Silva Fennica vol. 50 no. 5 article id 1680
Category: research article

SILVA FENNICA

www.silvafennica.fi
ISSN-L 0037-5330 | ISSN 2242-4075 (Online)
The Finnish Society of Forest Science
Natural Resources Institute Finland

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Environmental control of growth variation in a boreal Scots pine stand – a data-driven approach

Kulmala L., Žliobaitė I., Nikinmaa E., Nöjd P., Kolari P., Koupaei K.K., Hollmén J., Mäkinen H. (2016). Environmental control of growth variation in a boreal Scots pine stand – a data-driven approach. Silva Fennica vol. 50 no. 5 article id 1680. 21 p. http://dx.doi.org/10.14214/sf.1680

Highlights

- High water potential and carbon gain during bud forming favoured height growth.
- High water potential during the elongation period favoured height growth.
- A spring with high carbon gain favoured diameter growth.
- The obtained regression models had generally low generalization performance.

Abstract

Despite the numerous studies on year-to-year variation of tree growth, the physiological mechanisms controlling annual variation in growth are still not understood in detail. We studied the applicability of data-driven approach i.e. different regression models in analysing high-dimensional data set including continuous and comprehensive measurements over meteorology, ecosystem-scale water and carbon fluxes and the annual variation in the growth of app. 50-year-old Scots pine stand in southern Finland. Even though our dataset covered only 16 years, it is the most extensive collection of interactions between a Scots pine ecosystem and atmosphere. The analysis revealed that height growth was favoured by high water potential of the tree and carbon gain during the bud forming period and high water potential during the elongation period. Diameter growth seemed to be favoured by a winter with high precipitation and deep snow cover and a spring with high carbon gain. The obtained models had low generalization performance and they would require more evaluation and iterative validation to achieve credibility perhaps as a mixture of data-driven and first principle modeling approaches.

Keywords height growth; diameter growth; Gross primary production; turgor pressure; predictive modelling; Least Angle Regression
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Received 14 July 2016 **Revised** 8 December 2016 **Accepted** 12 December 2016

1 Introduction

Both primary and secondary tree growth are sequential processes that include division, subsequent enlargement and wall formation of new cells. Under a strong hormonal control (e.g. Aloni 2013), growth process is driven by temperature, the availability of resources for biosynthesis and a sufficient turgor pressure for cell expansion (e.g. Hölttä et al. 2010; Pantin et al. 2012). Photosynthesis is the primary driver for ecosystem productivity as it absorbs solar energy for plant metabolism. Other important drivers are nitrogen, which is an essential constituent of proteins (Ågren 1996; Hari et al. 2013), and water availability, as drought prevents sufficient turgor pressure needed to expand the growing tissues (De Schepper and Steppe 2010; Hölttä et al. 2010) and inhibits photosynthesis (Mäkelä et al. 1996).

In the boreal zone, the annual cycle in light and temperature regulates the timing of tree growth. The year-to-year variation of radial growth (i.e. secondary growth) has been widely studied and connected with the variation in weather such as warm temperature in spring (Hordo et al. 2011; Babst et al. 2012; Henttonen et al. 2014) and in summer (Misson 2004; Korpela et al. 2011; Seo et al. 2011; Xu et al. 2014), especially in the northernmost regions and at high altitudes. The growth variation has been connected to precipitation as well (Zweifel et al. 2006; Pichler and Oberhuber 2007; Zubizarreta-Gerendiain et al. 2012; Henttonen et al. 2014) but the effect is clearer in the temperate zone where water is limiting. The growth variation of boreal trees has also correlated with light intensity (Hari and Siren 1972; Li et al. 2014) and air humidity (Li et al. 2014). As regards the primary growth of pines, Lanner (1976) confirmed that the height growth is affected both by conditions during bud formation and by conditions during the elongation period. Recent studies have emphasized the environmental conditions during bud formation in the previous summer in determining the extent of height increment (Salminen and Jalkanen 2007; Schiestl-Aalto et al. 2013).

In addition to the immediate environmental responses of growth, delayed responses have been observed. For example, Babst et al. (2012) studied conifers, mainly Scots pine (*Pinus sylvestris* L.), in southern Finland and Sweden and found that the temperature in previous July–August was negatively correlated with radial growth. Henttonen et al. (2014) found a similar negative correlation between radial growth and temperature of previous August in southern Finland and Estonia. Winter temperature and precipitation have also correlated with annual growth variation (Misson 2004; Seo et al. 2011; Babst et al. 2012). The variation of snow cover depth and its melting, for example, may cause these effects (Helama et al. 2013). Also, the storage of non-structural carbohydrates can cause such delayed responses (Sala et al. 2012).

