring station plot (right).

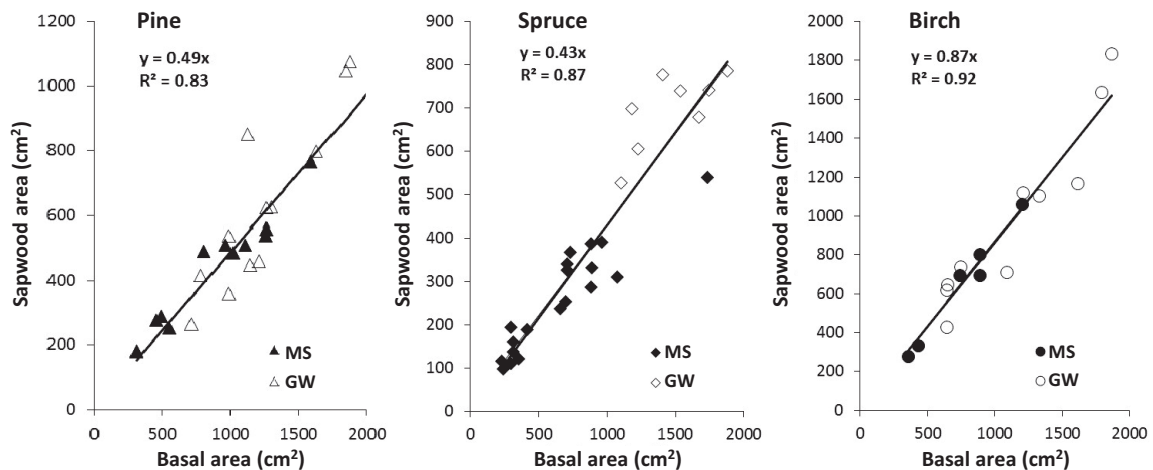


Fig. 4. Correlation of determined sapwood area and the basal area for pine, spruce and birch at the monitoring station plot (MS, filled symbols) and the groundwater plot (GW, open symbols).



plots, while sap flux for both species was quite similar from July until the end of September. Birch tended to slightly higher sap flux in June and lower sap flux from then on if compared to Scots pine and Norway spruce at both plots (Fig. 2, for significances see Fig. 7).

Xylem sap flux for each tree species correlated best with VPD and global radiation ( $R^2 = \sim 0.6$ ) followed by air temperature ( $R^2 = \sim 0.4$ ) (Table 4). Other meteorological parameters and soil moisture

showed only weak correlation with sap flux (data not shown).

