

Article

Intra-Annual Variation of Stem Circumference of Tree Species Prevailing in Hemi-Boreal Forest on Hourly Scale in Relation to Meteorology, Solar Radiation and Surface Ozone Fluxes

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Abstract: (1) Background: Continuous monitoring of the tree stem increment throughout the year is crucial for the understanding of trees' reactions to changes in meteorology, solar radiation and surface ozone and evaluating the adaptive capacity of prevailing tree species to recent environmental global changes; (2) Methods: Data on tree intra-annual sequences based on electronic dendrometer data of *Picea abies* (L.) Karst, *Pinus sylvestris* L., *Betula pendula*, and *Betula pubescens*, growing under different nutritional and humidity conditions in the north-eastern part of Lithuania, together with their stem sap flow intensity, common meteorology and O₃ fluxes, were used to meet the objectives of the study; (3) Results: Stem shrinking/contraction during the day, due to transpiration, and the swelling/expansion during the night was significantly related to meteorology, sun activity and O₃ flux intensity. These variations were negatively related to current time and temperature, but positively to precipitation and relative humidity. O₃ fluxed through the stomata stimulated the shrinking process more intensively than it inhibited the swelling process, but only for pine and birch trees. Spruce trees demonstrated the highest sensitivity to O₃ impact due to its significant effect on the stem swelling process. Pine trees were less sensitive to O₃ damages and birch trees were the least sensitive. An over-moisture regime at mesoeutrophic organic soil forest site increased the significance of the effect of O₃ on the tree increment of the considered tree species; (4) Conclusion: The most intensive tree ring formation of *Scots pine* trees in relation to recent environmental changes indicated their high resiliencies and adaptations to a local specific condition. Reduced tree growth intensity and weak relationships between the birch tree radius increment and main meteorological parameters indicated the lowest adaptive capacity of this tree species to recent environmental changes.



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Keywords: stem increment; hourly scale; swelling; shrinking; meteorology; PAR; ozone flux

1. Introduction

The growth of forests under changing environmental conditions has been extensively studied during recent decades [1]. Special attention is being paid to the effects of climate changes, which have become the main drivers of environmental changes owing to a significant rise in global mean surface temperatures and extreme weather events [2]. Their potential impacts and the risks to forest ecosystems are best studied and understood as they relate to wood production [3]. Tree-ring width and its formation are considered to be appropriate indicators of changes in environmental conditions [4,5] and are a proxy for ecosystem health [6].

Climate change is expected to increasingly impact forest ecosystems in the present century [7–9]. It may increase growth rates in temperate and boreal forests [10,11], while temperature-induced drought stress endangering the survival of trees and forest communities could determine the opposite effect, reducing it [10,12], especially in some southernmost areas [13]. The state of knowledge revealed that this effect varies across geographic areas, species, stand composition, tree age, and soil fertility [14]. In a hemiboreal vegetation zone, which is a transition zone between boreal and temperate zones such as the Lithuanian

forest, this effect on tree growth is suggested to depend on site conditions and can be either positive or negative [1]. Therefore, the accurate prediction of climate effects on forest ecosystems represents a critical research gap [15].

Field-measured forest productivity and its time-series are crucial for understanding the impact of climate change on the main tree species increment and stand productivity in general [16]. Climate warming is the main factor responsible for the increase in the tree-growth intensity of hemi-boreal European forest tree species, mainly *Scots pine* and *Birch* sp., with the exception of the *Norway spruce*, whose growth has significantly decreased in central Europe [17]. Recurrent drought events reinforced the effect of climate warming on spruce growth through changes in tree physiological processes, modifying the functioning and vitality of individual trees [18,19] and increasing the susceptibility to bark beetle attacks [20] and, finally, tree mortality [21]. Therefore, resilience to extreme meteorological factors is of the greatest concern due to high vulnerability under the pressure of recent global changes [22–25]. Despite this, our earlier obtained results confirmed that the hemi-boreal forest in the north-eastern part of Europe is favorable for the growth of *Norway spruce* trees [26]. On-going temperature and precipitation increases, which are typical for this region of Europe, had essential impacts on the recovery of spruce tree vitality and increased their incremental growth in Lithuanian forests up to a mature age.

Based on our results, *Scots pine* trees are likely to be the tree species that are the most sensitive and most resilient to environmental changes in hemi-boreal forests. These results also contradict the findings obtained for central or southern Europe, where the incremental growth of *Scots pine* trees was found to be least sensitive to environmental changes and differed least under different growth conditions [27]. Pine trees growing on dry mineral oligotrophic soils, with a natural moisture regime, had no higher requirements for precipitation, which indicated their very high resistance to the drought effect. At this forest site, which is typical for *Scots pine* growth, only positive effects on pine increment from temperature during the dormant and vegetative periods were detected [26]. Only drought may significantly reduce *Scots pine* growth, especially at the southernmost distribution limit forest sites in the future [13].

In central Europe, above-average summer temperatures have resulted in the positive tree-ring formation of birch trees, whereas below-average summer temperatures and a dry winter have resulted in negative growth intensity [28]. These findings also contradict our obtained results on birch tree-ring formation in Lithuania. The increment of mature and over-mature birch trees decreased significantly. Meteorological factors, which resulted in the increment increase of coniferous tree species, were responsible for reductions in birch trees [26].

In Europe, divergent forest productivity trends have recently been reported both at the local and regional levels, challenging the projections of boreal tree growth dynamics, which are mainly detected on the annual increment scale [29]. Continuous monitoring of the tree ring formation throughout the year is crucial for the understanding of tree reactions to changes in environmental conditions, such as temperature, sun radiation, soil water potential (SWP), vapor pressure deficit (VPD) and rainfall [30].

Zweifel et al. [31], analyzing published results, presumed that stem growth, including cell division and cell enlargement, is attributable to the activity in the cambium that is strongly related to water content in storage tissues [32]. The replenishment of water in storage tissues [31], that is, potential water friction losses, which leads to increasing the potential fluctuation of water, resulting in xylem diameter variation along the hydraulic pathway [33]. Therefore, both these physiological processes—tree stem growth and water uptake—finally resulted in stem circumference rhythm, which is difficult to detect with empirical treatment of stem radius variation records [34].

Automated dendrometers at intra-daily resolution offer great potential to link environmental conditions with tree physiology at the seasonal scale [35]. These dendrometers are believed to provide a better estimation of the average radial growth than point dendrometers because they summarize the growth of all radii [36]. The main disadvantage

lies in the difficulty of interpreting the obtained results. Dendrometer measurements do not distinguish between xylem, phloem and periderm increments, and these are also confounded with the overall swelling and shrinkage of the stem [37,38].

High-resolution analysis of stem circumference variation on an hourly scale provides insights into the temporal patterns in reversible tree water-related stem swelling and shrinking processes due to changing water potentials, including irreversible stem increments due to cell division and cell enlargement in the cambium in relation to environmental variables [32,39–42]. These two processes need to be separated to obtain drivers of growth and tree water deficits [35]. Therefore, automatic measurements of stem radius variations provide an effective and sensitive proxy, not only for plant water status assessment, but also for tree stem increment and its modelling in relation to environmental changes [35]. This process, based on graphical analyses of the time series on the stem increment has recently been extensively studied [30,35,38,42] and remains an intriguing issue given the potential impact of climate change on plant adaptive capacity to recent environmental changes [43].

Recently, climate change in the north-eastern part of Europe, including Lithuania, is associated with an increase in sun irradiance, temperature and precipitation amount vs. its decrease in middle and southern Europe, and also a decrease in surface ozone concentration [26,44]. Such environmental changes contributed to the regeneration of forest health and an increase in productivity [26,45]. However, the independent effect of each individual predicted variable on tree growth is still under investigation. Cambial phenological phases, which are influenced by the prevailing climatic conditions in forest stands at different forest sites of different fertility and humidity levels, have also scarcely been explored [39].

Notwithstanding this, in this study I tried to better understand how the daily stem radial activity of the prevailing forest tree species in Lithuania—*Scots pine*, *Norway spruce* and silver and downy birch were affected by variations in relative humidity, air temperature, solar radiation, wind speed and SWP as well as VPD. Special attention was paid to surface ozone concentrations and their fluxes through the stomata, which were detected by analyzing tree sap flow data. These data related to the seasonal growth behavior of the major tree species for forest sites in response to O₃ exposure are still lacking, especially when applying an hourly data approach [46,47].

The state of knowledge revealed that the current O₃ levels in the Northern Hemisphere are already high enough to negatively affect trees, especially fast-growing deciduous trees [48]. It can reduce the photosynthetic capacity and growth of forest trees [49,50] due to the humid climate increasing stomatal conductance and long light days extending diurnal periods with open stomata, both facilitating ozone uptake [47]. The degree of damages depends on the actual amount of pollutants that reach the target sites, as well as the capacity of the cells to restore homeostatic equilibrium by adapting to metabolic changes. Stomata conductance plays a fundamental role in determining the flux of O₃ into the apoplastic region of plants [47,50]. Plants that show more rapid stomatal closure are reported to be resistant to O₃ [51].