Despite the numerous studies on annual variation in tree growth, the year-to-year growth variation is still not understood in detail. During recent decades, various human-induced threats (acid rain, climate change, etc.) have caused a range of direct and indirect environmental changes and, as a result, the rates of forest ecosystem processes have been altered, (e.g. Olesen et al. 2007). In addition, the growth response to environment may be changing (Briffa et al. 1998; Vaganov et al. 1999; Berninger et al. 2004; D'Arrigo et al. 2004). This has raised interest in increasing our understanding about the linkages between tree growth, whole-tree physiology and the environmental drivers.

Since the 1970s and 1980s, measuring techniques have rapidly developed. This has facilitated field measurements on tree metabolism and tree growth with high temporal resolution. For example, the long time series of eddy covariance (EC) measurements are used to analyse the relationship between tree growth and the carbon and water fluxes between forests and atmosphere. Some of the studies have not found a coupling between ring width and the EC-derived net ecosystem productivity (NEP) (Rocha et al. 2006; Gough et al. 2008), but positive connections between the growth and NEP or gross primary production (GPP) have also been reported (Ohtsuka et al. 2009; Zweifel et al. 2010; Gea-Izquierdo et al. 2014; Babst et al. 2014; Schiestl-Aalto et al. 2015). The conflicting results may be due to the large range on uncertainty involved, largely because short data sets on different spatial and temporal resolution have been combined.

SMEARII station (Hari and Kulmala 2005) was established in 1995 and since 1996 the continuous and comprehensive measurements over forest-atmosphere interactions have created a massive high-dimensional data set that is unique in the world. The versatile measurements open a new possibility to combine different metabolic phenomena in the analysis of forest ecosystems. In this study, we analysed the relationship between tree growth and the SMEAR measurements using established data-driven computational methods such as data mining, pattern mining and iterative regression. These offer potential for new insights to understand factors affecting tree growth with the flexibility to consider a wide range of variables. In addition to traditional statistical analysis, data-driven approaches can distil information from a large numbers of variables and samples. However, a high number of partly intercorrelated candidate variables may result in tangled models with low accuracy and with explanatory variables unlikely driving the growth.

Our objectives were to study, 1) whether there are any persistent correlations between the growth and the environmental variables over prolonged periods before or during the growth, 2) whether it is possible to model the growth variation with a single variable or combination of a few variables at fixed times, and 3) does a manual preselection of candidate explanatory variables improve the accuracy of the prediction.

2 Materials and methods

2.1 Study site

The study site at the SMEAR II (Hari and Kulmala, 2005) is a Scots pine stand established by sowing in 1962. It is located in southern Finland (61°52´N, 24°17´E) on a medium fertile site, classified as *Vaccinium* type (Cajander 1926). In 2012, the dominant height and mean stem diameter at 1.3 m were 17.5 m and 19.6 cm, respectively, (Bäck et al. 2012) with the density of 700 stems ha^{-1}. In 2002, the stand was partly thinned from below decreasing the stand basal area from 24.3 $m^2\ ha^{-1}$ to 17.9 $m^2\ ha^{-1}$ on the thinned area.

The site belongs to the middle boreal zone and has a harsh boreal climate with long cool days in the summer and short cold days in the winter. The mean annual temperature is +3.5 °C and mean monthly temperature varies from −7.7 °C in February to 16.0 °C in July (mean for 1980–2009) (Pirinen et al. 2012). Mean annual rainfall is 711 mm distributed evenly throughout the year.

2.2 SMEAR II data

The SMEAR II station was set up in 1995, with an extensive range of measurement including atmospheric physics, meteorology, material and energy fluxes, tree physiology, and soil and soil water characteristics. For our analysis, we selected 31 explanatory variables with less than 15% of the records missing (Table 1). Except for the snow depth, all the other measurements were available as 30 min averages during the years 1997–2013. Snow depth was measured mostly weekly during the snow-covered season. Linear interpolation was used for days when no snow measurements were available.

