Growth limiting factors and climate response variability in Norway spruce (*Picea abies* L.) along an elevation and precipitation gradients in Slovenia

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Abstract:

Norway spruce (*Picea abies* L.) is among the most sensitive coniferous species to ongoing climate change. However, previous studies on its growth response to increasing temperatures have yielded contrasting results (from stimulation to suppression), suggesting highly site-specific responses. Here, we present the first study that applies two independent approaches, i.e. the non-linear, process-based Vaganov-Shashkin (VS) model and linear daily response functions. Data were collected at twelve sites in Slovenia differing in climate regimes and ranging elevation between 170 and 1300 m a.s.l. VS model results revealed that drier Norway spruce sites at lower elevations are mostly moisture limited, while moist high-elevation sites are generally more temperature limited. Daily response functions match well the pattern of growth limiting factors from the VS model and further explain the effect of climate on radial growth: prevailing growth limiting factors correspond to the climate variable with higher correlations. Radial growth correlates negatively with rising summer temperature and positively with higher spring precipitation. The opposite response was observed for the wettest site at the highest elevation, which positively reacts to increased summer temperature and will most likely benefit from a warming climate. For all other sites, the future radial growth of Norway spruce largely depends on the balance between spring precipitation and summer temperature.

Keywords: Vaganov-Shashkin model; climate-growth correlations; tree rings; process-based modelling; dendroTools; dendroclimatology

1. INTRODUCTION

Norway spruce (*Picea abies* L.) is among the most important European tree species from both an economic and ecological point of view (Caudullo et al. 2016; Brus et al. 2012). In previous centuries, it was preferred for planting in managed forests due to its fast growth, high quality wood, wide ecological amplitude and adaptive capacity to various site conditions (Klimo et al. 2000; Spiecker 2003). In recent decades, however, Norway spruce has suffered from natural hazards such as windthrows, ice-storms, insect outbreaks and droughts (Schelhaas et al. 2003; Seidl et al. 2016), resulting in a decline in its share in the national growing stocks of many European countries, including Austria (BMLFUW 2017), the Czech Republic (MZe 2018), Germany (BMEL 2015), Latvia (Tērauds et al. 2011), Slovakia (MPSR 2019), Slovenia (Skudnik et al. 2019) and southern Sweden (Valinger et al. 2014). Furthermore, some projections show that this trend will continue for the whole of Europe in the future (Buras and Menzel 2019; Hanewinkel et al. 2013). Extreme climate conditions, increasing temperatures and altered precipitation patterns are among the highest risks related to less suitable habitat conditions for Norway spruce in future decades (Lévesque et al. 2013; van der Maaten-Theunissen et al. 2013). Despite the evident threats associated with a warmer and drier climate, there is evidence that Norway spruce is exhibiting faster growth than that recorded in the past century, especially at higher elevations close to the timberline (Pretzsch et al. 2014; Cienciala et al. 2018; Kahle et al. 2008; Ponocná et al. 2016; Hartl-Meier et al. 2014). Norway spruce has shown contrasting responses to climate at lower and higher elevations (Andreassen et al. 2006; Kolář et al. 2017; Sidor et al. 2015), indicating that site-specific conditions need to be considered to more accurately estimate its future growth, vitality and habitat suitability (Reyer et al. 2017).

Although Norway spruce is among the most studied European species, predictions of its response to diverse growth conditions (environmental changes) remain challenging. Models based on realistic underlying processes would improve our understanding of the performance of the species in the future. Furthermore, silvicultural practices could be more effectively adjusted in order to mitigate the effects of climate change (Klopčič et al. 2017). Process-based modelling provides a unique insight into underlying processes resulting in tree growth (Guiot et al. 2014). One frequently applied process-based model for simulations of intra- and inter-annual tree-ring characteristics of conifers is the Vaganov-Shashkin (VS) model (Vaganov et al. 2006; Shishov et al. 2016), which incorporates the nonlinear and nonstationary relationship between climate and radial tree growth. The VS model incorporates the principle of growth limiting factors through the calculation of growth potential on a daily basis as a result of soil moisture, temperature and solar irradiance. The most limiting factor defines the potential for growth for each day. With the parameterization process, the effect of climate on radial conifer growth is defined and available for interpretation. To the best of our knowledge, the VS model has not yet been applied to Norway spruce, although Tumajer et al. (2017) studied moisture and temperature limitations in Norway spruce in the Czech Republic with the VS-Lite model (Tolwinski-Ward et al. 2011), which is a simplified VS model based on monthly climatic data.

To better understand the underlying growth limiting factors of Norway spruce and how they vary with respect to different site conditions, we analysed spruce chronologies from twelve sites in Slovenia. Slovenia is characterized by a transitional climate with wide local climatic variability and pronounced gradients that support the growth of this species on a wide variety of sites. Thus, the findings of our study could be applied to different sites across Europe with similar growth conditions. The main objectives of our study were 1) to parameterise the VS model for the selected Norway spruce sites, 2) to extract daily growth rates and infer about

95 limiting growth factors and how they vary in time, 3) to further use daily growth rates to infer
96 about growing season patterns and 4) to analyse climate-growth correlations with daily
97 response function and compare the results with the VS model. We hypothesise that specific
98 sites will show variable growth patterns and responses to climatic conditions, i.e. growth
99 stimulation/reduction due to increasing temperature in moist/dry sites.

100

101 **2. METHODS**

102 **2.1 Site description and climate data**

103 Twelve spruce sites were selected for sampling in 2016–2018. The sites ranged from dry and
104 warm low elevation sites in eastern Slovenia to moist and cold high elevation sites in the
105 central, north-western and southern parts of the country (Figure 1). All sampled sites are
106 managed forests in the adult developmental stage, with Norway spruce as the dominant tree
107 species. The main differences between the selected sites are elevation, climate regimes and
108 soil types (Table 1). For each site, daily precipitation sums and mean temperature data were
109 extracted for the closest grid point from the E-OBS gridded climate datasets (Cornes et al.
110 2018). E-OBS version 21.0e on a 0.1-degree regular grid was used, which starts on January 1,
111 1950. To account for differences in longitudes, latitudes and elevations between E-OBS grid
112 points and site locations, climate data was spatially interpolated using cokriging, where
113 elevation was used as covariate for the cokriging method (Apaydin et al. 2004; Adhikary et al.
114 2017).

115 **Table 1:** Site descriptions with annual mean temperature (T) and precipitation (P) sums in
116 the period 1950–2018.