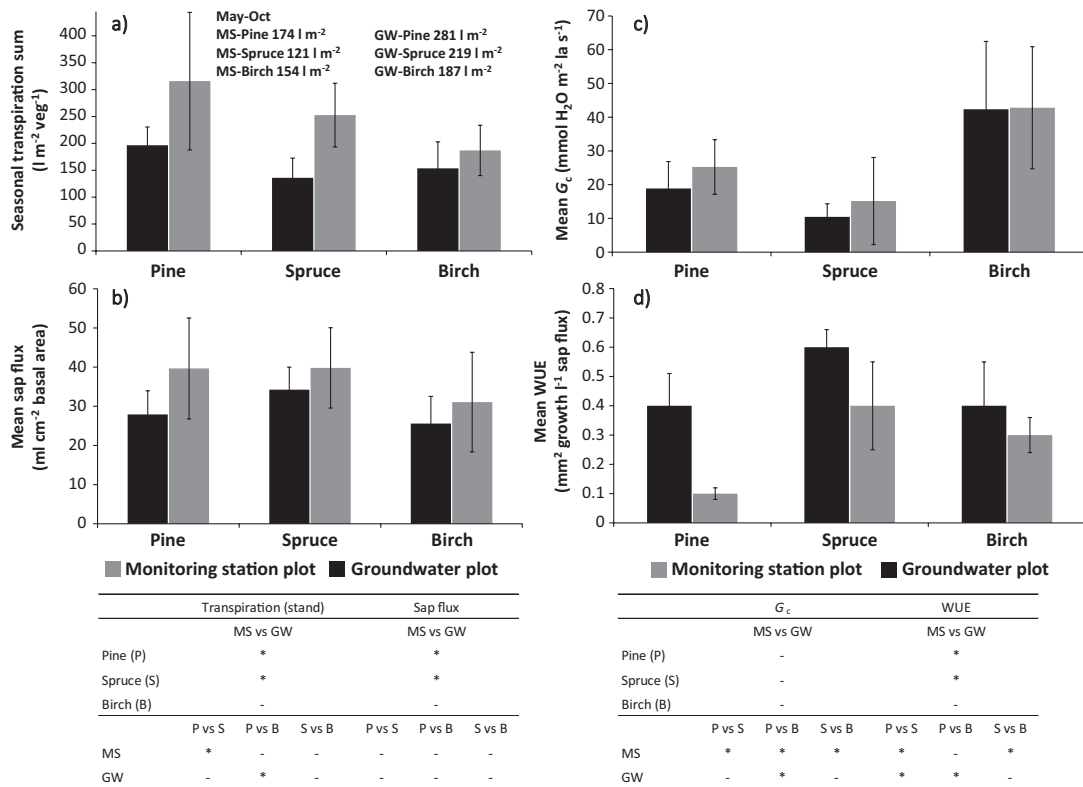
Canopy conductance was in a similar dimension and followed the same course during the vegetation period for all species at both plots, with birch exhibiting highest values compared to Scots pine and Norway spruce (Fig. 2). Canopy conductance of Scots pine tended to be higher than that of Norway spruce, both slightly increased at the GW compared to the MS plot. Reduced canopy conductance led to no substantial reduction in transpiration (Fig. 2).

**Table 4.** Correlation of sap flux of Scots pine, Norway spruce and birch sample trees throughout the monitoring station plot and the groundwater plot with water vapour pressure deficit (VPD), global radiation (GR) and air temperature (AT) monitored at the climate station at the monitoring station plot for the main growing season. Regression coefficient:  $R^2$ . Linear trend equation:  $y = \text{sap flux (ml cm}^{-2} \text{ basal area h}^{-1})$ .

species	x = VPD (hPa)	x = GR (W m <sup>-2</sup> )	x = AT (°C)
Pine	$R^2 = 0.65$ $y = 0.30x + 0.27$	$R^2 = 0.74$ $y = 0.05x + 0.23$	$R^2 = 0.46$ $y = 0.11x - 0.33$
Spruce	$R^2 = 0.66$ $y = 0.29x + 0.38$	$R^2 = 0.52$ $y = 0.001x + 0.32$	$R^2 = 0.39$ $y = 0.09x - 0.21$
Birch	$R^2 = 0.60$ $y = 0.21x + 0.17$	$R^2 = 0.59$ $y = 0.004x + 0.22$	$R^2 = 0.40$ $y = 0.09x - 0.35$

### 3.6 Average species-specific stand transpiration, sap fluxes and $G_c$

Whole season (April-Nov, May-Oct for birch) species-specific stand transpiration (calculated by assuming pure stand conditions for each species, in 1 m<sup>-2</sup> ground surface area) was significantly different between the two plots for Scots pine and Norway spruce but not for birch (Fig. 5a). Species-specific stand transpiration was higher at the GW plot compared to the MS plot for all species. Species-specific stand transpiration of Scots pine was significantly different to Norway spruce at the MS plot and to birch at the GW plot and tended to show highest species-specific stand transpiration at both plots compared to the other species. Norway spruce and birch showed 70% and 88%



**Fig. 5.** Seasonal averages  $\pm$  standard deviations for species-specific stand transpiration, xylem sap flux per basal area, canopy conductance ( $G_c$ ) and water use efficiency of growth WUE for Scots pine, Norway spruce and birch at the monitoring station plot (MS) and the groundwater plot (GW) for the whole measuring period from April – November 2016 (calculated from hourly means). a) Species-specific stand transpiration sum in 1 m<sup>-2</sup> ground surface area (calculated from stand basal area per hectare for virtual pure stands), values upper right mean species specific transpiration (estimated for virtual pure stands) for May – October, b) mean daily sap flux per basal stem area, c) mean daily  $G_c$ , and d) mean WUE of growth. la: leaf area (coniferous species: whole foliage area, birch: projected leaf area). Tables below figure: result of statistical test. \* indicates statistically significant differences ( $p < 0.05$ ).

at the MS plot and 77% and 67% at the GW plot if compared to Scots pine. Birch transpiration tended to about 30% and 40% lower transpiration compared to Scots pine and Norway spruce during the entire season, respectively (Fig. 5a).