Recently, ozone flux after the passage of O₃ through the stomata into the leaf inter-cellular space is also of the greatest concern when evaluating the effect of O₃ on forest trees [44,52,53]. Transpiration rate, which is established by applying tree sap flow data obtained from the tissue heat balance method, allows the detection of O₃ flux through the stomata and the detection of its effect on the increment formation of the prevailing forest tree species in Lithuania under different site conditions. It is also very beneficial to detect tree water-use efficiency (WUE), which is a key plant response mechanism to moderate severe soil water deficits and is therefore quite often used to assess the adaptive capacity of trees to recent environmental changes [54].

The present study was conducted with the aim of confirming the hypothesis that the boreal forest coniferous species, Scot pine and *Norway spruce*, are adaptive to recent climate changes and their capacity to mitigate climate change is higher than that of deciduous tree

species, mainly Birch spp., which was established based on annual increment sequences relating to the monthly mean time series of meteorology and environmental contaminants, including surface ozone [7]. *Norway spruce*, with the rapid increases recorded in growth intensity since 1980, was found to be well adapted to recent environmental changes, which makes it one of the most favorable tree species for silviculture in the northeastern part of Europe. Scot pine demonstrated the highest level of resilience and capacity to adapt to recent global changes because its reaction to both negative and favorable environmental factors was best expressed. The sap flux of these considered coniferous tree species was lowest, which increased their WUE during the drought period [54]. Therefore, the requirement to create well-designed process-based models for climate responsibility to cambium phenology, adaptation, distribution or the replacement of these tree species in response to climate change is of great concern not only in Lithuania but also across all of Europe.

Only a significant decline in the growth intensity of silver and downy birch trees and the absence of significant reactions to environmental factors indicated that these tree species demonstrated a reduced resistance to recent changes in environmental conditions, especially in the mature and over-mature age groups at the driest site [26]. Their WUE was also the lowest there [54].

To validate these results at the hourly scale, it is suggested that a stem-cycle approach should be used, separating increment formation changes into distinct phases [30,35,41,55] and generalizing the obtained data by applying a diurnal approach that extracts the summary metrics per day [42]. Based on this, the presented study was conducted on stem shrinking and swelling processes separately, detecting key predicted variables resulting in the intensity of these opposite processes, when the reliability of the obtained results was checked through a comparative analysis with the common results obtained at the diurnal scale.

To meet the aims of this study the objectives were as follows:

- To detect differences in the tree stem increment of the prevailing tree species in Lithuania, growing under different site conditions;
- To detect key environmental factors that have the most significant effect on tree stem shrinking and swelling processes during vegetation;
- To detect the direct effect of surface ozone fluxes on the tree stem radius increment;
- To evaluate the adaptation capacity of the prevailing tree species to recent climate changes.

The obtained data should allow an explanation of the difference in tree stem increments and evaluation of the adaptive capacity of the prevailing tree species in Lithuania to recent environmental changes.

2. Materials and Methods

The investigation was conducted in the coniferous–deciduous forest in the northeastern part of Lithuania at the Aukstaitija Integrated monitoring station (IMS), which was established in Aukstaitija National Park (NP) in 1993 (Figure 1). It was established in the strict reserve zone of NP in the Azvintiniai mature and over-matured natural forest. Bearing in mind differences in the physiological reactions of the tree species to environmental stressors at sites with different moisture and fertility availabilities, seasonal reactions of the prevailing tree species in Lithuania—*Scots pine* (*Pinus sylvestris* L.), *Norway spruce* (*Picea abies* Karst.) Silver and Downy birch (*Betula pendula* Roth. and *B. pubescens* Ehrh.)—were investigated at three different forest sites (FS). A more detailed description of FSs can be found in our earlier studies [26,56–58].

2.1. Site Description

The main dendrometric characteristics of the monitored FSs are compiled in Table 1. The sample trees chosen for the intensive investigation of fluctuations in their stem circumference suitably reflected the mean dendrometric parameters of each considered tree species.

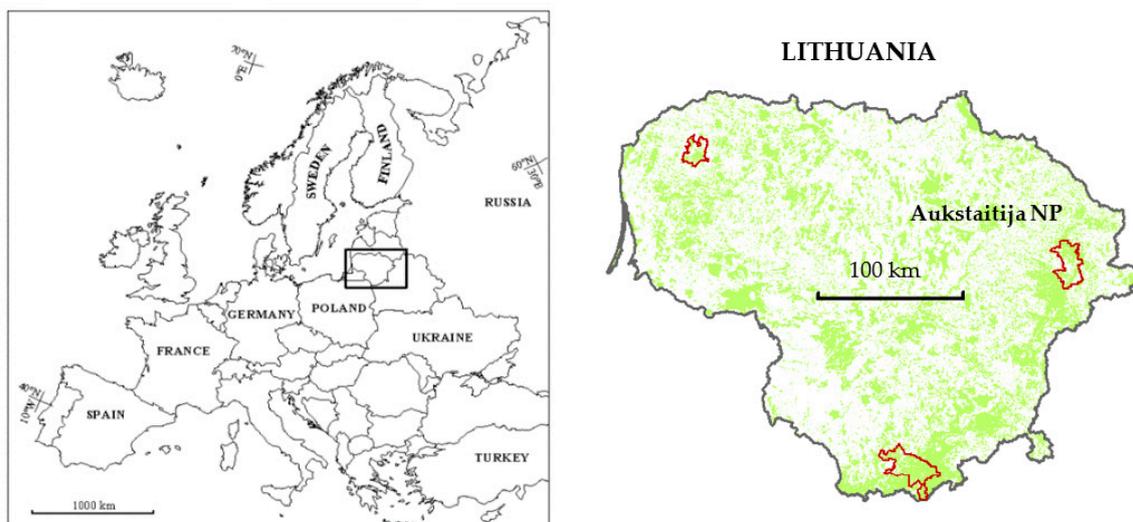


Figure 1. Location of the studied object and Aukstaitija National Park in Lithuania.

Table 1. Main dendrometric characteristics of the considered mixed stands.

Species	Dendrometric Parameters				
	DBH	Height	Basal Area	Density	Age
	cm	m	m ² ha ⁻¹	unit ha ⁻¹	year
Oligotrophic mineral soil forest site FS-1					
Birch	33.4	30.5	13.1	149	65
Pine	31.8	29.5	23.7	299	95
Spruce	29.8	29	3.5	50	65
Total			40.2	497.6	
Mesoeutrophic organic peatland forest site FS-2					
Birch	36.6	30.0	16.5	160	80
Pine	40.0	31.5	13.6	106	110
Spruce	43.5	32.0	11.5	78	75
Total			41.6	344	
Mesoeutrophic mineral forest site FS-3					
Spruce	42.3	32.5	32.9	234	75
Total			32.9	234	

Site FS-1 was established on oligotrophic mineral soil. There, *Pinus sylvestris* with *Betula pendula* and *Picea abies* dominated in the first stand layer. *Sorbus aucuparia*, *Frangula alnus* and *Juniperus communis* were present in the shrub layer. *Vaccinium myrtillus*, *V. vitis-idaea* and *Melampyrum pratense* dominated in the herb layer. *Pleurozium schreberi*, *Hylocomium splendens* and *Dicranum polysetum* dominated in the moss layer. The soil type of FS-1 is *Haplic Arenosol*, the water table is deeper than 6 m [26,54]. The pure and mixed groups of the considered tree species, which were indicated as “pure” or “mix,” were selected for the hourly estimation of stem increment. Several suppressed spruce trees from the second stand layer comprised the group called “press”.

FS-2 was established on mesoeutrophic peatland organic soil. *Pinus sylvestris* with *Betula pendula* and *Picea abies* also dominated in the stand. *Sorbus aucuparia*, *Frangula alnus* and *Corylus avellana* were present in shrub layer. *Vaccinium myrtillus*, *Maianthemum bifolium*, *Oxalis acetosella*, *Mercurialis perennis*, *Trientalis europea* and *Equisetum pratense* were present in the herb layer. *Pleurozium schreberi*, *Hylocomium splendens* and *Plagiomnium affine* dominated

in the moss layer. The soil type of FS-2 is *Terric Histosol*, the depth of the water table was approximately 0.5 m [26,54]. Only the pure groups of the considered tree species were selected for the analysis of the stem increment. These groups were called “peat”.

FS-3 was established in the spring of 2017 as a pure spruce stand, typical for this region, located 200 m from the FS-2 at a mesoeutrophic mineral forest soil site. *Frangula alnus* and *Corylus avellana* were present in the shrub layer. *Oxalis acetosella*, *Vaccinium myrtillus*, *Maianthemum bifolium*, *Trientalis europea*, *Dryopteris filix-mas* and *Equisetum* were present in the herb layer. *Pleurozium schreberi*, *Hylocomium splendens*, *Eurhynchium angustirete* and *Plagiomnium affine* dominated in the moss layer. The soil type of FS-3 is *Gleyic Arenosol*; the water table was about 1.5 m. Only one pure spruce tree group was selected for the present study and it was called “pure”.

Data on soil water potential suitably reflected periods with sufficient humidity in the soil and periods with a lack of moisture, that is, drought periods (Figure 2). Soil water potential at a depth of 40 cm was higher than that at depths of 10 and 20 cm and, in general, agreed well with the precipitation amount at all FS.