Global shortwave radiation, reflected shortwave radiation, photosynthetic photon flux density (PAR), reflected PAR, ultraviolet radiation A and B (UVA and UVB) and precipitation were measured at the height of 18 m at 1 min intervals. Air temperature, CO_2 and water vapour (H_2O) concentrations, relative humidity (RH), wind speed and wind direction were measured at the height

Table 1. Measurements from SMEAR II station. The Manual selection indicates subjective pre-selection to the any time model by LARS (see 2.4.2).

Manual selection	Variable	Abbreviation	Units	Specifications	Missing values
√	Precipitation	Prec	mm	includes snow	1%
√	Air temperature	T	°C		–
	Atmospheric pressure	P	hPa		–
√	Air relative humidity	RH	%		–
	CO_2 concentration in air	CO_2	ppm		–
	Water vapour in air	H_2O	ppth		–
	Soil volumetric water content	M_O	$m^3\ m^{-3}$	O horizon	50%
√	Soil volumetric water content	M_A	$m^3\ m^{-3}$	A horizon	50%
	Soil volumetric water content	M_B	$m^3\ m^{-3}$	B horizon	50%
	Soil volumetric water content	M_C	$m^3\ m^{-3}$	C horizon	50%
	Soil temperature	T_O	°C	O horizon	1%
	Soil temperature	T_A	°C	A horizon	1%
√	Soil temperature	T_B	°C	B horizon	1%
	Soil temperature	T_C	°C	C horizon	1%
√	Net ecosystem exchange	NEE	$\mu mol\ m^{-2}\ s^{-2}$	for CO_2	–
√	Total ecosystem exchange	TER	$\mu mol\ m^{-2}\ s^{-2}$	for CO_2	–
√	Gross primary production	GPP	$\mu mol\ m^{-2}\ s^{-2}$	for CO_2	–
√	Evapotranspiration	ET	$\mu mol\ m^{-2}\ s^{-2}$		1%
	Sensible heat flux	H	$W\ m^{-2}$		–
	Vapour Pressure Deficit	VPD	kPa		–
√	Global shortwave radiation	SW	$W\ m^{-2}$		9%
	Reflected shortwave radiation	SW_R	$W\ m^{-2}$		10%
√	Photosynthetically active radiation	PAR	$\mu mol\ m^{-2}\ s^{-2}$	400–700 nm	–
	Reflected PAR	PAR_R	$\mu mol\ m^{-2}\ s^{-2}$		11%
	Ultraviolet A	UVA	$W\ m^{-2}$	320–400 nm	6%
	Ultraviolet B	UVB	$W\ m^{-2}$	280–320 nm	7%
√	Snow depth	d_{snow}	cm		3%
√	Snow presence	Snow	present/absent		3%
	Wind speed	WS	$m\ s^{-1}$		–
	wind direction E–W	WD_{EW}	°	cos of direction	8%
	wind direction N–S	WD_{NS}	°	sine of direction	8%

of 16.8 m at 1 min intervals. Vapour Pressure Deficit (VPD, kPa) was computed as a function of relative humidity, and the saturated water pressure as in Parry (1983).

Soil volumetric water content ($m^3\ m^{-3}$) was measured at 15 min intervals (Ilvesniemi et al. 2010) by time domain reflectometry (TDR) and soil temperature with thermocouples from the A, B and C horizons (2–5, 5–23 and 23–60 cm, respectively). The soil moisture during November–April was excluded from the analysis since the soil moisture in winter is close to field capacity but the measurement signal is biased in frozen soil. More information about the measuring devices used is available in Vesala et al. (1998).

The ecosystem CO_2 net exchange (NEE) was measured with a closed-path eddy-covariance measuring system (Vesala et al. 2005). The net exchange was partitioned into gross primary production (GPP) and total ecosystem respiration (TER) that was modelled from night time observations using an exponential function with the temperature in soil organic matter as the explanatory factor (Kolari et al. 2009). The evapotranspiration and sensible heat fluxes were calculated using standard methodology with stability filtering described in Mammarella et al. (2009) and Launiainen (2010), respectively.

The measurements were averaged over four-week time windows over the year since average over one month is traditionally used in growth studies and a shorter period is not expected to affect noticeably the final increment. There were 43 of four-week time windows in all. Measurements from the growth year and from the previous year were included as candidate variables for the analyses. At the study site, the height growth is completed in late June – early July and the tracheids in stems expanded to their full widths in early August even the cell wall formation continues till late autumn (Schiestl-Aalto et al. 2015). Thus, we considered data from January in the year before to August of the current year.