Beyond the vegetation period during the months April, October and November the coniferous species still transpired water. In these months 11% from the entire seasonal transpiration at the MS plot and 11% and 13% at the GW plot amounted for Scots pine and Norway spruce.

Assuming a species composition of 70% of Scots pine, 20% of Norway spruce and 10% of birch the estimated mixed stand transpiration for the entire vegetation period 2016 (April-October) would arise to about 200 (180 ± 30) mm at the monitoring plot and about 300 ± 100 (291 ± 109) mm at the groundwater plot which is accompanied by 370 mm of precipitation in the same period. Regarding the water supply in the month April, May and June and in September the monthly precipitation sums would have been below the estimated monthly species-specific stand transpiration sums at both plots

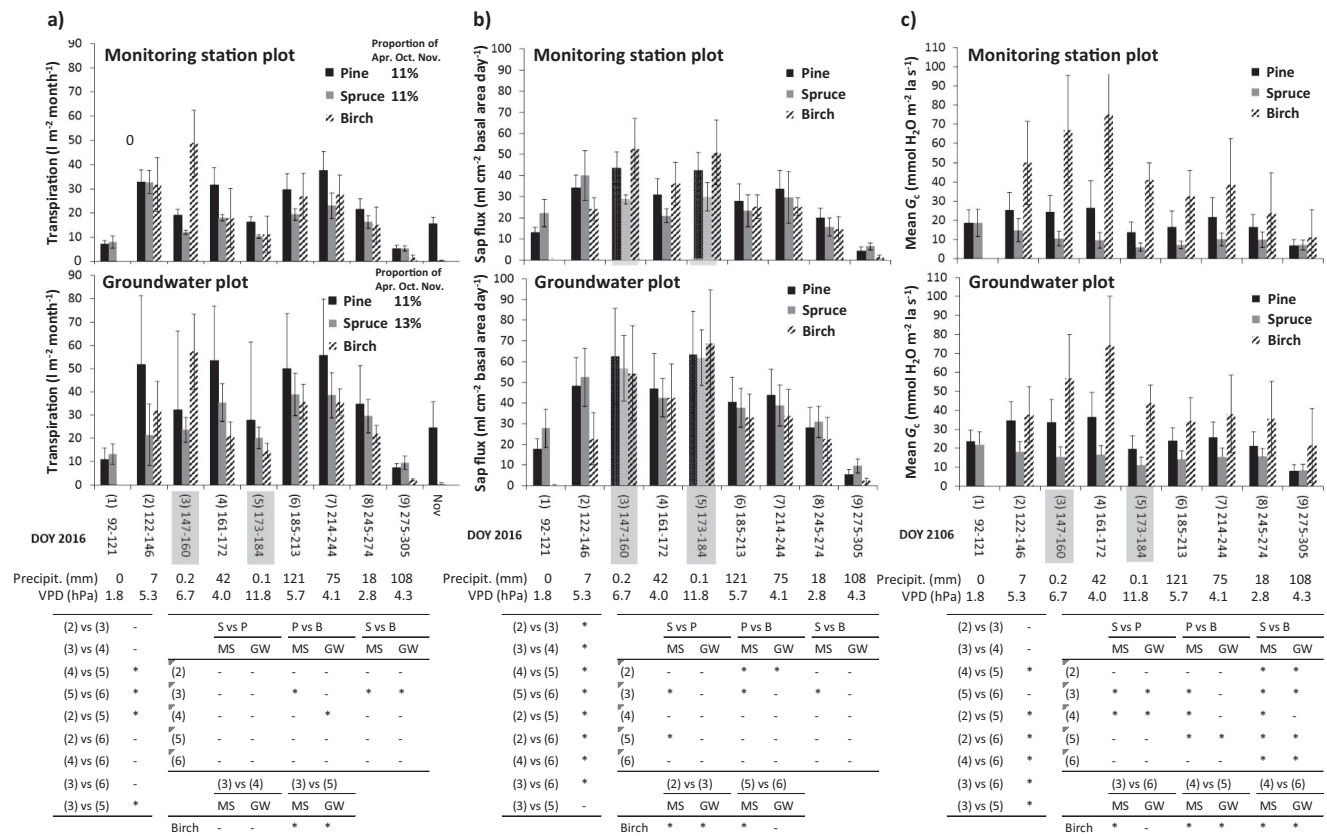
assuming virtual “pure” stands (Fig. 1, Fig. 6a).