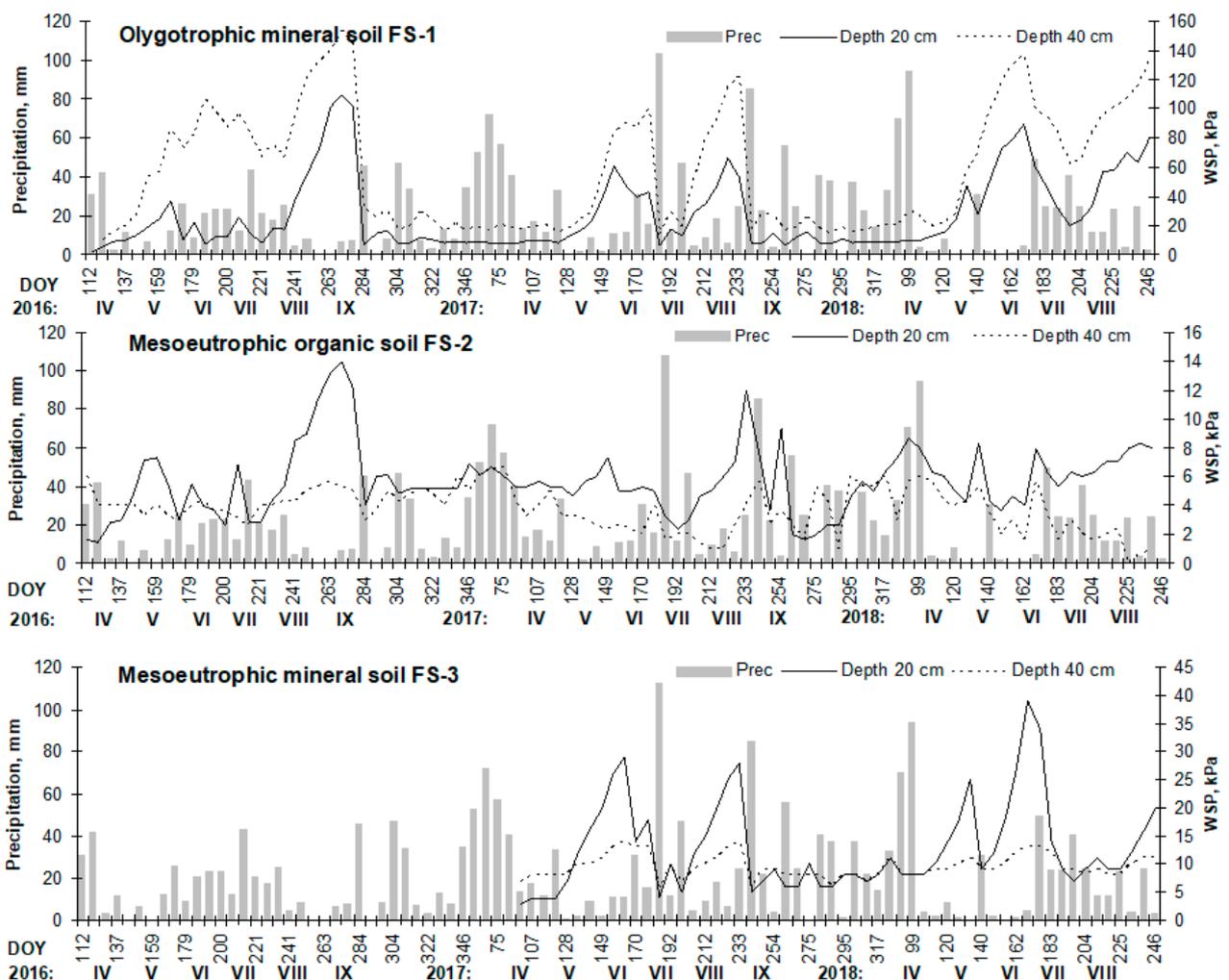


Figure 2. Seasonal dynamics in water soil potential (WSP) and precipitation amount per week at the considered FS during 2016–2018 period. (Roman numbers represent month).

2.2. Variation in Meteorology, Solar Activity and Surface Ozone during 2016–2018 Period

Meteorological parameters, temperature, precipitation amount, humidity, atmospheric pressure, wind speed, solar radiation, soil water potential (SWP) and vapor pressure deficit (VPD), as well as data on surface ozone, were obtained from Aukstaitija IMS (Figure 2).

A positive diurnal stem circumference increment was applied to identify the start of the growing period, and a negative applied to identify the end of the growing period. This period is marked by a textbox in Figure 3.

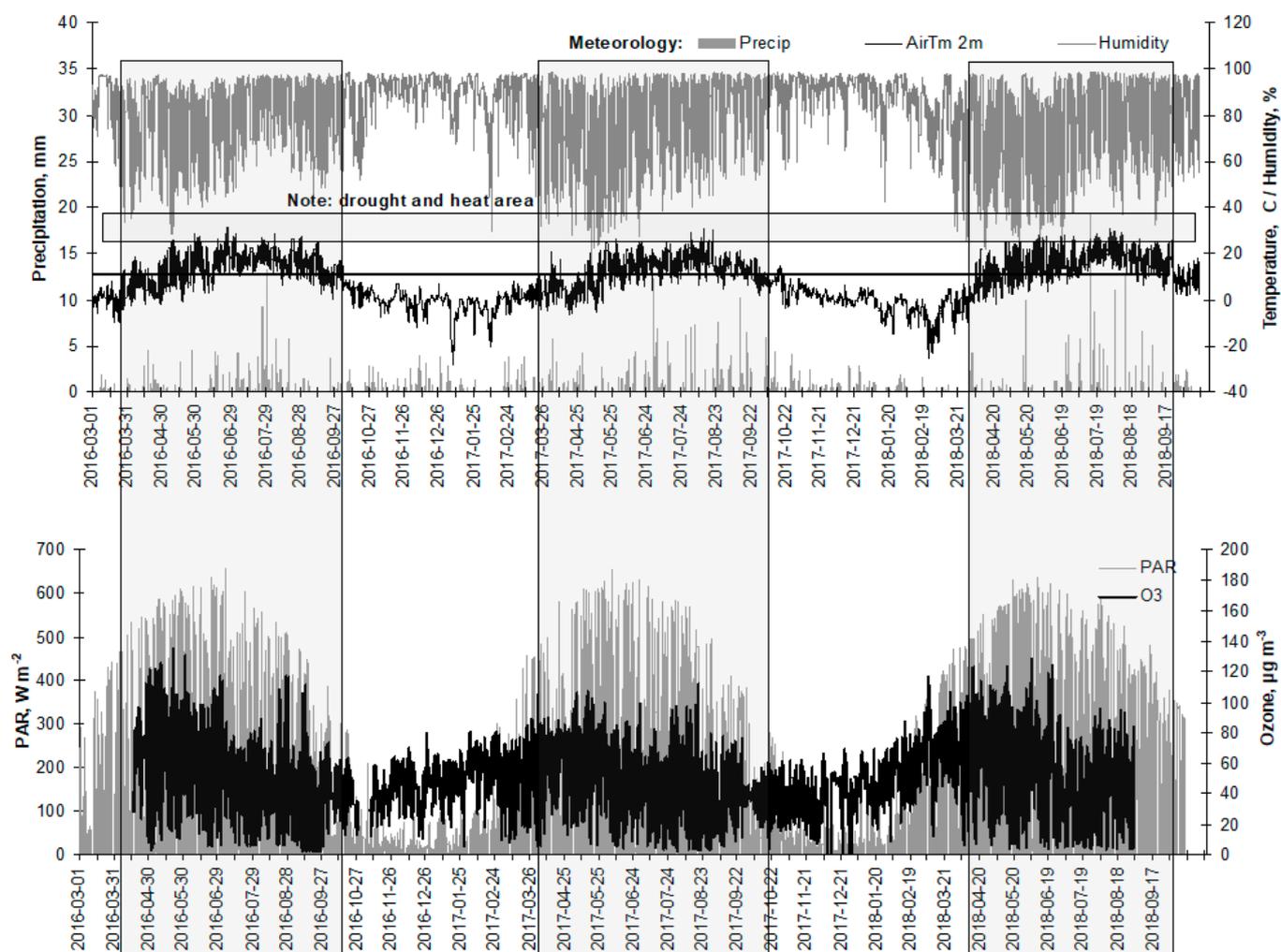


Figure 3. Values of the main meteorological parameters (precipitation, mm per h; temperature, °C; humidity, %) and sun radiation (photo synthetically active radiation, $W m^{-2}$ and surface ozone, $\mu g m^{-3}$) on hourly scale in Aukstaitija IMS, 2016–2018. Periods when mean temperature exceeded 5 °C are in box.

The drought effect was most expressed in 2018. In that year, sun PAR radiation together with air temperature was the highest. The maximal value of surface ozone was registered in 2016. Drought was detected during the period when mean daily humidity decreased below 40% and air temperature exceeded 25 °C.

Soil water potential was analyzed by applying data from 4 × 3 watermark soil moisture sensors (10, 20, 40 cm depth), which were installed under the canopy at all forest sites.

The vapor pressure deficit in hPa was obtained from relative humidity and air temperature data.