Site	Short	Lon	Lat	Elevation [m]	Annual T [°C]	Annual P [mm]	Soil type
Apače	APA	15.55	45.68	210	9.3	979	Dystric Fluvisol
Brežice	BRE	15.64	45.95	170	10.6	1011	Eutric Cambisol
Dole	DOL	15.07	46.03	640	9.1	1194	Chromic Cambisol
Loče	LOC	15.53	46.33	310	9.8	1069	Eutric Cambisol
Masun	MAS	14.42	45.62	1000	6.4	1605	Chromic Cambisol
Pohorje	POH	15.39	46.45	1285	6.8	1166	Dystric Cambisol
Pokljuka	POK	13.94	46.37	1300	5.3	1852	Rendzic Leptosol
Ravnik	RAV	14.29	45.90	750	9.2	1641	Rendzic Leptosol
Sorško Plain	SOR	14.38	46.19	370	9.4	1464	Eutric Cambisol
Sviščaki	SVI	14.41	45.58	1200	6.3	1652	Rendzic Leptosol
Verd	VER	14.32	45.93	595	9.6	1587	Rendzic Leptosol
Vitanje	VIT	15.28	46.42	940	6.9	1181	Dystric Cambisol

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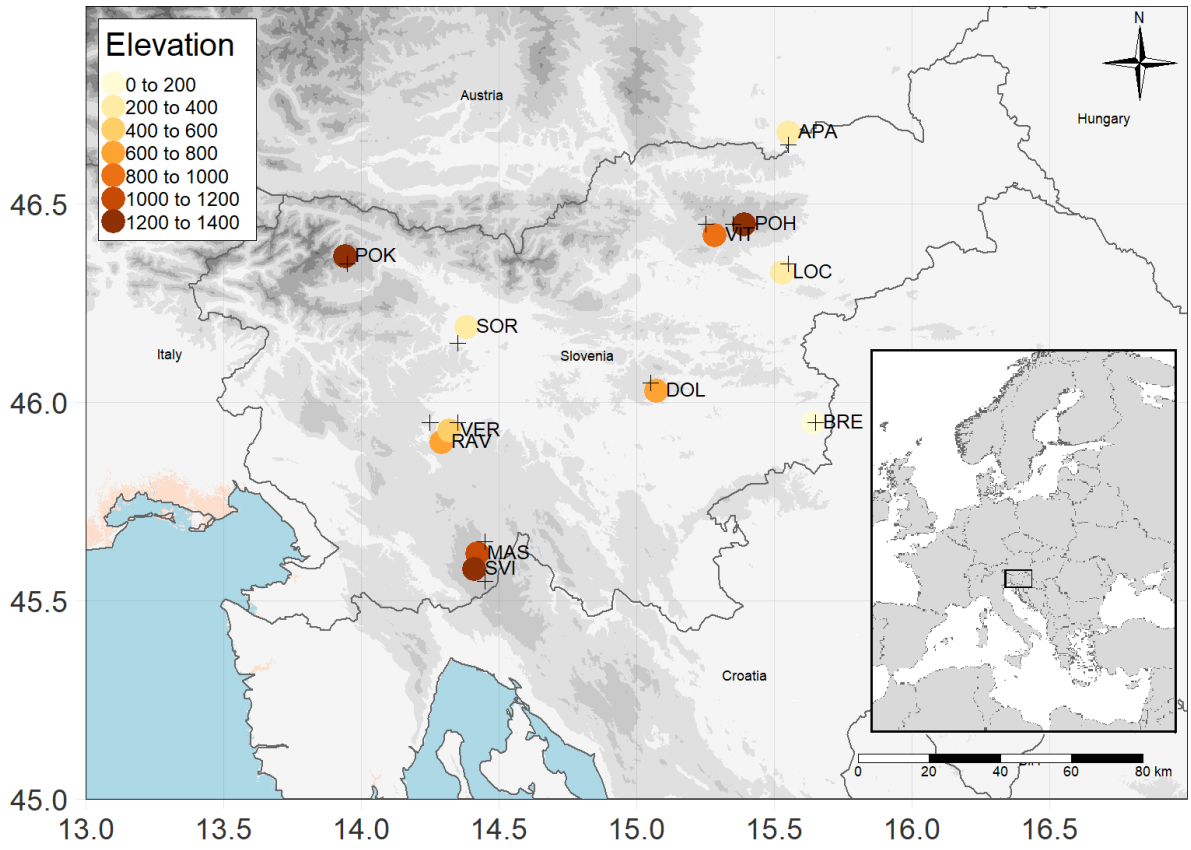


Figure 1: Site locations (coloured dots) with elevation in meters and the closest grid points (crosses) from the E-OBS daily dataset.

2.2 Dendrochronological analysis

At each site, at least 20 dominant or codominant adult trees were cored from the opposite sides using a Pressler borer. Tree cores were dried in the laboratory, fixed in wooden holders and sanded to obtain a smooth surface with clearly visible borders between the tree rings. High resolution images were taken with the ATRICS (Levanič 2007). Tree-ring widths were then measured in CooRecorder & CDendro software (Cybis), and the final cross-dating was done in PAST-5 (SCIEM). A few series showed low correlations with site chronologies and were therefore not used in further analysis. All series were standardised using the *detrend()* function from the dplR R package (Bunn 2008). A modified negative exponential function was fitted to the raw tree-ring width series and to obtain final tree-ring indices (TRWi), measured

values were divided by fitted ones. To build site chronologies, TRWi were pre-whitened and averaged using a robust biweight mean. The basic parameters of the site chronologies are given in Table 2.

Table 2: Descriptive statistics for site chronologies with number of trees (and cores), mean chronology length, earliest and recent year, and mean *Pearson* correlation among detrended series (*rbar*).