Significant differences for average mean sap fluxes were only detected between plots for Scots pine and Norway spruce, but not for birch. No differences between species were found (Fig 5b).

Average  $G_c$  for the vegetation period was not differing within species at both plots (Fig. 5c). Significant differences for average  $G_c$  were found between all species at the MS plot, but only between Scots pine and birch at the GW plot (Fig. 5c).

### 3.7 Determination of temporary moderate dry periods

In order to determine moderate dry periods, we used meteorological data (precipitation sums, VPD), soil water data (SMT, modelled PAW) and  $G_c$ , derived from sap flow data (see 3.5). Several periods without precipitation, lasting at least 10 to 15 days, could be selected during the study year 2016. Such periods with a lack of rainfall occurred already at the beginning of the vegetation period from end of March until the 12th of May, during the main growing season from the 26th of May until the 8th of June (DOY 147-160), from the 21st of June to the 2nd of



**Fig. 6.** (a) Species-specific stand transpiration in l m<sup>-2</sup> ground surface area (calculated from stand basal area for virtual pure stands), (b) mean daily xylem sap flux [ml cm<sup>-2</sup> basal area day<sup>-1</sup>] and (c) mean daily canopy conductance  $G_c$  (mmol H<sub>2</sub>O m<sup>-2</sup> la s<sup>-1</sup>) including standard deviation for selected periods during the whole measuring period (April – November 2016) for Scots pine, Norway spruce and birch at the monitoring station plot (MS) and the groundwater plot (GW). Values upper right in a) mean proportion of the transpiration during the months April, October and November for coniferous species from whole season transpiration. Time period and corresponding DOY 2016 are shown as number in bracket and its following number below x-axis. Grey shaded field indicates dry period. Monthly precipitation and mean VPD for the respective time period are also shown below DOY 2016. Left tables below figure: result of statistical test between time periods (both plots, MS and GW) for above shown parameters. \* indicates statistically significant differences ( $p < 0.05$ ) between time periods throughout species. Right tables below figure: result of statistical test between species in the same time period, and between time periods in birch at each plot.

July (DOY 173–184), from the 5th to the 20th of September (DOY 249–264) and at the end of the vegetation period from the 10th to the 21st of October (DOY 284–295) (Fig. 1). These periods are each characterised by distinctly increased VPD (Fig. 1).

Extremely low precipitation during the winter month 2015/2016 and the complete lack of rainfall from April until the end of May lead to a reduced  $FC_{eff}$  (~60–70% of  $FC_{eff}$ ) in the main rooting zone at the MS plot already at the beginning of the vegetation period, whereas no soil water limitation could be detected for the GW plot (Fig. 3).

Thus, we segregated drought periods only for the MS plot. There, SMT in 40 cm soil depth and modelled PAW for the rooting zone indicated a period with limited soil water supply, especially from the end of May until the beginning of July and from the beginning of September until the beginning of October (Fig. 3). Assuming soil water conditions near field capacity at the beginning of our measurements at the MS plot, SMT fell below more than 60% of its initial values already at the end of May. A further decline in SMT occurred at the end of June, which was persisting more or less until the beginning of September, followed by a further decline in SMT lasting until October (Fig. 3).