Ozone uptake was evaluated by combining hourly canopy conductance data with ambient ozone concentrations. Canopy conductance for water vapor was derived from xylem sap flow data measured in tree trunks. Sap flow density was estimated with the heat dissipation method [59], using SFM1 Sap Flow Meters (SFM1 instrument, ICT International, Australia). Sap flow sensors were installed on all monitored trees at approximately 120 cm stem height in N-exposition and sheltered with aluminum foil caps. 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). Measuring intervals of 15 min were summarized to hourly values as the basis for all further calculations [54].

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).

Using the tree stem sap wood area obtained at the measured height, sap flow density was upscaled to the whole tree. Using the total leaf area for pine and spruce trees and the projected leaf area for birch trees, the whole tree sap flow was scaled to the ground area related whole-tree transpiration (E_C). E_C data were time shifted according to the ambient solar radiation and VPD, in order to obtain current, more accurate ozone uptake results.

Whole-tree canopy conductance to water vapor scaled to ground area (G_C) was determined from the time ratio of the time shifted ground area related to whole-tree transpiration (E_C) versus ambient (VPD) according to [60]:

$$G_C = E_C / \text{VPD}. \quad (1)$$

The whole tree O_3 uptake was then calculated according to the flux equation:

$$F_{CO_3} = O_3 \times G_C \times 0.613, \quad (2)$$

where F_{CO_3} is the whole-tree canopy O_3 flux or uptake rate scaled to ground area, O_3 is the ozone concentration of the ambient air, G_C is the whole-tree canopy conductance for water vapor scaled to ground area, and 0.613 is a conversion factor to account for the lower diffusivity of O_3 relative to water vapor in air [61].

2.3. Data Sampling Methods

Ten averaged data series of tree ring stem increments on an hourly scale based on electronic dendrometers data (DRL 26, EMS Brno Regio 621 00 Czech Republic) were prepared to detect the regional peculiarities of tree increment including reversible stem shrinking and swelling and irreversible increment in relation to meteorology and surface ozone. At least three hourly sequences of stem circumference variation of each considered tree species obtained from DRL 26 were used to calculate the stem basal area increment (BAI) and complete their averaged data series.

The obtained data allowed for examining the reversible and irreversible fluctuations in stem circumference, which were related to daily changes in stem water potential and fluctuations in bark, phloem and in xylem [62–64]. To meet the objectives of the presented study stem basal area increment (BAI) based on stem circumference data was detected.

2.4. Data Analyses

Pearson correlation analysis was used to examine the relationship between stem BAI and meteorological parameters on an hourly scale and to detect the key parameters most significantly related to changes in stem BA: its shrinking and swelling including increments during 2016–2018 vegetation periods. The period of stem growth was separated into two distinct phases based on changes in stem circumference: data with negative values were used to analyze the key environmental factors responsible for stem shrinking, and positive values were used to analyze the key environmental factors responsible for stem swelling. Generalizing the obtained results, a diurnal approach was applied to all data to meet the objectives of presented study.

To solve this problem, a linear multiple regression technique implemented in the statistical software STATISTICA version 8.0 www.statsoft.com (accessed on 21 June 2021) was applied. Single hourly values on the considered predict variables during the vegetation season were included in the multiple regression models. While developing the models, the selected parameters were excluded from the regression model by a stepwise procedure

based on the lowest level of significance [65]. Finally, variables with a high level of significance ($p < 0.05$) were used to run the models. These parameters were evaluated as key factors limiting hourly fluctuations in the stem BAI of the prevailing tree species in Lithuania under different growth conditions. The goodness-of-fit of each model was assessed by determining the coefficient of determination (R^2) and the level of statistical significance (p).

The effect of surface ozone was detected by using different methodological approaches: firstly, detecting relationships between ozone concentration and variation in stem BAI; secondly, analyzing the effect of ozone fluxes through stomata; and finally, the significance of the O_3 effect was established by developing regression models and calculating the differences in R^2 and p with the ozone effect and without it.

3. Results

3.1. Annual Increment, Sap Flow Intensity and WUE of the Prevailing Tree Species

The swelling and shrinking processes of stem circumference during the dormant period, that is, from the beginning of September up to the beginning of new vegetation in April or May, were not included in the analysis. The period of the investigation was characterized by an over moisture regime in 2017, when the precipitation during the vegetation period exceeded 680 mm, which was close to the long-term annual average of precipitation at this location and the longest duration of vegetation period, which exceeded 220 days (Table 2). That year, the vegetation period was the coolest and least polluted by surface ozone if compared with the other two considered years (Figure 3).

Table 2. Duration and main meteorological characteristics (precipitation, Pr and temperature, Tm) of the considered vegetation periods.

Year	Vegetation Period (DOY)			Solar Radiation	Meteorology and Ozone of Vegetation Period				
	Start	End	Length	PAR	Precipitation	Temperature		Surface Ozone	
						Mean	Max	Mean	Max
	DOY	DOY	days	kW m^{-2}	mm	$^{\circ}\text{C}$	$^{\circ}\text{C}$	$\mu\text{g m}^{-3}$	$\mu\text{g m}^{-3}$
2016	85	303	218	552	403.2	13.8	31.7	51.7	135.6
2017	75	295	220	555	685.1	12.1	31.1	49.4	112.4
2018	94	293	199	650	378.0	14.7	31.1	55.2	128.8

Precise measurements of the stem circumference at an hourly scale indicated that, on the 10–12 May, the first signs of the tree ring formation of coniferous trees were detected, first of all at the mineral soil forest site (FS) (Figure 4). After a few days, their growth started at the organic peatland FS. Birch tree growth started a few days after the coniferous tree species at both considered FSs. Rather, regular growth with stem shrinking during the daytime and swelling at night, including growth, was observed until the middle of June, when the drought period started. Drought, which continued for about two weeks during each considered year, that is, from approximately the middle or end of June up to the beginning of July, had a significant impact on the tree stem increment.

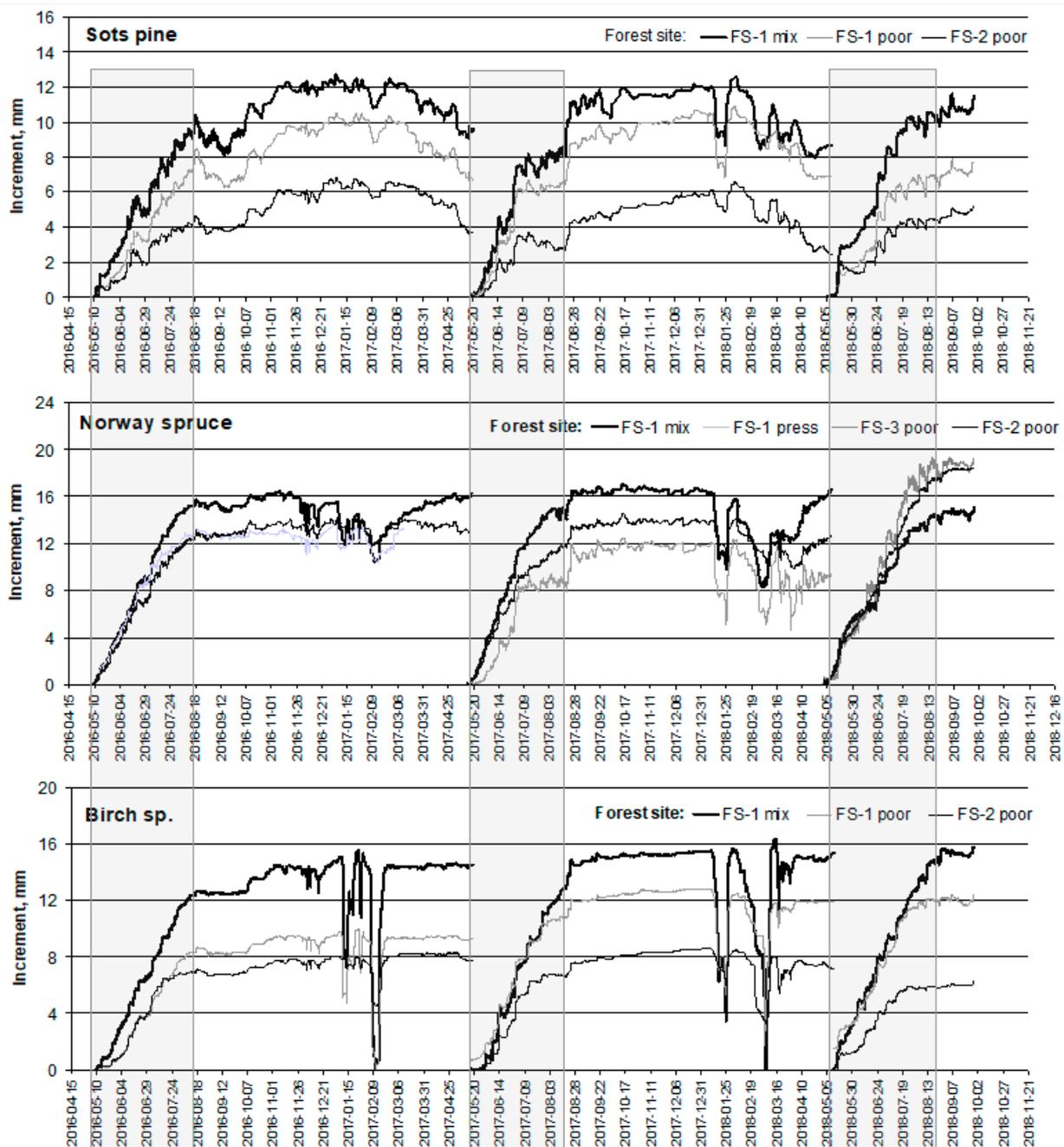


Figure 4. The cumulative seasonal prolongation of stem circumference (mm) of the prevailing tree species in Lithuania at three forest sites in Aukštaitija IMS, 2016–2018. Trees growth periods are in box.