Site	N	Length	First year	Last year	rbar
APA	20 (40)	95	1889	2018	0.44
BRE	20 (39)	76	1910	2017	0.42
DOL	19 (38)	100	1879	2018	0.37
LOC	19 (35)	108	1883	2017	0.42
MAS	21 (42)	110	1863	2016	0.29
POH	20 (40)	124	1882	2016	0.38
POK	21 (41)	136	1867	2016	0.33
RAV	20 (39)	97	1870	2016	0.37
SOR	20 (39)	98	1862	2016	0.40
SVI	20 (39)	141	1821	2016	0.46
VER	21 (41)	111	1800	2017	0.38
VIT	22 (43)	132	1839	2017	0.45

2.3 Vaganov-Shashkin (VS) process-based model

The VS model simulates the kinetics of radial growth of conifers, more specifically the characteristics of a representative radial file of tracheids, such as their number, lumens and cell-wall thicknesses (Guiot et al. 2014). It has been successfully tested in various biomes, e.g. near the polar forest limit, in the taiga and steppe, in semiarid and monsoon climates

(Vaganov et al. 2006), in a Mediterranean climate (Touchan et al. 2012), in a humid continental climate (St. George et al. 2008), in the cold and dry continental climate of north-western China (He et al. 2018; He et al. 2017b; He et al. 2017a) and in the continental climate of Siberia (Shishov et al. 2016; Tychkov et al. 2019).

The radial profile is the result of the simulation of cambium activity, where cells divide and grow depending on daily weather conditions (Vaganov et al. 2006). The characteristics of the radial files can also be summarized into annual characteristics to obtain estimates for tree-ring parameters such as width and density. For the VS parameterization (see below) and simulation purposes, we used VS-oscilloscope (Shishov et al. 2016), while there is also a MATLAB version available (Anchukaitis et al. 2020). VS-oscilloscope is an interactive visual tool of the VS model that enables the selection of an optimal combination of model parameters while simultaneously comparing the observed and modelled TRWi. Input variables for the VS model are daily temperature and precipitation, while daily solar irradiation is calculated from latitude and day of the year. Precipitation is used to estimate soil moisture. This model incorporates the principle of growth limiting factor, which defines the growth rate for each day. In the first step, the VS model calculates the partial daily growth rates *Gr(t)* for temperature, soil moisture and solar irradiance. In the second step, the minimum from daily temperature and soil moisture growth rates is multiplied by the solar irradiance growth rate to obtain *G(t)* (Evans et al. 2006). The resulting integral daily growth rate expresses the potential for radial growth on each day and varies between 0 and 1. Values close to 0 indicate dormancy or climatically unfavourable days of the growing season, usually in winter or during summer drought periods, while values close to 1 indicate favourable climate conditions for radial growth, such as warm summer days with both daily temperature and moisture in optimal intervals.

2.4 VS model parameterization and evaluation

All chronologies were split into a period for model parameterization (calibration), i.e. 1980–2016 (or the most recent year), and a period for model evaluation (verification), i.e. 1950–1979. To evaluate the accuracy of VS model simulations, the *Pearson* correlation coefficient (r), root-mean-square error (RMSE), mean bias and Gleichläufigkeit statistics (Buras and Wilmking 2015; Eckstein and Bauch 1969) were calculated between simulated and observed TRWi. In addition, to account for differences in simulated and observed variability, a simple variance ratio was calculated as the quotient between simulated and observed variance.

Partial daily growth rates were further used to analyse growth limiting factors for each site and how they vary in time. In addition, trends in growing season timing since 1950, namely the date of the onset and end of the growing season, were analysed and used to infer about temporal changes in cambial phenology. The onset of the growing season was defined as the first day in the year when the cumulative temperature sum exceeds the minimum temperature threshold for growth, while the end of growing season was defined as the day in the year when the cumulative temperature sum falls below the temperature threshold for growth and growth rate is less than the critical value. See more information about the final parameter values in Supplementary Table 1.

2.5 Daily response functions

To further supplement the VS model simulations, daily correlations were calculated between TRWi and climate data using the dendroTools R package (Jevšenak and Levanič 2018; Jevšenak 2020). The function *daily_response_seascor()* was applied, which uses a moving window of variable widths and calculates partial correlation coefficients between an aggregated climate variable and selected tree-ring proxy, while simultaneously controlling for the second climate

193 variable. The function was applied to both climate variables: temperature, while considering
194 precipitation as a control, and vice versa. To calculate daily correlations, all window widths
195 between 21 and 270 consecutive days were considered, and partial correlations were
196 calculated using a bootstrap procedure with 1000 replicates. Such calculations provide robust
197 correlation estimates but are also computationally expensive.

198

199 **3. RESULTS**

200 The VS model was parameterised for each of the twelve Norway spruce sites in Slovenia, and
201 the final parameter values are presented in Supplementary Table 1. VS parameters related to
202 temperature thresholds correlated negatively with site elevations, while parameters related
203 to soil moisture thresholds generally showed less significant and positive correlations with
204 elevation (Supplementary Figure 1). Warmer low elevation sites had a higher minimum
205 threshold temperature (7 °C) and higher temperature sums (80 °C) for trees to start growing
206 season, while for high elevation and colder sites, e.g. the coldest site SVI, the minimum
207 temperature to start growth was 4 °C and the temperature sum was 69 °C.

208 VS simulations provided significant correlations between modelled and actual TRWi for all
209 analysed sites (Figure 2, Table 3). On average, the correlation coefficient was 0.598 ($p < 10^{-4}$)
210 for the calibration period and 0.508 ($p < 10^{-2}$) for the verification period. The best results were
211 obtained for low-elevation site BRE, where correlations for calibration and verification
212 periods were both above 0.75 ($p < 10^{-5}$). The lowest verification results were obtained for site
213 SVI, where correlations for calibration and verification were around 0.34 ($p < 0.05$).

214

215 **Figure 2:** Simulated (blue lines) and observed (red lines) TRWi chronologies for the calibration
216 (1980–2018) and verification (1950–1979) periods. Chronologies are sorted based on a
217 precipitation gradient from drier sites (upper panels) to wetter sites (lower panels).

Table 3: Evaluation results for the comparison between simulated and observed TRWi chronologies for the calibration and verification period: Pearson correlation coefficient (r), root-mean-square error (RMSE), mean bias, Gleichläufigkeit (GLK%) and variance ratio (VR).