2.3 Tree growth: response variables RWI and HII

The annual ring widths were measured from increment cores taken at breast height (1.3 m) of 29 randomly selected trees in late summer 2014. One core per tree was sampled and the year 2014 was excluded from the analysis. All trees were germinated from sown seeds and were of the same age (50-years in 2012), even if the diameter of the sample trees ranged from 8.6 to 31.4 cm with a mean of 19.4 cm. Ring widths were measured using an Addo tree ring analyser (Parker Instruments, Malmo, Sweden). One tree was later discarded from the analysis since the growth had been barely noticeable for years.

The annual height increments were measured from seven trees felled either in 2012 or 2013. The annual height increment was determined from the distances between the whorls of branches along stems. Five of them grew in the unthinned and two in the thinned part of the stand (see Chapter 2.1). The measured tree heights ranged from 12.2 to 20.1 m. The thinning resulted in no differences in annual height increments between the treatments.

A modified negative exponential function was fitted separately for each tree (1984–2014) for detrending the size related changes from the tree ring width series whereas for height growth, a smoothing spline was fitted for each tree for the same purpose (1982–2012). R package dplR (Bunn 2008) calling ModNegExp (modified negative exponential with the default parameter settings) and Spline (smoothing spline with the default rigidity parameter 0.67) were used for fitting the negative exponential and spline smoothing functions, respectively. The long-term trend of height growth resembled a concave function (Figures S1–S2, available as a supplementary file at http://dx.doi.org/10.14214/sf.1680), which cannot be accurately modelled by the negative exponential function, and therefore, a spline was used for height growth. Autocorrelation was not removed from the growth series since the time span was too short for its reliable estimation. In addition, previous season weather variables were related to tree growth.

Tree ring widths and height growth were standardized by dividing the original measurements of each tree by the values of the fitted function. Thereafter, the annual increment indices were calculated as the bi-weight mean of the individual trees (Cook 1985; Cook and Kairiūkštis 1990).

The final correlation and regression analyses were performed over the period 1998–2013, for which data from SMEAR II was available. Even though the detrending was successful, the shortened period included again a minor trend in the obtained ring width and height growth indices (RWI and HII). We removed it by fitting a simple linear regression function, subtracting the fitted values from the observed values, and dividing by the standard deviation of the response variable. The resulting standardized response variable has zero mean and unit variance (Fig. 1).

We computed the intercorrelations of the detrended target variable (bi-weight mean over all other trees), and each individual tree (Figure S3, available as a supplementary file at http://dx.doi.org/10.14214/sf.1680). Most of the individual trees were highly correlated with the master chronology. There were 6 outliers out of 28 trees with respect to ring widths; with respect to

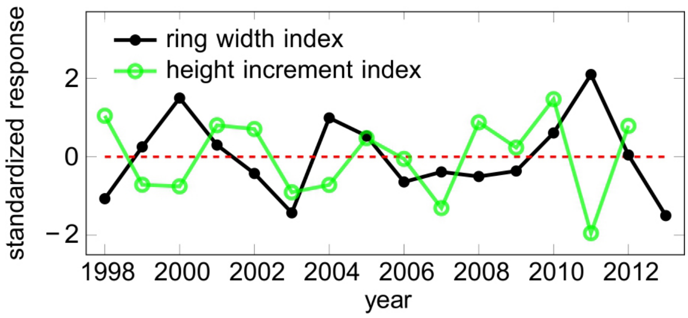

Fig. 1. Standardized response variables i.e. indices for ring width (RWI) and height increment (HII).

height growth, only the smallest tree was an outlier. The expressed population signals using R package dplR were 0.74 and 0.52 for detrended ring widths and height increments, respectively. Even though we had relatively few trees, especially for height growth, the analysed trees showed reasonably consistent signals.

2.4 Data analysis methods

2.4.1 Fixed time analysis with one to four predictors

As a starting point, we computed linear correlations between each independent variable before and during the growth period and each target variable. We used linear models in order to restrict the search space and reduce the risk of overfitting (Hastie et al. 2001), i.e., a situation where a model is so flexible that it fits the sample data to every detail, but fails to capture the essential features of the unseen data. The correlations were statistically significant (two tailed t-test) at 5% level of significance if the absolute correlation with the radial increment indices was higher than 0.49, and with the height increment indices higher than 0.51. The goal of this analysis was to get a basic understanding about the relationships at a single variable level, while further modelling analysed the combinations of variables.