Precipitation, which interrupted the effect of drought on tree growth, affected the tree increment remarkably. After episodes with abundant precipitation, the highest growth rate, including stem swelling, was recorded for spruce trees and the lowest for birch trees at all investigated FSs. The end of tree ring width formation was detected at approximately the same time, that is, 15–18 August.

FS conditions also had no impact on this phenological stage of monitored trees. The obtained data revealed that, in the middle of August, tree ring width formation stopped and afterwards only stem circumference fluctuations with higher shrinking rates were recorded.

Therefore, the 95-day period from tree ring width formation, starting on the 12 May up to its end on 18 August, was chosen for the detailed investigation of the causative effects of meteorology and surface ozone at the level of stem circumference fluctuations at the

hourly scale. The exceptional case was the end of the growth of spruce trees at the peatland FS in 2018 when the stem increment/circumference swelling continued until the beginning of October (Table 3).

Table 3. Main characteristics of the monitored trees at different forest sites, their transpiration, water use efficiency and O₃ flux intensity.

Year	Forest Site	Growing Period (DOY)			Annual Increment			Transpiration	WUE	O ₃
		Start	End	Duration	Circumference	Basal Area	Volume			
		DOY	DOY	Days	mm	cm ²	dm ³			l
<i>Sots pine—Pinus sylvestris L.</i>										
2016	FS-1 mix	131	221	90	10.28	13.8	19.0	3169	166.8	0.463
2016	FS-1 pure	132	225	93	8.5	10.3	13.2	2492	188.1	0.347
2016	FS-2 peat	134	226	92	4.6	7.93	10.8	5469	506.4	0.750
2017	FS-1 mix	144	220	101	9.22	12.9	17.1	3290	192.4	0.650
2017	FS-1 pure	145	220	75	7.85	9.5	12.3	2481	201.7	0.548
2017	FS-2 peat	146	220	74	3.41	5.8	7.9	4124	522.0	0.770
2018	FS-1 mix	136	219	83	11.62	16.4	21.6	4633	214.5	0.762
2018	FS-1 pure	137	219	82	7.9	10.7	13.8	3506	254.1	0.679
2018	FS-2 peat	137	220	83	5.09	9.1	12.3	4044	328.8	0.679
<i>Norway spruce—Picea abies Karst.</i>										
2016	FS-1 mix	129	226	97	15.43	20.6	22.6	1891	83.7	0.241
2016	FS-1 press	130	227	98	13.01	14.0	16.3	1827	112.1	0.248
2016	FS-2 peat	131	227	98	13.15	25.8	37.8	6904	182.6	0.766
2017	FS-1 mix	127	230	103	16.44	21.9	23.5	3313	141.0	0.680
2017	FS-2 peat	128	229	101	13.43	25.3	37.3	8962	240.3	2.164
2017	FS-3 pure	141	226	85	11.76	17.2	27.3	5813	212.9	0.651
2018	FS-1 mix	96	239	143	14.92	22.8	29.4	3301	112.3	0.717
2018	FS-2 peat	99	240	141	18.45	43.3	63.5	10693	168.4	2.192
2018	FS-3 pure	130	239	109	19.27	37.3	55.5	8477	152.7	0.960
<i>Silver & downy birch—Betula pendula L. & B. pubescens L.</i>										
2016	FS-1 mix	132	231	99	12.68	15.0	16.1	3926	243.9	0.521
2016	FS-1 pure	134	231	97	8.74	13.7	18.3	2865	156.6	0.373
2016	FS-2 peat	132	231	99	7.16	13.2	16.6	3332	200.7	0.467
2017	FS-1 mix	143	236	93	14.92	17.8	19.0	3716	195.6	0.823
2017	FS-1 pure	142	236	94	11.4	18.2	24.4	4760	195.1	1.053
2017	FS-2 peat	145	236	91	7.59	13.8	17.6	1916	108.9	0.638

Table 3. Cont.

Year	Forest Site	Growing Period (DOY)			Annual Increment			Transpiration	WUE	O ₃
		Start	End	Duration	Circumference	Basal Area	Volume			Flux
		DOY	DOY	Days	mm	cm ²	dm ³			/1000
2018	FS-1 mix	129	235	106	15.6	19.1	20.4	2546	124.8	0.499
2018	FS-1 pure	131	225	94	10.64	17.7	23.7	4922	207.7	0.957
2018	FS-2 peat	133	207	74	5.9	10.8	13.7	1924	140.4	0.360

The obtained results revealed that spruce trees demonstrated the highest growth rate during this period at both considered forest sites. Only the growth rate of the pine and birch trees differed significantly. At the mineral *oligotrophic* soil FS, the growth rate of the pine trees exceeded the growth rate of silver birch trees, while at the organic soil FS, the growth rate of downy birch trees exceeded the growth rate of *Scots pine* trees.

Winter shrinkage exceeded the growth rate of a whole season, which has been mentioned by other scientists [40], and was especially noticeable in the birch tree growth series in January and February.

The mean parameters of the monitored trees revealed that pine trees demonstrated the biggest stem increment in 2018 after a very humid vegetation period in 2017 (Table 3). This tendency was detected at both pine FSs. The comparison of tree increments among FSs showed that pine trees growing together with deciduous trees at oligotrophic mineral FS-1 were the most productive. Their increment was the biggest. The pine increment at FS-1, growing in group with other pine trees, was a little lower and the least increment was detected for pine trees growing at the mesoeutrophic organic (peatland) FS-2, which is not typical for pine growth in Lithuania.

Different results were obtained comparing sap flow intensity data, which were in a close relationship with water contents at the site. The highest sap flow intensity was observed for pine trees growing at the peatland FS-2. There, the water use efficiency (WUE) of pine trees was the lowest, that is, for 1 dm³ of timber production pine used up to 500 L of water. The highest WUE was detected for pine trees growing at the oligotrophic mineral FS-1 together with deciduous trees, that is, WUE reached 200–300 L of water for 1 dm³ of timber.

Spruce trees demonstrated different results. The biggest annual increment was observed for spruce trees growing at mesoeutrophic mineral FS-3, while their WUE was one of the lowest, that is, about 150–200 L per 1 dm³ of timber. The highest WUE was detected at oligotrophic mineral FS-1 with a lack of humidity, that is, only 80–150 L of water for 1 dm³ of timber. At mesoeutrophic organic FS-2 with an over-moisture regime, WUE was the lowest and made 180–240 L per dm³ of timber. Water availability was the key factor responsible for spruce tree productivity and WUE.

Birch trees growing in pure stands at oligotrophic mineral FS-1 demonstrated the highest productivity and their WUE made about 200 L per dm³ of timber and did not differ significantly from the WUE of pine trees. Significant differences among birch tree WUE on FS-2 were not detected.

3.2. Intra-Annual Fluctuation in Stem Basal Area of the Prevailing Tree Species

Maximal growth rate, which exceeded the regular growth rate, was recorded in periods with rather abundant precipitation and a lower temperature. Such conditions were first of all favorable for stem swelling including the increment. The time and duration of these processes differed among the considered tree species. An increase in the stem circumference of pine trees was recorded at 6 p.m. and reached its maximal value at 8 p.m.; meanwhile, for spruce trees, the maximal value in increment was reached at midnight. Such expansion of circumference including growth/new cells formation continued for pine

trees up to 5–6 a.m. meanwhile for spruce trees up to 8–9 a.m., that is, a few hours longer than for pine trees. By contrast, birch tree stem swelling started at 3 p.m. and reached its maximal value at 7 p.m. and stopped at 7 a.m., that is, earliest if compared with coniferous species. At the organic soil forest site, no significant difference in stem increment formation was detected.

Exceptionally different growth rates were established for the considered tree species during the drought period. During this period, the mean daily temperature exceeded 25 °C, humidity decreased by up to 40% (Figure 3). These environmental conditions were unfavorable for tree growth and mainly resulted in stem shrinking and the inhibition of ring increment over a 10 h period, that is, from 8 a.m. up to 6 p.m., and the suppression of the stem swelling during the night.

The results obtained on the balance of stem BA shrinking and swelling at the diurnal scale were rather surprising. Spruce trees demonstrated the greatest decrease in stem BA during the daytime and the greatest increase during the nighttime at both FSs. An approximately twofold lower reduction and increase in stem BA were recorded for pine trees during these time periods and only birch stem BA shrinking and swelling processes were close to zero. At organic soil FS-2, the intensity of these processes was less expressed for all considered tree species than at mineral soils FS-1. There, spruce stem BA swelling was significantly higher than shrinking, which indicated that, even during drought episodes, more humid site conditions were more favorable for spruce tree growth than for pine and birch tree growth.