Site	Period	Years	r	RMSE	bias	GLK%	VR
BRE	Calibration	1980 – 2017	0.77	0.14	0.00	0.73	0.40
BRE	Verification	1950 – 1979	0.75	0.10	0.00	0.76	0.81
LOC	Calibration	1980 – 2017	0.59	0.16	-0.01	0.73	0.54
LOC	Verification	1950 – 1979	0.56	0.11	0.00	0.66	1.03
APA	Calibration	1980 – 2018	0.54	0.22	-0.02	0.71	0.25
APA	Verification	1950 – 1979	0.37	0.15	0.02	0.62	0.85
VIT	Calibration	1980 – 2017	0.64	0.16	-0.01	0.73	0.73
VIT	Verification	1950 – 1979	0.45	0.16	-0.01	0.55	1.68
DOL	Calibration	1980 – 2018	0.56	0.17	0.02	0.66	0.61
DOL	Verification	1950 – 1979	0.41	0.15	-0.02	0.52	1.52
POH	Calibration	1980 – 2016	0.42	0.17	-0.01	0.58	0.41
POH	Verification	1950 – 1979	0.45	0.12	0.01	0.52	1.24
SOR	Calibration	1980 – 2016	0.78	0.17	-0.01	0.86	0.11
SOR	Verification	1950 – 1979	0.54	0.11	0.01	0.62	0.21
VER	Calibration	1980 – 2017	0.67	0.09	0.01	0.76	0.58
VER	Verification	1950 – 1979	0.72	0.12	-0.04	0.83	0.28
MAS	Calibration	1980 – 2016	0.57	0.10	0.01	0.75	0.62
MAS	Verification	1950 – 1979	0.42	0.09	0.00	0.59	1.31
RAV	Calibration	1980 – 2016	0.66	0.13	-0.01	0.81	0.26
RAV	Verification	1950 – 1979	0.62	0.13	0.03	0.66	0.22
SVI	Calibration	1980 – 2016	0.33	0.15	-0.01	0.64	0.92
SVI	Verification	1950 – 1979	0.35	0.14	0.01	0.69	1.39
POK	Calibration	1980 – 2016	0.64	0.11	-0.02	0.75	0.46
POK	Verification	1950 – 1979	0.45	0.09	0.01	0.72	1.03

Daily growth rates revealed different growth limiting patterns for the analysed sites (Figure 3). To explain the differences in growth limitations among spruce sites, the annual precipitation pattern turned out to be more appropriate than elevation. At the beginning of growing seasons, all sites are temperature limited, while in late spring and summer seasons, sites that receive less than 1200 mm annually are mostly precipitation limited, while high elevation sites with more than 1600 mm of annual precipitation generally remain temperature limited. Some moderately wet sites (i.e. SOR, VER and RAV) showed mixed-precipitation and temperature signal. We observed a very moderate increase in temperature limitation for most of the higher elevation sites, while the temporal changes in moisture limitation are non-significant (Supplementary Figure 2). Those results indicate that temporal changes in growing season limiting factors for Norway spruce in Slovenia are only minor and mostly nonsignificant.

The temporal changes in onset and end of growing season were estimated from daily growth rates (Figure 4). The calculated trends indicated earlier onset and later end of the growing season for recent years, resulting in a longer growing season for the majority of the sites. A minor deviation from this pattern was observed for site MAS, which showed a slightly delayed onset of the growing season for recent years, while site BRE indicated earlier end of growing season. The estimated increase of the growing season duration ranged from 5.6 (SOR) to 1.0 (BRE) days per decade. We did not observe any systematic pattern of growing season prolongation related to elevation, climate regimes or prevailing growth limiting factors.

Daily response functions revealed a consistent pattern of climate signal in TRWi: Higher precipitation sums had a positive effect and higher mean temperature had a negative effect on radial tree growth (Figure 5). The only clear exception was the wettest site POK, which showed almost no significant correlations with precipitation and the positive influence of

higher temperature. No significant precipitation correlation was observed also for site SVI, which receives a relatively high amount of annual precipitation.