During the low rainfall period (end of May–beginning of July) low SMT values occurred in 40 cm soil depth and also slightly reduced SMT values in the upper soil (10 cm and 20 cm soil depth). We presume that the rain events in June (9th–20th (DOY 161–172), 42 mm) only marginally reached 40 cm soil depth which is constancy with no limitations in transpiration. Similarly, the continuous rainfall from 3rd of July until mid of August (DOY 185–228) following the low rainfall periods, did not increase soil water supply substantially because of the high water consumption by tree transpiration (Fig. 1, 2, 3).

Thus, in order to determine dry periods at the MS plot, we included the canopy conductance serving as a plant related factor (Fig. 2). Hence, we found a reduction of canopy conductance for all tree species from the 26th of May until the 7th/8th of June (DOY 147–160) and a further clear reduction from 21st of June until the 17th of July (173–194). During these periods we found decreased canopy conductance for all three tree species, with no considerable reduction in sap flux (Fig. 2).

To segregate dry periods now, we combined periods with reduced canopy conductance and periods with a lack of precipitation and increased VPD. As stem increment growth occurred mainly during May until the end of July, we considered drought events limited to this period.

Thus, based on meteorological, soil water and plant-related parameters, two dry periods were segregated, the first between 26th of May and 8th of June (DOY 147–160, dryperiod1) and the second between 21st of June and 2nd of July (DOY 173–184, dryperiod2), with precipitation sums of 0.2 mm and 0.1 mm and a mean VPD of 6.7 hPa and 11.8 hPa (see Fig. 6), respectively, and concurrently low SMT values during the whole period (Fig. 1, 2, 3).

Both selected dry periods were tested significantly different to their preceding and subsequent sap flux, whereas no significant differences could be found between the both dry periods (Fig. 6).

### 3.8 Species-specific stand transpiration, sap fluxes and $G_c$ for the selected dry periods

For the species-specific stand transpiration significant differences could be detected for the period 3 (dryperiod1) between Scots pine and birch at the MS plot and between Norway spruce and birch at both plots (Fig. 6a). Only birch showed significant differences between the two dry periods 3 and 5 at both plots, with lower values in period 5 (dryperiod2) (Fig. 6a).

Significant differences for sap fluxes were detected between Scots pine and birch and between Norway spruce and birch at both plots for period 2, whereas for period 3 (dryperiod1) differences between all three species were found only at the MS plot (Fig. 6b). For period 5 (dryperiod2) significant differences were detected only between Norway spruce and birch, with Norway spruce exhibiting lowest values. For birch, we found significant differences between the dry periods and the previous and subsequent period (Fig. 6b). In summary, for the dry periods Scots pine, Norway spruce and birch at the MS plot significantly differed in sap flux compared to the adjacent time periods, whereas no differences were found between the two dry periods (Fig. 6b). At the GW plot no significant differences could be detected for the dry periods (Fig. 6b).

For the period 3 (dryperiod1), all species showed significant differences at both plots, except for Scots pine between birch at GW plot (Fig. 6c). During the intermediate period 4,  $G_c$  was significantly different between all species at the MS plot, but only between Norway spruce and Scots pine at the GW plot (Fig. 6c). For the period 5 (dryperiod2), significant differences were found between Scots pine and birch as well as between Norway spruce and birch (also different for period 6) (Fig. 6c).  $G_c$  differed significantly for birch between period 3 and 6, period 4 and 5, and period 4 and 6 (Fig. 6c).