Generalizing the shrinking–swelling processes during the vegetation, it was established that stem the BA shrinking process continued for up to 35% of the hours while the swelling process was up to 65% of the hours (Table 4). This means that during the day shrinking occurred for 8 h and swelling was two-fold longer, that is, 16 h. No significant differences among tree species and forest site conditions were established.

Table 4. Swelling and shrinking of tree stem basal area of the considered tree species under different growth conditions during 2016–2018.

Tree Species Forest Site		2016		2017		2018	
		Shrinking	Swelling	Shrinking	Swelling	Shrinking	Swelling
Spruce-mix FS-1	mm ²	−12.94	33.56	−14.36	36.35	−32.68	55.51
	h	742	1580	863	1644	1208	2282
	mm ² /h	−0.017	0.021	−0.017	0.022	−0.027	0.024
	h, %	32.0	68.0	34.4	65.6	34.6	65.4
Spruce-press FS-1	mm ²	−11.19	25.23				
	h	1035	1282				
	mm ² /h	−0.011	0.020				
	h, %	44.7	55.3				
Spruce-pure FS-3	mm ²			−43.14	60.39	−129.7	167.0
	h			775	1374	966	1707
	mm ² /h			−0.056	0.044	−0.134	0.098
	h, %			36.1	63.9	36.1	63.9
Spruce-peat FS-2	mm ²	−39.12	64.92	−24.1	49.43	−47.79	91.24
	h	808	1489	867	1613	1164	2256

Table 4. Cont.

Tree Species Forest Site	2016		2017		2018		
	Shrinking	Swelling	Shrinking	Swelling	Shrinking	Swelling	
	mm ² /h	−0.048	0.044	−0.028	0.031	−0.041	0.040
	h, %	35.2	64.8	35.0	65.0	34.0	66.0
Pine-mix:	mm ²	−27.31	41.09	−20.94	33.88	−15.71	32.06
FS-1	h	767	1369	681	1168	854	1450
	mm ² /h	−0.036	0.030	−0.031	0.029	−0.018	0.022
	h, %	35.9	64.1	36.8	63.2	37.1	62.9
Pine-pure	mm ²	−11.37	21.67	−7.23	16.75	−12.38	23.1
FS-1	h	812	1418	703	1119	961	1343
	mm ² /h	−0.014	0.015	−0.010	0.015	−0.013	0.017
	h, %	36.4	63.6	38.6	61.4	41.7	58.3
Pine-peat	mm ²	−15.23	23.16	−9.95	15.7	−13.09	22.12
FS-2	h	836	1397	777	1047	978	1326
	mm ² /h	−0.018	0.017	−0.013	0.015	−0.013	0.017
	h, %	37.4	62.6	42.6	57.4	42.4	57.6
Birch-mix:	mm ²	−9.71	24.75	−10.49	28.29	−17.39	36.49
FS-1	h	866	1532	935	1307	900	1632
	mm ² /h	−0.011	0.016	−0.011	0.022	−0.019	0.022
	h, %	36.1	63.9	41.7	58.3	35.5	64.5
Birch-pure	mm ²	−10.09	23.74	−9.41	27.6	−13.7	31.38
FS-1	h	898	1427	969	1311	850	1433
	mm ² /h	−0.011	0.017	−0.010	0.021	−0.016	0.022
	h, %	38.6	61.4	42.5	57.5	37.2	62.8
Birch-peat	mm ²	−8.82	21.83	−7.28	21.1	−8.73	19.48
FS-2	h	850	1548	805	1406	647	1134
	mm ² /h	−0.010	0.014	−0.009	0.015	−0.013	0.017
	h, %	35.4	64.6	36.4	63.6	36.3	63.7

Differences in the annual increment resulted in changes in the hourly rate of BA shrinking and swelling processes. For birch trees, the hourly rate of stem shrinking was significantly lower than the hourly rate of stem swelling. For pine trees, the hourly rate of stem shrinking was lower than or equal to the hourly rate of stem swelling. For spruce trees, the hourly rate of stem shrinking was lower than or equal to the hourly rate of stem swelling at FS-1 and FS-2 and higher at FS-3.

3.3. Intensity of Shrinking and Swelling of Stem Basal Area on Hourly Scale in Relation to Environmental Factors

It is well established that the timing and magnitude of diurnal variations in stem size are mainly determined by the course of transpiration and soil water content [37], both of which are mainly related to precipitation amount and air humidity, that is, to microclimatic conditions, and can rapidly change under different weather conditions [66].

To detect the key environmental parameters responsible for water contents in xylem and cambium, which resulted in fluctuations in stem circumference, a separate analysis of stem BA shrinking and swelling processes in response to environmental conditions was

performed. The considered predicted variables had a more significant effect on variation in stem BA shrinking than its swelling. The key factor that stimulated the shrinking process for spruce trees was low humidity level and a higher temperature together with SWP and VPD. The other considered variables only stimulated stem shrinking, the most significant of which was the negative effect of PAR (Figure 5). The effect of O₃ fluxes on stem shrinking was not significant, especially at FS-1 for spruce trees suppressed by neighboring trees (Figure 5, Norway spruce, Press).

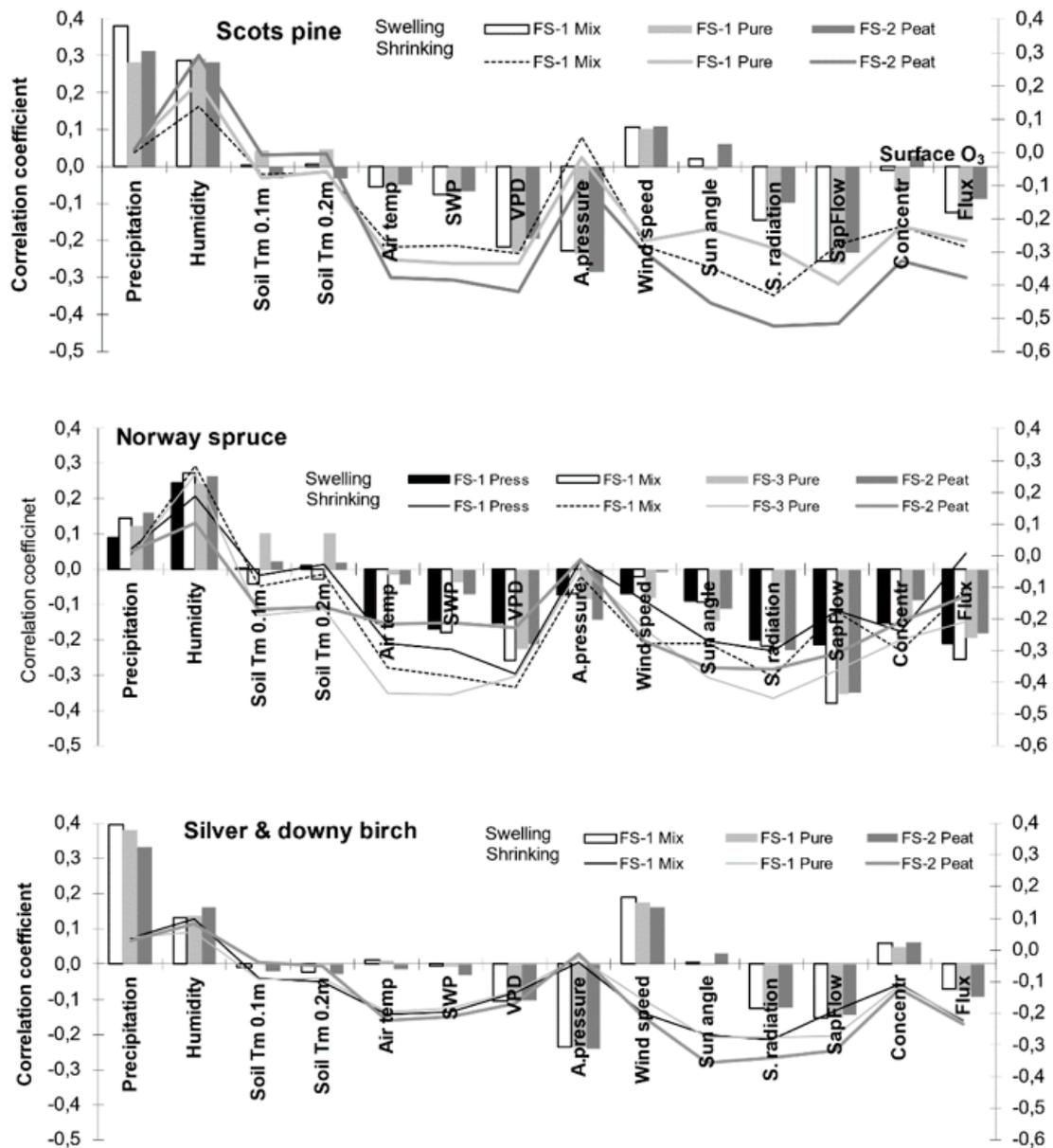


Figure 5. Relationship between values of the stem basal area fluctuations (shrinking and swelling) on hourly scale of the considered tree species and meteorology at different forest sites. Silver birch on FS-1 and downy birch on FS-2.