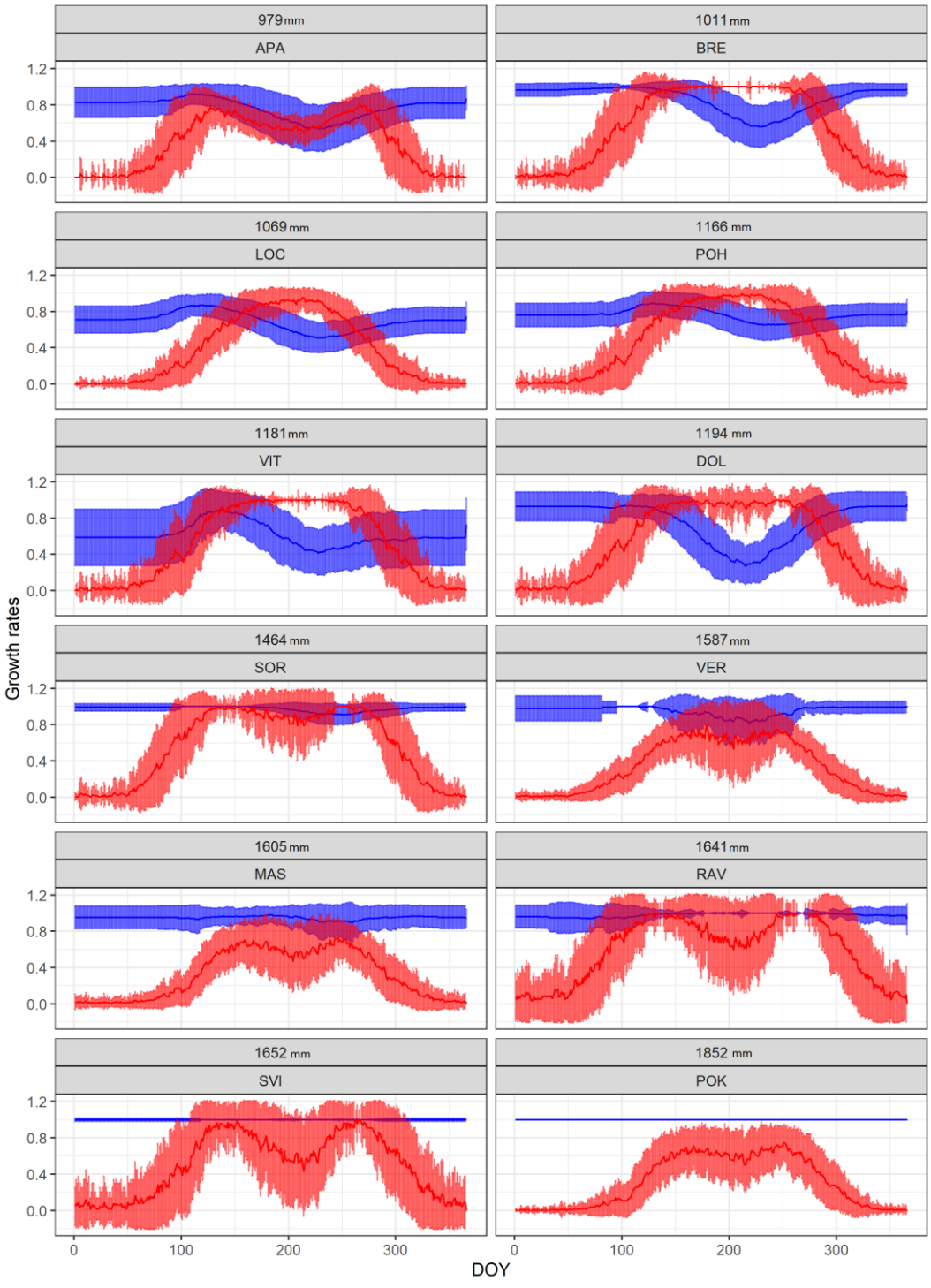


Figure 3: Daily growth rates as predicted by the VS model for the analysed sites based on precipitation (blue colour) and temperature (red colour). Shown values represent the average and standard deviation of each day of the year (DOY) for the entire analysed period, i.e. 1950–2016. Above site abbreviations, mean annual sums of precipitation in millimetres (mm) are given for the period 1950–2017.

4. DISCUSSION

4.1 The effect of climate on radial tree growth

4.1.1 Growth limiting factors

The VS model describes the effect of climate on radial tree growth by applying the principle of growth limiting factor through realistic mechanistic equations. Drier Norway spruce sites at lower elevations are mostly moisture limited, while moist high-elevation sites are generally more temperature limited. We observed an interesting pattern of constant soil moisture effect for both the wettest sites (SVI and POK), where partial growth rates for soil moisture limitation are always close to 1, indicating the optimal soil moisture conditions throughout the year. Such results are expected and in accordance with previous studies focused on the analysis of limiting growth factors of Norway spruce across environmental gradients (Rabbel et al. 2018).

To distinguish between precipitation and temperature limited sites, precipitation seems to be more appropriate than commonly used elevational gradients (Touchan et al. 2016). Below 1200 mm of annual precipitation, spruce sites are mostly precipitation limited, while above 1600 mm, temperature defines tree growth through most of the growing season. Moderately wet sites, i.e. with annual precipitation sums of 1200-1600 mm showed a mixed precipitation-temperature signal. However, the defined thresholds are only approximate, and there are other site factors, such as soil type, slope, exposition and seasonal precipitation distributions, that interact with climate and define tree growth. For example, sites SOR and VER received a similar amount of annual precipitation, 1464 and 1587 mm, respectively, but SOR is more moisture limited, while VER is more temperature limited.

The identified growth limiting factors for Norway spruce correspond to those reported by Tumajer et al. (2017), who analysed moisture and temperature limitations in Norway spruce

294 in the Czech Republic tree-ring network with the VS-Lite model (Tolwinski-Ward et al. 2011).
295 They found a clear pattern of temperature limited sites at higher elevations (above 800 m)
296 and moisture limited sites at lower elevations (below 500 m), while mid-elevation
297 chronologies were mostly characterised as mixed signal chronologies. However, our studies
298 differ in the identified temporal shifts; while Tumajer et al. (2017) reported increasing soil
299 moisture limitation for most of the analysed chronologies, we observed insignificant changes
300 for soil moisture limitation and minorly increased temperature limitation for higher elevation
301 sites. The differences between the two studies might arise from different methodological
302 approaches, i.e. VS model vs VS-Lite model, different sampling strategies (random in the
303 Czech Republic vs dominant trees in Slovenia) and different strategies to analyse temporal
304 shifts. The growth limiting factor shifts from our study correspond to the actual climate trends
305 at the analysed sites (Supplementary Figure 3), where mean annual temperatures exhibit a
306 moderate increasing trend and precipitation patterns show no significant changes.

307 To put our results into a wider context, the VS model has often recognized soil moisture to be
308 the prevailing driver of tree growth in dry areas, such as the cold Tibetan Plateau (He et al.
309 2017a), warm Mediterranean (Touchan et al. 2012) and Siberia (Tychkov et al. 2019; Popkova
310 et al. 2018). Often, temperatures play an important role at the beginning of the growing
311 season (Rossi et al. 2008), while during the growing season, the environmental signal may
312 change, and water availability becomes the main factor affecting growth (e.g. St. George et
313 al. 2008). Temperature defined the onset of the growing season for all Norway spruce sites
314 analysed in our study. However, to understand global drivers of tree growth and how they
315 relate to local climate conditions, additional studies are needed to reveal the underlying
316 physical dependences between tree growth and limiting site factors (Carrer et al. 2012).

317

4.1.2 Daily response functions

The results of daily response functions (Figure 5, Supplementary Table 2) correspond well with the pattern of growth limiting factors from the VS model (Figure 3). In general, prevailing growth limiting factors correspond to the climate variable with higher correlations, although both temperatures and precipitation are significant at most sites. Some more moisture limited sites (e.g. BRE, LOC, VIT and SOR) showed more significant correlations with aggregated precipitation data, while more temperature limited sites showed more significant correlations with aggregated temperature data (e.g. APA, DOL, and POK) (Supplementary Table 2). Importantly, how the VS model and dendroTools correspond is more obvious for sites with higher correlations and better VS model performance. The benefit of applying the response functions is the information related to the positive/negative effect of a particular climate variable, which is not obvious from observing the growth limitation patterns (Figure 3). For the drier low-elevation sites APA, BRE and LOC, we observed positive spring and summer correlations with precipitation sums, while higher precipitation in autumn resulted in negative correlations and decreased ring widths. This shift in correlations corresponds to a shift in the growth limiting factor, where soil moisture becomes less limiting and temperature limitation prevails (Figure 3).

All previous studies that considered a sufficiently wide elevation gradient reported two different response types for Norway spruce: 1) positive summer temperature correlations and (less significant) negative precipitation correlations for higher elevations close to timberline and 2) negative summer temperature correlations and positive precipitation correlations for lower elevations, e.g. for all of Norway (Andreassen et al. 2006), the Giant Mountains in the Czech Republic (Kolář et al. 2017), the Alps (Hartl-Meier et al. 2014) and the Eastern Carpathians in Romania (Sidor et al. 2015). Similarly, the analysis of colder sites from the

upper timberline from East-Central Europe (Ponocná et al. 2016) and the far north to the Arctic timber line (Mäkinen et al. 2000) revealed positive summer correlations and a barely significant positive precipitation effect. Positive precipitation correlations and negative correlations for summer temperature are commonly reported for Norway spruce from mid to low elevations, e.g. for south-western (van der Maaten-Theunissen et al. 2013) and western (Rabbel et al. 2018) Germany, the Eastern Carpathians in Romania (Bouriaud and Popa 2009) and the lowlands of Poland (Koprowski and Zielski 2006).