For the second objective, we built and analysed regression models on one, two, three or four independent variables to predict the annual variation in height and cambial growth. The models are referred to as greedy fixed-time models, because in these models all the independent variables come from equal time intervals. First, we generated all possible models using the standard linear regression. There were 465 models with two explanatory variables, 4495 models with three variables, and 31 465 with four variables. Then the models were filtered out based on their testing accuracy score using a pattern mining approach. Testing accuracy score is measured as the coefficient of determination (R^2) on data not used in model fitting via cross-validation procedure, described later. The main principle of the pattern mining approach is that for a more complex model to be selected, the testing accuracy for this model has to be better than the accuracy of any of the models built on subsets of its variables. For example, a model built on A, B, C must be better than models built on A and B, B and C, A and C, and models built only on A, only on B, and only on C.

One-variable fixed-time models were the simplest models build with only one explanatory variable. A separate model was built for each environmental variable in Table 1. The time of year, which had the maximum absolute correlation with the response variable, was selected.

Traditional fixed-time models included two explanatory variables, which are often used in modelling tree growth (e.g. Garcia-Suarez et al. 2009): air temperature and precipitation. The times of year for each variable were chosen such that they had the maximum absolute correlation alone with the response variables.

For each model, we report two performance measures: *R^2 fit* and *R^2 test*. *R^2 fit* is the traditional coefficient of determination, measured on the data used for model fitting. It gives information about the goodness of the model fit. For the baseline predictor that always predicts a constant value, *R^2 fit* = 0. R^2 can be negative, which means that the performance is worse than the baseline. *R^2 test* is a coefficient of determination, computed in the same way, but the predictions are made on data that has not been used for model fitting. We used the leave-one-out cross-validation procedure (LOOCV), see e.g. Hastie et al. (2001) for more details. Firstly, parameter estimation was done on all observations except one. Then, a prediction was made for the remaining observation. The procedure was repeated as many times as there were observations in the dataset. For example, ring width observations were available for the years 1998–2013. First we selected the year 1998 as a test-year. Models were fitted on the years 1999–2013 and tested on 1998. Next, the year 1999 was a test year. Models were fitted on the years 1998, 2000–2013, and tested on 1999, etc.

Before each model fitting, we standardized the explanatory variables to zero-mean and unit-variance. When LOOCV procedure was used, the parameters for standardization were computed on the training data while no parameter fitting was done on the testing data. Missing values were replaced by the mean. When LOOCV procedure was used, means were estimated on only training data. The response variables were converted back to the original representation (growth indices) before computing R^2 measures.

We also report a consistency index, which indicates how consistent the best time of year is during LOOCV. It was computed as the number of observations for which the most frequent time of year appeared, divided by the total number of observations. Consistency, 1 means that at each iteration of the cross validation cycle the same four-week period is nominated as the most informative. If the value is close to 0, then the time selection is very inconsistent.

2.4.2 Variable time analysis with different number of predictors

Least Angle Regression (LARS, Efron et al. 2004) is a regression technique designed for high dimensional data. It iteratively adds predictors to the regression model taking into account dependencies between predictors. The result is a linear model, but the procedure of parameter fitting results to different coefficients from the standard linear regression. We selected LARS technique to analyse how the number of variables affects the model accuracy, i.e. to what extent high number of partly intercorrelated explanatory variables result in tangled models with low accuracy, and whether the results can be improved by the expert-based pre-selection of candidate variables.

We used the R package 'lars' implementation where the maximum number of variables was set to 10 and analysed the occurrence of the parameter values (from 1 to 10). Models obtained by LARS did not have any time constraints. Explanatory variables from any time of year (43 time windows) could have been included, also containing several time periods for an explanatory variable. We used LARS technique for fitting the regression models with three approaches in variable selection:

1: BB, black-box had no restrictions on candidate variables, the selection pool was 31 × 43 = 1333 variables (Table 1),

2: MS, manual pre-selection of 13 variables that have occurred in earlier studies (indicated in Table 1), the selection pool was 13 × 43 = 559 variables, and

3: TR, traditional pre-selection, where only two variables: air temperature and precipitation were allowed, but they could come from any time of year, the selection pool was 2 × 43 = 86 variables.