Quite a similar relationship was detected between fluctuations in pine stem BA and the considered environmental factors. The significant adverse effect of atmospheric pressure is noticeable, but this effect can be explained mainly through the collinearity of this parameter with the rest of the considered parameters, first of all, temperature and humidity. O₃ fluxes had a more significant effect on stem shrinking than on stem swelling.

Contrary to the results obtained for coniferous trees, the direct effects of temperature and humidity were lower for both stem swelling and shrinking processes of the birch tree (Figure 5). The direct effect of surface ozone fluxes had a more significant effect on stem shrinking than on stem swelling. The effect of precipitation on stem swelling process intensity was expressed most significantly. A much lower effect of PAR and ozone fluxes was detected on stem shrinking during daytime in comparison with their effect on the stem shrinking of pine trees. The obtained data revealed that, in general, the effect of the considered environmental factors on birch stem BAI was less expressed than that on coniferous trees.

Multi regression models of tree BAI revealed that wind speed, PAR, soil water potential, vapor pressure deficit and ozone fluxes are the key factors resulting in pine tree stem BA shrinking (Table 5). They explained up to 20% of the variation in shrinking intensity at oligotrophic mineral soil FS-1 and up to 30% of its variation at mesoeutrophic organic soil FS-2.

The predicted variables, with the exception of O₃ fluxes, explained up to 24% of the variation in spruce stem BA shrinking at FS-1. O₃ fluxes had no significant effect on spruce tree stem shrinking at this FS-1, while their effect at FS-2 and FS-3 was significant. In addition, temperature, PAR and VPD were also key variables at these FSs. These parameters explained about 12% and 22% of the variation in spruce tree stem shrinking, respectively.

Wind speed, temperature, PAR and O₃ fluxes were the key parameters resulting in birch tree stem shrinking variation. However, their explanation rate was the lowest if compared with the rate obtained for coniferous tree species, that is, only up to 10%.

None of the considered parameters with the effect of mitigating the stem shrinking process remained in the models.

The multi-regression models created revealed that only the direct effect of precipitation amounts, relative humidity and wind speed resulted in statistically significant intensity of stem BA swelling (Table 6). SWP was responsible for the mitigation of the swelling process only for spruce trees at FS-1. Surface ozone fluxes demonstrated highly significant inhibition of stem BA swelling of all tree species at all considered FSs.

3.4. Integrated Effect of Environmental Factors on Hourly Fluctuation in Stem Basal Area

During the entire period of tree ring formation, only precipitation and relative humidity stimulated tree stem increment (Figure 6). Based on the obtained results, birch trees were least tolerant to the lack of precipitation at both considered FSs, while spruce trees demonstrated the highest resiliencies to this factor. The key factor resulting in spruce stem increment was relative humidity.

Lower values of VPD and SWP also stimulated spruce tree stem increment most significantly if compared with the other considered tree species. On the other hand, higher temperature together with solar PAR also most significantly resulted in a decrease in spruce stem increment through its shrinking.

Different results were obtained when investigating the effect of air humidity on the stem increment of the considered tree species. Both coniferous tree species demonstrated higher requirements for humidity for a greater rate of tree stem increment than birch trees, and surprisingly at the organic soil forest site. Temperature and sun characteristics, that is, photoperiods (sun angle) and PAR, which stimulated stem BA shrinking processes, inhibited the tree stem increment process. The effect of these factors was reinforced by higher wind speed and atmosphere pressure. Consequently, surface ozone, especially its fluxes, also reduced the stem increment.

Table 5. Key factors contributing to the shrinking of tree stem basal area of the considered tree species under different growth conditions and their significance expressed by means of multiple regression model statistics.

Tree Species	Site No	Precipitation	Humidity	Temperature	Wind Speed	Sun PAR	SWP	VPD	O3 Flux	R2	F(a, b)	Std. Error	p<	O3 Flux Effect
Scots pine	FS-1 mix				○	○	○		○	0.225	166	3.02	0.05	8.7
	FS-1 pure				○	○	○	○	○	0.156	91	1.83	0.05	0.8
	FS-2 pure				○	○	○	○	○	0.300	221	1.68	0.05	0.2
Norway spruce	FS-1 mix				○	○	○	○		0.243	226	2.56	0.05	NF
	FS-1 press					○		○		0.151	92	1.78	0.05	NF
	FS-2 pure			○	○			○	○	0.117	94	3.86	0.05	0.8
	FS-3 pure			○	○			○	○	0.223	163	10.1	0.05	1.5
Birch	FS-1 mix				○	○			○	0.092	91	1.64	0.05	0.6
	FS-1 pure					○			○	0.079	116	1.53	0.05	0.2
	FS-2 pure			○	○				○	0.079	66	1.19	0.05	1.3

○—negative effect; NF—no effect.

Table 6. Key factors contributing to swelling of tree stem basal area of the considered tree species under different growth conditions and their significance expressed by means of multiple regression model statistics.

Tree Species	Site No	Precipitation	Humidity	Temperature	Wind Speed	Sun PAR	SWP	VPD	O3 Flux	R2	F(a, b)	Std. Error	p<	O3 Flux Effect
Scots pine	FS-1 mix	●	●		●				○	0.212	267	3.33	0.05	1.1
	FS-1 pure	●	●		●				○	0.174	204	2.37	0.05	0.3
	FS-2 pure	●	●		●				○	0.176	200	2.14	0.05	0.1
Norway spruce	FS-1 mix	●	●				○		○	0.122	189	2.33	0.05	2.3
	FS-1 press	●	●				○		○	0.071	24	1.98	0.05	0.7
	FS-2 pure	●	●						○	0.095	186	3.31	0.05	1.1
	FS-3 pure	●	●						○	0.081	87	7.41	0.05	1.6
Birch	FS-1 mix	●	●		●				○	0.205	287	2.83	0.05	0.8
	FS-1 pure	●	●		●				○	0.187	240	3.17	0.05	0.5
	FS-2 pure	●	●		●				○	0.161	195	2.21	0.05	0.9

●—positive effect; ○—negative effect; NF—no effect.

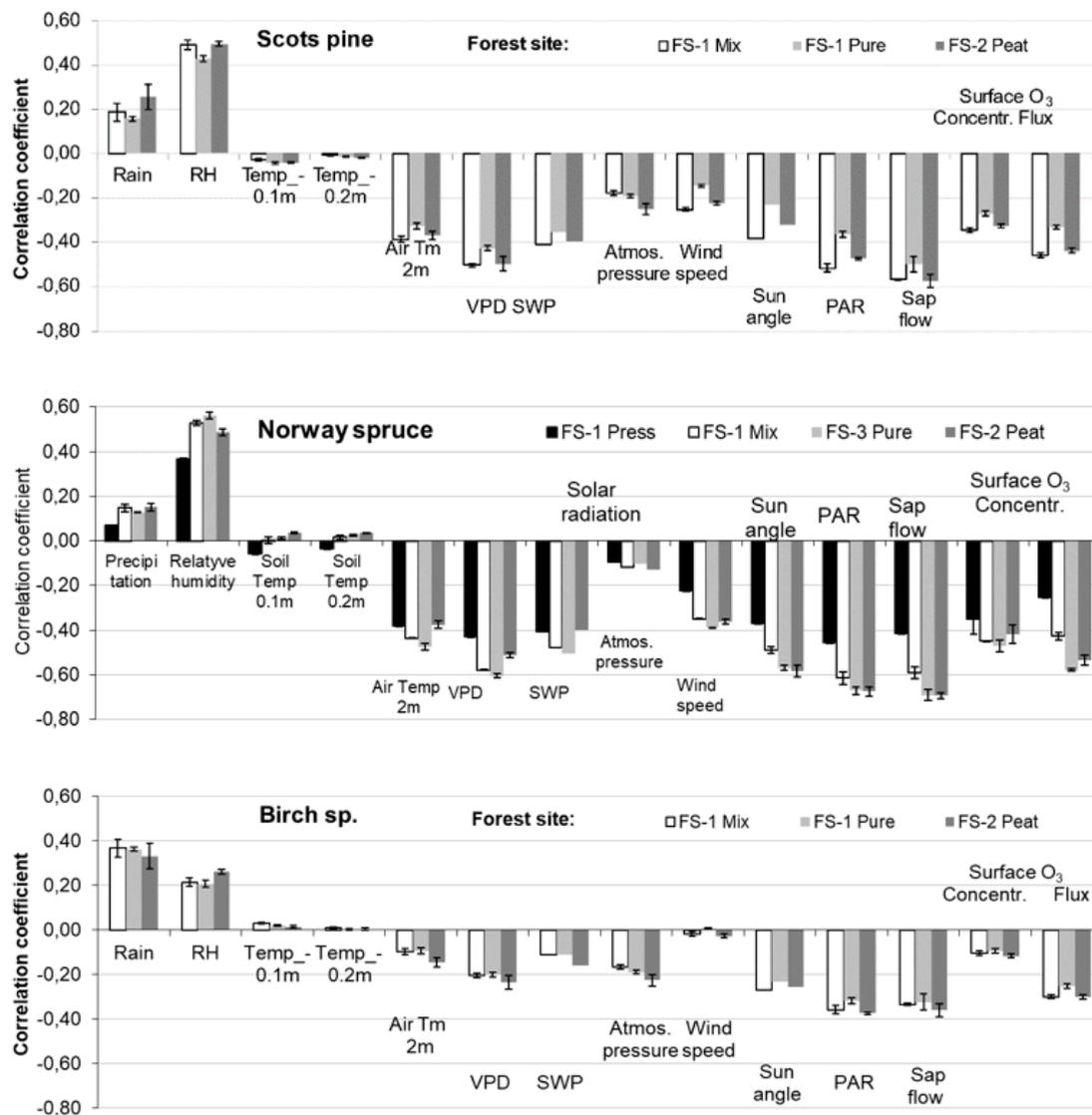


Figure 6. Relationship between data on meteorology on hourly scale and growth rates of the prevailing tree species under different growth conditions in 2016–2018.