The results of our response analysis are in accordance with previous studies: higher winter and spring precipitation amounts have a positive effect on tree growth, while higher summer temperature is related to negative correlations for all low- and mid-elevation sites. In contrast, Pokljuka (POK) – the wettest site from the highest elevation – shows the opposite pattern. Sites SOR and POK were used in a comparison study by Levanič et al. (2008) and exhibited the same climate-growth patterns as shown in our study.

The shift between a positive and negative effect of temperature on the radial growth of spruce was reported to be somewhere between 13-13.5 °C (June temperature) (Sidor et al. 2015; Andreassen et al. 2006), which corresponds well with the results from our study. We calculated the positive effect of higher temperatures for the Pokljuka (POK) site, where the mean June temperature (1950–2018) was 12.2 °C. Next the coldest (June) sites were SVI (13.5 °C) and MAS (13.6 °C) which already exhibited a negative effect of higher temperatures.

4.2 Simulated growing season patterns

The changes in growing season phenology were inferred from daily growth rates, which indicate the onset and end of the growing season (see Section 2.3 for definitions). The typical onset of the growing season was calculated to be on DOY 98, while the typical end of the

366 growing season was on DOY 311. Those estimates can be compared with direct observations
367 by Gričar et al. (2014), who studied the xylogenesis at low- (400 m) and high-elevation (1200
368 m) Norway spruce sites for three consecutive years (2009–2011). They reported the average
369 onset DOY 103 (low elevation) and DOY 117 (high elevation), while the average end of the
370 growing season was on DOY 241 (low elevation) and 228 (high elevation). Xylem formation
371 phenology for sites SOR and POK were studied in 2002–2004 by Levanič et al. (2008), so we
372 can directly compare the observed and simulated onset and end of the growing season
373 (Supplementary Table 3). The agreement between the simulated and measured onset and
374 end of the growing season was better for site POK, where the simulated onset was on average
375 for 12 days earlier, while the simulated end was on average 48 days later than the measured.
376 Therefore, there is a general agreement between the VS model simulations and xylogenesis
377 observations, where the onset estimates are closer to field observations than those of the
378 end of the growing season. Buttò et al. (2020) reported systematic overestimations in the
379 predicted timing of tracheid differentiation phases by 1-20 days and concluded that the
380 current formulation in the VS model is unable to explain the events in autumn. VS model
381 currently lacks an appropriate module that would account for carbon storage processes which
382 usually occur at the end of the growing season (Furze et al. 2019), when climate conditions
383 are favourable. Ongoing efforts aim to improve the performance of the VS model by more
384 properly accounting for carbon storage processes and subsequent carry-over effects in the
385 subsequent spring. Although there are differences between the observed and simulated
386 onset and end of the growing seasons, we assume that, in relative terms, temporal changes
387 are systematic and VS simulations can be used to infer the cambial phenology trends and
388 intra-annual variability.