### 3.9 Water use efficiency of growth (WUE)

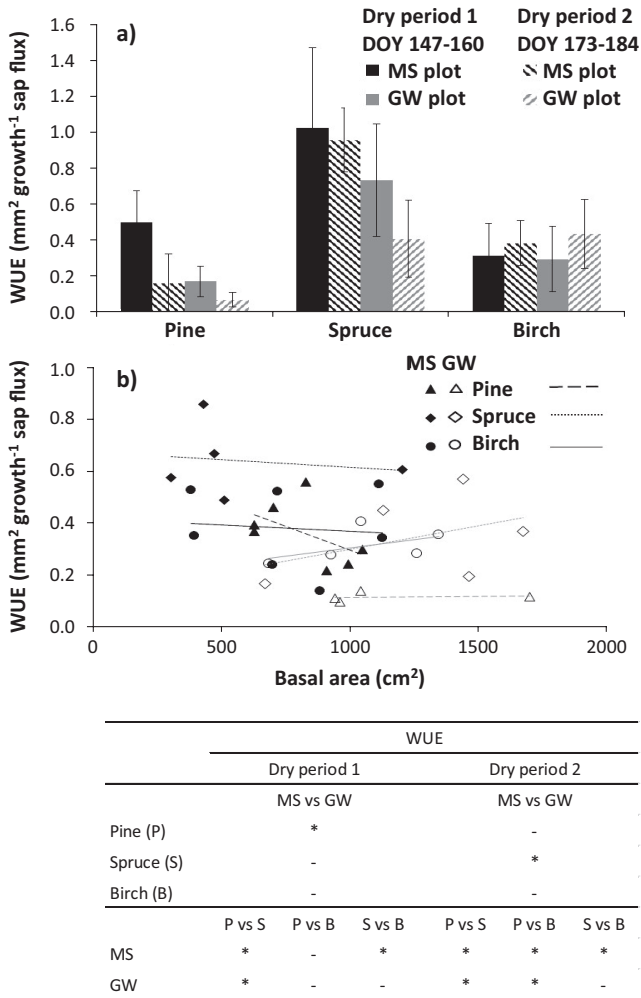
Average WUE of growth for the vegetation period was statistically significantly higher at the MS plot compared to the GW plot, except for birch (Fig. 5d). Analysing tree species WUE was significantly differing between Norway spruce and Scots pine or birch, but not between Scots pine and birch at the MS plot; at the GW plot we found differences between Scots pine and Norway spruce or birch and none between birch and Norway spruce (Fig. 5d), with each highest WUE for Norway spruce.

During the first dry period Norway spruce showed significantly higher WUE compared to Scots pine and birch, whereas no differences could be found between Scots pine and birch at the MS plot (Fig. 7); at the GW plot WUE of Norway spruce was significantly higher.

During the second dry period all tree species showed significantly different WUE at the MS plot, but at the GW plot only between Scots pine and Norway spruce or birch, whereas all species differed significantly between plots. Again, Norway spruce exhibited highest WUE at both plots with significantly differing in its height at the MS and the GW plots (Fig. 7).

As no correlation of basal area and WUE could be found, thus, it is assumed that WUE was independent of tree size (Fig. 7).

In the second dry period no or nearly zero growth was



**Fig. 7.** (a) Water use efficiency of growth (WUE) for the dry period 1 and 2 (DOY 147–160, 0.2 mm precipitation, and DOY 173–184, 0.1 mm precipitation, respectively) for Scots pine, Norway spruce and birch at the monitoring station (MS) plot and the groundwater (GW) plot. (b) Correlation of WUE and basal area of the sample trees. Closed symbols: MS plot, open symbols: GW plot. Table below indicates result of statistical test \* indicates significant differences of WUE ( $p < 0.05$ ) between plots in each species and between species in each plot.

determined for more than 40% of the Scots pine sample trees at the MS plot and for 25% at the GW plot, whereas no zero growth was detected for the other species during the dry periods (data not shown, personal comm. A. Augustaitis).

#### 4. Discussion

Tree species specific water related parameters such as xylem sap flux, WUE and stand transpiration (estimated for pure stand conditions) were analysed for dominating adult Scots pine, Norway spruce and birch in a mixed forest at sites with different susceptibility to drought in the Aukstaitija National Park. The study period can be characterized as an average year concerning meteorological conditions compared to the last 20 years. But low precipitation in winter season and at the beginning of the vegetation period lead to soil drought between

late May and early July at the “water-limited” site also in deeper horizons (monitoring station plot, MS, arenosol) prevailing during the main growing season. During the end of May until the beginning of July two biweekly periods with nearly no precipitation occurred, but water availability in combination with VPD is known to be the dominant driver for tree growth and transpiration (Eilmann and Rigling 2012). Canopy conductance during these segregated dry periods was reduced for all species but did not lead to considerably reduced sap fluxes. Even if water supply was already restricted at the beginning of the vegetation period at the water-limiting site, we have to conclude that the temporary drought incidents during the one-year study period were moderate and of limited duration and thus, maybe shortly compensated by the use of other rooting zones of the sample trees.