The analysis was based on the variable selection while fitting LARS regression via cross-validation. For each iteration of LOOCV, a regression model was built. For each variable, we took an average over all the regression coefficients from all LOOCV models. We scaled each coefficient by the total number of candidate variables considered. This way the magnitude of the regression coefficients produced by all three types of any-time models (BB, TS and TR) became comparable. The higher the absolute magnitude of the coefficient, the more important the variable is when considered in a set together with all other variables.

In addition to LARS models, we considered a Baseline model, which does not use any explanatory variables, but always predicts a constant value, equal to the mean of the target variable.

We made the dataset as well as the code implementing our experiments in R publicly available (https://github.com/zliobaite/tree-growth-smear).

3 Results

3.1 Fixed time models

3.1.1 Correlation analysis

There were several periods when individual variables showed consistent correlations with RWI for three or more pixels (i.e. ≥8 weeks, Fig. 2):

1. During the supposed growing season, relative humidity and water vapour were negatively correlated with RWI. Air temperature, carbon gain (GPP), PAR and precipitation during the growing period did not strongly correlate with RWI.
2. Just before or in the early phase of the supposed growing season, air and organic soil temperature, GPP and water vapour concentration positively correlated with RWI while the correlations with global radiation and UVA were negative.
3. Snow depth in the previous winter positively correlated with RWI.
4. Correlations with soil water turned from positive to negative during previous summer
5. GPP in May–Sep in the previous summer (y-1) negatively correlated with RWI while the correlation with NEE was positive for the same period.
6. Soil and air temperatures, water vapour, evapotranspiration and all carbon fluxes (NEE, TER, GPP) negatively correlated with RWI in Jan–Feb in the winter in the previous year (y-1), while the correlation with RH was positive for the same period.

Likewise, several periods were consistently correlated with HII (Fig. 2):

1. During the supposed growing season, RH, soil water and global radiation positively correlated with HII while the correlations with air and soil temperatures and VPD were mostly negative during the same period.
2. Just before or in the early phase of the supposed growing season, RH and snow presence positively correlated with HII while air temperature, TER, GPP, VPD and PAR, UVA and UVB showed negative correlations.
3. Air and soil temperatures and water vapour concentration during winter positively correlated with HII while snow depth, PAR and global radiation showed negative correlations.
4. Precipitation, soil water, RH, GPP, TER and evapotranspiration in the previous summer (y-1) correlated positively with HII, while correlations with VPD, UVA and air temperatures were negative.
5. UVA and UVB in previous spring (y-1) correlated positively with HII while correlation with snow was negative.