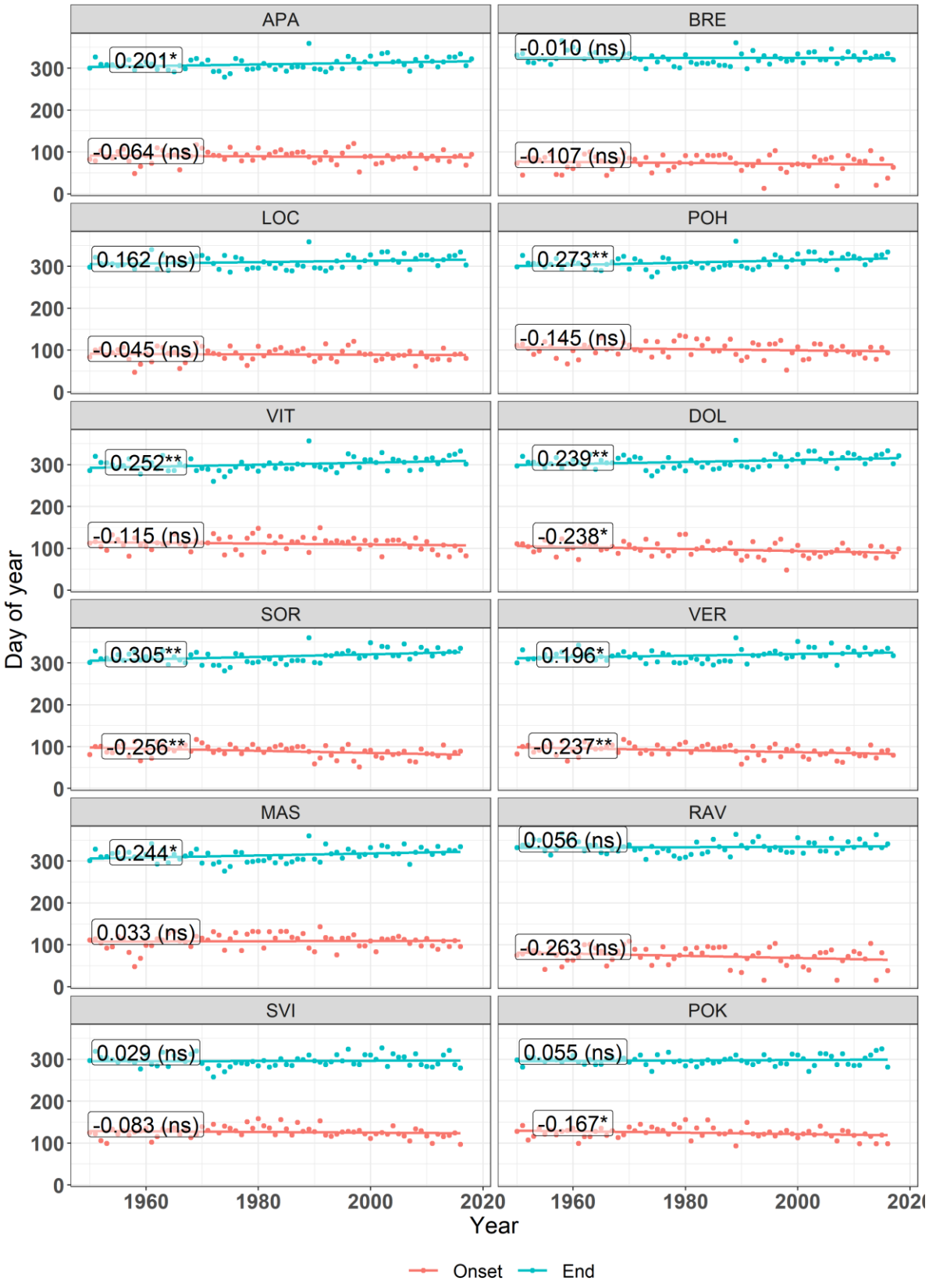


Figure 4: Changes in the onset and end of the growing season as calculated from the daily growth rates from the VS model. Labels depict slope parameters of calculated trends with the following significance codes: *** ($p < 0.001$), ** ($p < 0.01$), ** ($p < 0.05$) and ns (nonsignificant).

Mainly due to a warming climate, changes in growing season patterns have already been reported around the globe based on observations of leaf phenology (Menzel and Fabian 1999), satellite images (Park et al. 2016) and climatological records (Linderholm et al. 2008). Our analysis of growing season trends indicated the earlier onset and later end for recent years, which resulted in the prolongation of the growing season by 3.1 days per decade on average (Figure 4). A comprehensive overview of growing season changes is available by Linderholm (2006). Recently, Park et al. (2016) reported a prolongation of 2.60 days per decade (1984–2014) for the Northern Hemisphere based on an analysis of satellite observations. Our calculated trends based on VS simulations are within the intervals usually reported by others; therefore, we assume they realistically reflect growing season trends for the analysed sites.

4.3 VS model performance

The parameterization process resulted in realistic parameter values (Supplementary Table 1), which effectively reflected local site characteristics (Supplementary Figure 1). Temperature thresholds showed negative correlations with elevation, while precipitation thresholds showed less significant correlations with site characteristics. We assume that soil moisture parameters are much more related to local terrain characteristics and soil conditions and therefore show lower correlations. In general, low elevation sites had higher temperature thresholds to start growth, and sites with higher amounts of precipitation had a higher soil moisture threshold for the initiation of tree growth.

All correlations between modelled and actual tree-ring chronologies were significant ($p < 0.05$) for both calibration and verification data (Figure 2, Table 3). For the independent verification data, correlations ranged from 0.75 to 0.33. Importantly, none of the analysed

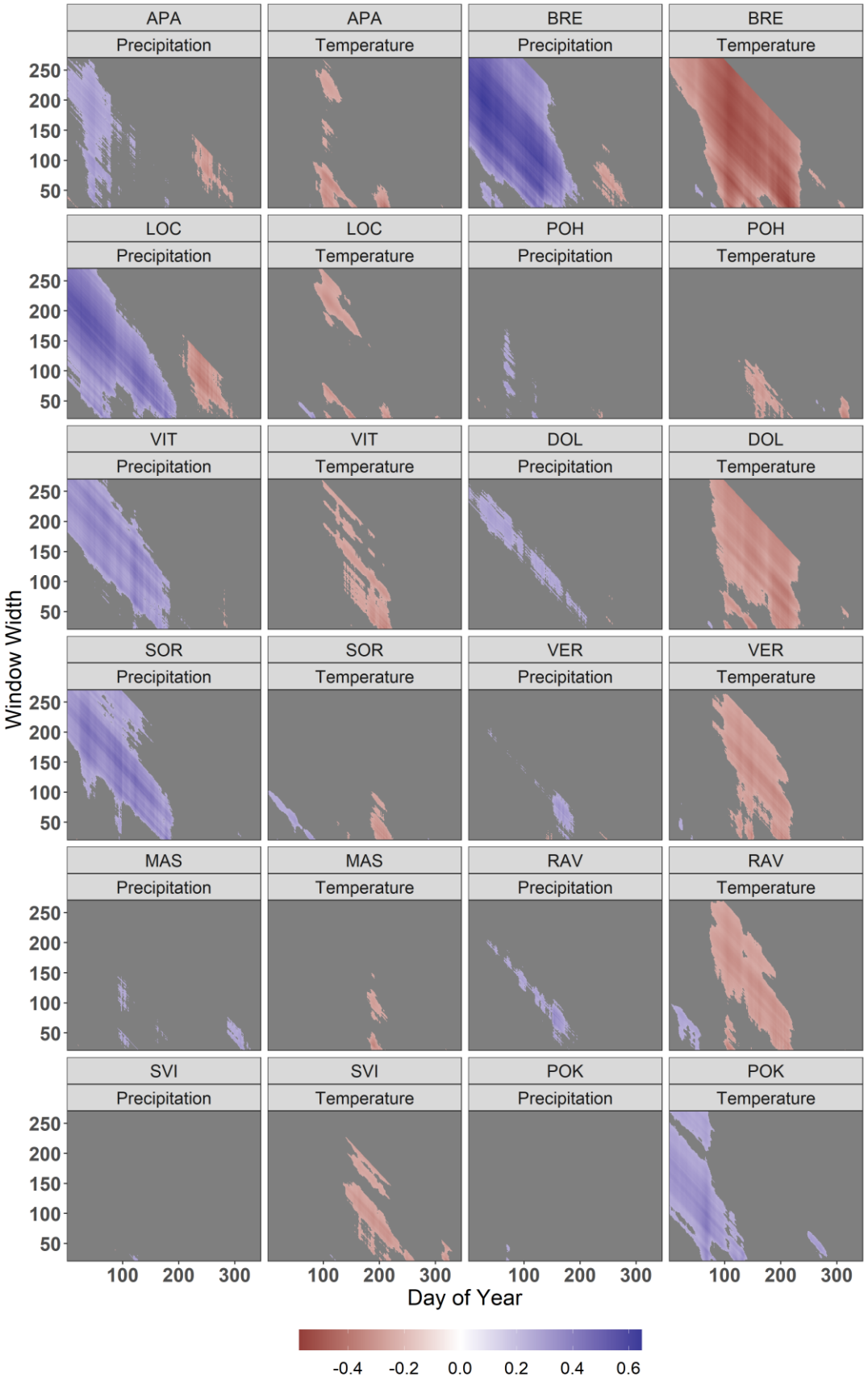
418 sites was from ecological margins of species distribution, which are often considered as
419 optimal for dendroclimatic investigations. In previous studies, the VS model has already
420 shown promising performance on independent verification data, e.g. for *Pinus halepensis*
421 from Tunisia (r = 0.63) (Touchan et al. 2012) and *Pinus sylvestris* from Siberia (r = 0.53)
422 (Tychkov et al. 2019). The results from VS-Lite are usually less significant. Tumajer et al. (2017)
423 reported a mean correlation of 0.24 (*Picea abies*), while Breitenmoser et al. (2014) reported
424 a mean value of 0.29 for the 2287 tree-ring chronologies from the ITRDB network.