#### 4.1 Relation of water consumption and trees growth at the study sites

Species specific sap fluxes as well as stand transpiration assumed for pure stands were clearly enhanced at the water-saturated peat site (GW plot, histosol). As soil water tension was persistently high during the whole season at the water saturated site (~+70–80% higher mean whole tree transpiration at GW plot), WUE was quite low for each tree species there. Water consumption of Scots pine trees was highest followed by birch and Norway spruce, whereas average stem radial increment was quite similar for Scots pine and birch in this year, but clearly increased for Norway spruce at the water saturated site, which is in accordance to the long-term results of Augustaitis *et al.* (2018). Irrespective of high unlimited water supply at the GW plot, birch trees (silver and downy birch) showed no pronounced increase of mean daily sap flux at the GW plot compared to the MS plot (arenosol) (MS:  $4.36 \pm 1.03$  l cm<sup>-2</sup> basal area day<sup>-1</sup>; GW:  $5.38 \pm 2.01$  l cm<sup>-2</sup> basal area day<sup>-1</sup>, May–September). As stem radial increment of birches was similarly increasing during the main growing season at both plots, silver and downy birches seemed to be well adapted to the growth conditions in their respective niches. WUE was quite low and similar for both birch species at both plots, but neither silver birch nor downy birch showed an adjusting WUE during the dry periods at both plots, indicating no specific adaption to drought (Augustaitis *et al.*, 2018).

Even as no water-limitation was assumed for the whole sampling period at GW, Norway spruce had higher WUE compared to Scots pine due to an increased mean stem radial increment of Norway spruce while water consumption was lower compared to Scots pine. Also, Augustaitis *et al.* (2018) showed clearly higher stem increment of Norway spruce compared to Scots pine at the same site. Thus, Norway spruce growth seemed to profit from excessive water supply compared to Scots pine.

#### 4.2 Relation of water consumption during temporarily “dry periods”

WUE of Norway spruce was clearly enhanced compared to Scots pine at the temporarily water-limited site (MS plot) and during the two dry periods when tree water consumption was reduced again compared to growth. However, we assume only

moderate dry periods at the water limited site (MS plot) during our study period as water tree water consumption of all tree species wasn't considerably restricted. So, we conclude that water supply in the upper soil horizons was still sufficient which was supporting growth of the shallow rooted Norway spruce trees against drought (Cienciala *et al.*, 1998). In contrast to the drought intolerant Norway spruce (Innes, 1991), Scots pine is characterised as a drought avoiding species due to its deep rooting system combined with the strategy of immediate stomata closure (Richardson, 2000; Kallioikoski 2011) to counteract high susceptibility to cavitation (Martinez-Vilalta *et al.*, 2004). Regarding the mean daily sap flux at the MS plot, Norway spruce showed clear reductions during the dry periods, while Scots pine didn't restrict water consumption persistently during the main growing season from May until August, irrespective of dry conditions. Thus, Scots pine seemed to be quite unaffected by limited soil water supply even in deeper horizons or by temporarily lack of precipitation during the study period. Under sufficient water supply water absorption usually is most efficient close to the root tips, located in the upper soil layer (Bréda *et al.*, 2006). As, at sites susceptible for drought, Scots pine roots are able to explore also deep soil regions (Richardson, 2000), we presume that Scots pine at the MS plot established connection to the groundwater to ensure constant water supply (at ~300 cm soil depth at MS) regardless of variable soil water content in the upper soil.