The created generalized multiple regression models of tree increment based on an hourly scale allowed for the evaluation of the main detected environmental factors responsible for fluctuations in the stem BA of the considered tree species under different growth conditions (Table 7). Multivariate regression models showed that variations in the stem increment of all considered tree species were positively related to the amount of precipitation and relative humidity, especially for pine trees at all FSs and spruce trees at FS-1. A negative direct effect of temperature was not responsible for the tree stem increment.

Precise measurements of ring width formation indicated close temporal linkages between PAR and patterns of tree stem increment during diurnal cycles, confirming the state of knowledge in this area [67]. O₃ fluxes also remained among the key factors resulting in the BA increment of the considered tree species, inhibiting it. Finally, I can conclude that surface ozone fluxes stimulated shrinking and inhibited the swelling of the tree stem, which resulted in the reduction of tree ring width in general.

Table 7. Key factors of tree ring formation of the considered tree species on hourly scale under different growth conditions and their significance expressed by means of multiple regression models statistics.

Tree Species	Site No	Precipitation	Humidity	Temperature	Wind Speed	Sun PAR	SWP	VPD	O ₃ flux	R ²	F(a, b)	Std. Error	p<	O3 Flux Effect
Scots pine	FS-1 mix	•	•			○		○	○	0.343	656	3.68	0.05	1.6
	FS-1 pure	•	•			○	○	○	○	0.227	312	2.39	0.05	1.0
	FS-2 pure	•	•			○	○	○	○	0.347	564	2.17	0.05	1.9
Norway spruce	FS-1 mix	•	•		○	○	○		○	0.442	933	2.51	0.05	0.6
	FS-1 press		•			○	○		○	0.230	202	2.46	0.05	0.1
	FS-2 pure	•			○	○		○	○	0.473	1460	3.80	0.05	0.7
	FS-3 pure	•				○	○	○	○	0.489	891	8.93	0.05	1.0
Birch	FS-1 mix	•			•	○			○	0.260	630	2.74	0.05	0.9
	FS-1 pure	•			•	○			○	0.226	503	2.91	0.05	0.2
	FS-2 pure	•			•	○			○	0.243	552	2.10	0.05	0.4

•—positive effect; ○—negative effect; NF—no effect.

4. Discussion and Conclusions

Seasonal variability of environmental contaminants and the main meteorological parameters, such as air temperature and soil water regime, are suggested as key research areas for investigating climate change effects on forest ecosystems [53] including the intra-annual variability of environmental effects on tree health and productivity. This means that the continuous monitoring of stem circumference variation throughout the year is crucial for the understanding of tree reactions to short-term changes under environmental conditions such as temperature, air humidity, rainfall and parameters of solar activity as well as air contaminants, including surface ozone.

During the vegetation period, the reversible shrinking and swelling of stems contribute to a significant part of the variability in stem size changes, reflecting the use of water stored in tree tissues [68,69]. This higher variation in stem circumference allows us to gain a deeper insight into stem growth variations in relation to changing environmental conditions including meteorology, natural solar radiation, and surface ozone (O₃) [41,70,71]. Specific parameters, such as changes in hourly rate in the stem basal area, can only be obtained with the stem cycle approach [41,55,70]. To my mind, even the shrinking process cannot be ignored when investigating these rather complicated processes of tree ring width formation. It is most likely that, during deep drought processes, some part of the stem shrinking could not be reversible due to the limited plasticity of the cell membranes. Therefore, this stem-cycle methodological approach allows for separating the high-resolution dendrometer records into distinct phases of contraction, expansion and stem-radius increment. It is supported by many scientists investigating increment formation on the basis of short time sequences [41,66,70,72–74] and therefore was used to meet the main tasks in the presented study.

The obtained data confirmed the background knowledge in the area of short time tree stem increment formation. Stem increment is positively related to precipitation and relative humidity and negatively to temperature, sunshine hours and drought [41,75,76]. Night-time temperature was more effective for stem increment than daytime temperature [38]. This means that stems contract during the day, due to transpiration and photosynthesis, and expand during the night and on rainy days when water reserves are gradually replenished [66] and assimilated carbohydrates are allocated along the stem. These eco-physiological processes differed significantly under different growth conditions due to their different strategies when surviving different (favorable or unfavorable) environmental conditions [77,78]; first of all, heat and drought episodes. Therefore, in general, the obtained data confirmed the statement that weather fluctuations very well reflect seasonal stem increment variation and that different environmental conditions result in statistically significant differences in tree stem increment during the growing season.

Long term investigation of tree growth intensity revealed that, recently, *Norway spruce* trees have demonstrated greater stem radial increment in Lithuania than pine and birch trees [26]. An increase in precipitation amount followed by a decrease in soil water potential and vapor pressure deficit resulted in significantly higher spruce stem increment. Their stem shrinking was higher than that of pine and birch trees; however, stem swelling at nighttime exceeded the intensity of this process in pine and birch trees. These growth reactions indicated their better adaptation to recent climatic conditions in hemi-boreal forest, which contradicts the knowledge of the previous century, that is, that climate change reduces radial growth in spruce stems and especially in the subsequent vegetation period [4,78,79].

Pine trees also demonstrated a very sensitive reaction to environmental changes. Their stem shrinking and swelling processes in general were most expressed during the entire vegetation period. The highest reversible fluctuations in water storage in xylem, phloem and bark did not mask the signal caused by wood formation, which has been referred to by many authors [62,63,80,81], and this is why this species became most sensitive to changes in meteorology and air pollutants including surface ozone in the northeastern part of Europe. The considered meteorological parameters explained the variation in both stem

shrinking and swelling most significantly. These results contradict the findings obtained in Central or Southern Europe, where the increment of *Scots pine* was least sensitive to environmental changes and differed least between different growth conditions [27]. Our data obtained earlier indicated that meteorology and acidifying compounds explained the variation in annual pine tree ring width most significantly [56–58]. On an hourly scale, temperature, precipitation, humidity, sun activity and surface ozone play a major role in pine intra-annual tree ring width formation, confirming our data obtained on annual pine increment.

The integrated effect of meteorology and ozone fluxes on the intra-annual tree ring width formation of birch trees expressed by means of multi regression models was found to be remarkably lower than the effect on spruce or pine annual tree ring width formation. Information on the direct positive hourly effect of temperature and solar radiation on birch tree growth rate is more limited [67,82,83]. Stem shrinking, as well as the whole tree stem increment during the vegetation, was the least explained by meteorological factors. These data very well reflect data obtained at the annual scale. The air temperature of months also had no significant effect on birch growth and only the precipitation amounts during June at the mineral soil forest site stimulated birch tree ring width formation [26]. A very weak relationship between meteorological parameters and birch stem swelling and shrinking could be presented as a key factor which resulted in the gradual decrease in tree ring width in Lithuania.

Finally, the adaptive capacity of the considered tree species to the recent global changes was evaluated based on the reaction of these tree species to variations in hourly concentrations of surface ozone. Among air pollutants, ground-level ozone (O_3) is one of the main drivers of changes in forest conditions [53]. During the considered time, mean ozone concentration reached about $60 \mu\text{g m}^{-3}$, meanwhile its maximal values rarely exceeded $125 \mu\text{g m}^{-3}$ with the exception of 2016. This concentration could be evaluated as low with a negligible effect on tree growth; however, earlier results indicated that maximal values in surface ozone had a negative and significant effect on pine stem increment [52]. Despite this, our data confirmed the statement obtained by McLaughlin et al. [67] and the negative effect of ozone fluxes on short time tree increment formation was found to be weak but statistically significant ($p < 0.05$), especially under more humid conditions. Based on the obtained results, the coniferous tree species seems to be more sensitive to ozone damage than birch trees, and these data also agreed well with data obtained at the hourly scale [26].

On the basis of these results, I could conclude that birch trees, which demonstrated the lowest (positive or negative) reaction to the environmental changes, should be evaluated as not having capacity to adapt to existing environmental conditions and their prospects of composing sustainable succession is very problematic, especially when their annual growth gradually decreases. The hypothesis that the coniferous species are more adaptive to recent climate changes in Lithuania and their capacity to mitigate the threats of global changes is higher than that of deciduous tree species was confirmed on an hourly scale of variation in stem circumference.

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Conflicts of Interest: I declare no conflict of interest.

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