425 We obtained better VS results for dry sites, mostly at low elevations. For instance, sites BRE
426 and LOC showed very good model performance: In addition to high correlation coefficients
427 for calibration and verification data, the model realistically simulated the variance, which
428 resulted in very low error terms (Table 3). For some other sites, e.g. VER and SOR, the model
429 produced good correlation results, but the variance of simulated chronologies was lower than
430 the actual one. It must be noted here that parameterization was primarily guided to achieve
431 high correlation results, rather than low RMSE and bias. The least precise results in our study
432 were obtained for site SVI. This is not surprising given the concave shape of the local
433 topography (i.e. typical karst depression). This is also characterised as a cold air pool, which
434 is associated with local climate conditions and most likely not integrated in gridded climate
435 products.

436 For some sites, differences in the correlation coefficient between calibration and verification
437 data were greater, e.g. site DOL (from 0.56 to 0.41) and VIT (from 0.64 to 0.45). We further
438 explored the possible underlying drivers of this pattern by comparing the performance of the
439 VS model and associated rbars (Supplementary Figure 5). In general, a drop in the correlation
440 was associated with a drop in the rbar. A possible explanation of this phenomenon is through
441 common causality on rbar and VS performance – due to stronger climatic control on tree

442 growth, tree-ring width series of individual trees (Ponocná et al. 2018) and forest site
443 chronologies (Shestakova et al. 2016) become more tightly synchronized, resulting in
444 increasing rbar. At the same time, because of the purely climate-driven algorithm, the VS
445 model performs best in climatically strongly controlled sites and periods, where climate is the
446 prevailing driver of tree growth. However, there were some exceptions to the rbar and
447 correlation synchronicity, i.e. site VIT, where rbar was stable, while correlation was
448 importantly lower for the verification split. It must be noted that different combinations of
449 parameter values can potentially result in good calibration statistics and that the selected
450 combination might not be optimal for the entire period in such cases.

451 The VS model has proven to be a reliable tool for modelling radial tree growth as a function
452 of climate, where fixed environmental influence is defined by properly tuned parameters.
453 However, in its current form, it seems that approximately 50 % of the explained variance is
454 the maximum that can be achieved. In addition to the beforementioned consideration of
455 carry-over effects, a key to achieve even better performance might be related to other known
456 environmental factors that importantly contribute to radial tree growth and vary from year
457 to year, such as nitrogen deposition and atmospheric carbon dioxide concentration (Kahle et
458 al. 2008).



459

460 **Figure 5:** Bootstrapped partial correlation coefficients calculated from day-wise aggregated climate
461 temperature and precipitation data of variable widths. The reference position for each value is the
462 beginning of the considered window. Only significant correlations with $p < 0.05$ are shown.

5. CONCLUSIONS

For the majority of European sites, environmental changes will likely lead to less favourable growth conditions for Norway spruce due to its drought intolerance (Lévesque et al. 2013; Zweifel et al. 2009; Schuster and Oberhuber 2013; Vitali et al. 2017; Boden et al. 2014). Representative concentration pathway (RCP) scenarios for Slovenia predict a temperature rise by 2100 of approximately 1.3 °C (RCP2.6), 2 °C (RCP4.5) and 4.1 °C (RCP8.5). In contrast to temperature, projections of changes in precipitation are less reliable (e.g. Piniewski et al. 2017; Orth et al. 2016). In the case of the moderately optimistic scenario RCP4.5, no significant changes are expected initially, while by 2100 the annual mean precipitation amount is expected to increase by 10 % (summarised by Slovenian Environment Agency 2019). In addition to climate, the future growth of Norway spruce will largely depend on natural hazards, such as windstorms and insect outbreaks (de Groot and Ogris 2019). Indeed, a full understanding of climate change-disturbance-forest productivity interactions cannot be reached because such events may completely change future productivity projections, i.e. an estimated increase in productivity may be counterbalanced by increased risk of damage due to extreme weather events.

We showed that the climate-related growth of Norway spruce is mainly determined by summer temperatures (negatively) and spring precipitation (positively). The exception here are high-elevation sites with annual precipitation sums close to 1900 mm, which are positively related to higher temperature at the beginning of growing season. Recent trends of radial growth at analysed sites support such predictions (Supplementary Figure 4). Most of the temperature limited sites which exhibited negative correlations with summer temperature showed slight negative trends, i.e. VER, SVI, MAS, RAV, while site POK (positive correlations with higher summer temperature) exhibited a positive trend in radial tree-growth. For mostly

precipitation limited sites, i.e. SOR, POH, VIT, DOL and LOC, a slightly increasing or neutral trend was shown. Sites BRE and APA have exhibited positive and negative growth trends since 1950, which could be attributed to the interaction of a positive precipitation and negative temperature effect in the studied period. Based on the climate projections for Slovenia (see above), the only site that would most likely benefit from such scenarios is site POK. For all other sites, future radial growth will largely depend on interactions between spring precipitation and summer temperature and how the projected increase in annual precipitation will compensate for the projected increase in summer temperature. Longer growing seasons could partly buffer against the negative effect of increasing temperature, where growth rates will decline due to higher drought stress in summer, but, simultaneously, the growing season will start earlier and end later due to increasing spring and autumn temperatures (Figure 4). Consequently, the decline in total ring width might be less intensive.

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Code availability: R code used for the analysis is available upon request from the first author.

Author contribution statement: J.J analysed the data and prepared the first version of the manuscript; V.S., J.G. and T.L. supervised the study; I.T. and J.T. parameterised the VS model for all sites; T.L. designed the sampling scheme and collected tree-ring data; J.T. contributed to the discussion and improved the manuscript; and D.A, P.P and M.P commented on the manuscript.

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