WUE of Scots pine was enhanced at MS compared to GW plot, but WUE differed for the dry periods: while WUE was similar to the seasonal WUE during the first dry period, in the second dry period WUE was clearly decreased at the MS and GW plots mainly because of reduced to no growth while sap flux was rather unchanged. Reductions of WUE are often described as tree reaction to drought events (Reichstein *et al.*, 2007) but generally WUE is reduced because of decreased water consumption. Intra-annual comparisons of short-term water limited mature beech showed also significantly reduced tree volume growth compared to moist conditions while transpiration remained constant but VPD was clearly enhanced (up to 40 hPa) and stomatal conductance was reduced (Kühn and Baumgarten, unpublished). The reduction of stomatal conductance is a main driver for reductions of stem growth through reduced CO<sub>2</sub> assimilation (Beer *et al.*, 2009) and early stomatal closure is known to prevent Scots pine from cavitation due to drought (Richardson, 2000). So, we conclude that Scots pine, being the climax species in this Baltic region, exhibits high capacity to adapt to various climate conditions such as temporary drought events or excess soil moisture conditions. Also, Norway spruce was found to be well adapted to various soil moisture regimes and during moderate short term drought events, due to the fact that the clear increase of WUE during the drought conditions and the increased stem increment indicates a particular resilience and high phenotypic plasticity. Increased growth rates which are reported since the 1980th (Augustaitis *et al.*, 2018) support a further increase of proportions of Norway spruce in north eastern hemi-boreal forests at present, but future progression of climate change, especially accompanying with further temporary dry periods and increased temperatures in winter the season, leading

to additional water demand, could diminish sustainability of Norway spruce in this region.

#### 4.3 Summary and Perspectives

- In this study, we selected two temporary dry periods during the main growing season. Norway spruce exhibited significantly reduced sap fluxes and increased WUE compared to Scots pine and Norway spruce at the water limited site, which is indicating high capability to dynamically react to reduced water supply. However, as no severe restriction of water consumption for the trees could be detected during the dry periods, we couldn't assume the occurrence of severe drought during the investigation period. Thus, no evidence for extended drought sensitivity of Norway spruce could be determined. Long-term studies across several growing seasons are needed to test drought sensitivity of Norway spruce at Lithuanian various forest sites.

- As sap flux of Scots pine trees at the examination sites was more or less constantly high during the main growing season and WUE was quite low during the "dry periods", we assume that Scots pine trees are less affected by temporarily drought events than Norway spruce at the water limiting site. We assume that Scots pine is not forced to enhance WUE because of its ability to exploit water reservoirs also in deep soil regions.

- Despite highest canopy conductance, birch trees were also little affected by dry periods. Birch exhibited similar quite high sap fluxes and similar low WUE during the main growing season at the water limited and the water saturated site, even during the dry periods. Thus, birch may compete with Scots pine trees at the study sites in terms of water consumption and nutrient resources during dry conditions, but its heart-shaped root system with many fine roots in the top soil layer compared to the deep reaching taproot of Scots pines may mitigate competition as natural co-occurrence with Scots pine indicates.

- As no water-limitation occurred at the water saturated site (GW plot) during the study period, our hypothesis that birch trees react more sensitive to short term drought events or suddenly decreasing ground-water levels at water-saturated peat sites couldn't be tested. In this context, the abundance of downy birch and its tolerance to temporary drought in such niches should be investigated.

- With regards to the recently documented Norway spruce mortality in the Baltic region and the European part of Russia (Kharuk *et al.*, 2015), the investigations of the adequate mixture of species is a main task for future forest management in the boreal zone to adapt forests to a changing climate and to sustain forest functions and productivity (Ge *et al.*, 2011). Thinning adjusted to site characteristics in combination with various species mixtures can help to exploit the benefits of the effects of climate change under boreal conditions (Briceño-Elizondo *et al.*, 2006).

- Considerable transpiration rates (assuming pure stands) for the coniferous species were measured already during short-duration rises of air temperature beyond the main growing season in April and November. In November, transpiration of Scots pine seemed to be favoured by slightly higher soil temperatures in deeper horizons whereas in April Scots pine and Norway spruce both started transpiration when soil temperatures

reached 3–4°C. Even though climatic shifting or interruptions in the seasonal course are prognosticated (IPCC, 2013) also for the period of tree dormancy, there is a lack of knowledge about the consequences for tree water balance and about implications of subsequent severe frost events for tree growth and condition.

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