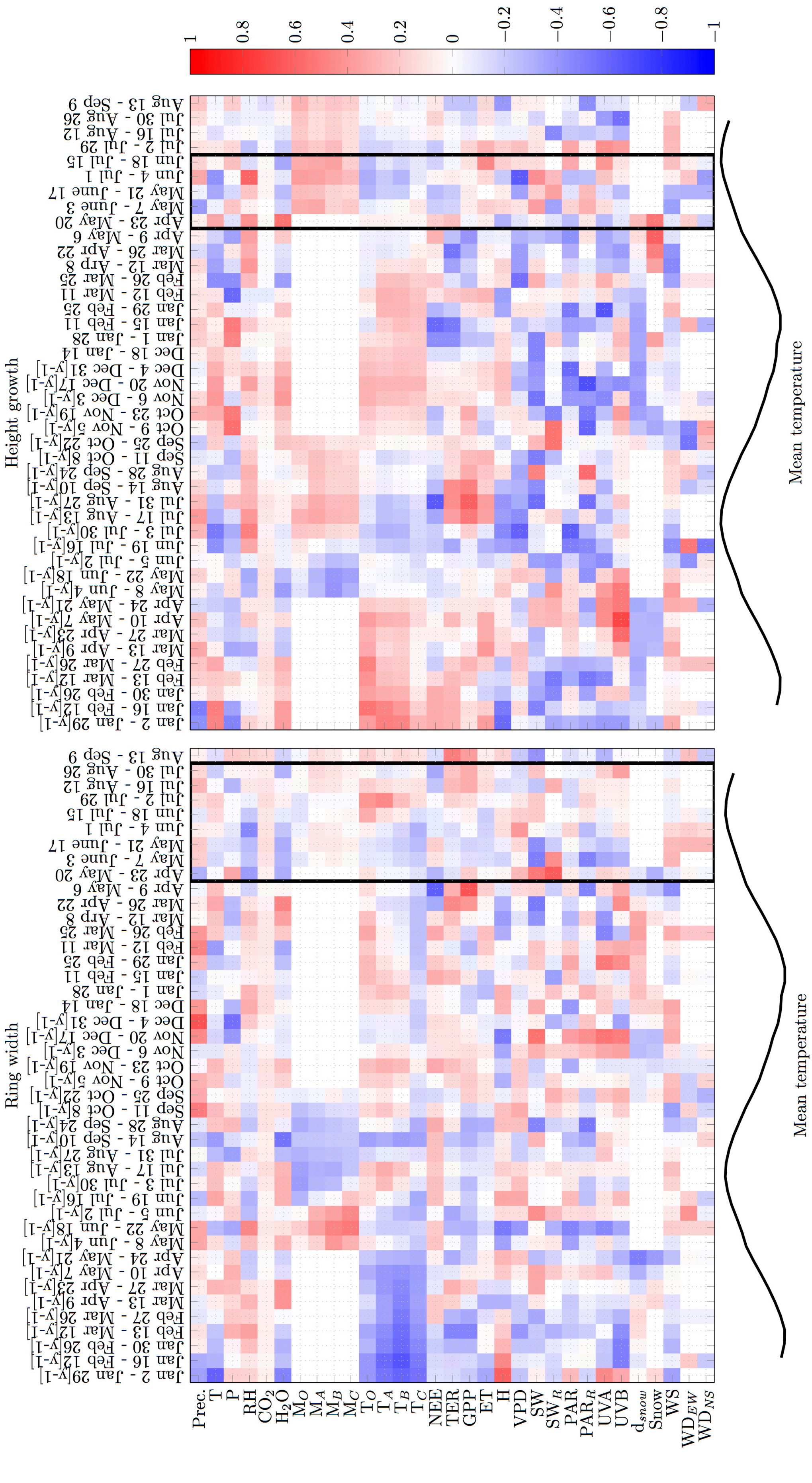

Fig. 2. Individual correlations. Black-lined rectangles indicate the most probable actual growing period according to Schiestl-Aalto et al. (2015). The vertical axis lists variables, the horizontal axis indicates times of year. Each square is a correlation of a given variable at a given time (four weeks interval) with the response variable. For reference the mean temperature for each time of year is plotted. There are white gaps in the measurements of soil water content since the measurement device does not work in winter time. Abbreviations are introduced in Table 1.

6. Soil and air temperatures, water vapour concentration, evapotranspiration and all carbon fluxes (NEE, TER, GPP) in Jan–Feb in the winter in the previous year (y-1) positively correlated with HII while the correlations with snow depth in Jan–Apr (y-1) and radiation in Jan–Mar (y-1) were negative.

3.1.2 One-variable models

The overall predictive power of individual explanatory variables was low for RWI and HII (Table 2ab). Even though R^2 was notable in many cases, the testing mostly resulted in negative R^2 values indicating that the performance was worse than the baseline. However, for both growth variables, there were a few single predictors individually producing positive R^2 *test* values with high stability. For RWI, those predictors were precipitation during the preceding Dec (y-1), as well as NEE and GPP in April. The predictors producing positive test values for HII were both from preceding year (y-1): UVB during April and NEE in August.

Table 2a. Predictive accuracies of explanatory variables for the ring width indices. Cons. indicates the consistency index for the best time, R^2 *fit* the coefficient of determination of the model fit on all data and R^2 *test* the coefficient of determination of leave-one-out cross-validation testing. The abbreviations are introduced in Table 1.

Feature	Best time	Cons.	R^2 *fit*	R^2 *test*
Prec.	Dec 4 – Dec 31 [y-1]	1	0.44	0.35
T	Jan 2 – Jan 29 [y-1]	0.9	0.37	–0.17
P	Dec 4 – Dec 31 [y-1]	0.9	0.3	–0.91
RH	May 22 – Jun 18 [y-1]	0.4	0.22	–2.23
CO_2	Aug 13 – Sep 9	0.8	0.02	–0.62
H_2O	Aug 14 – Sep 10 [y-1]	0.8	0.3	–0.48
M_O	Jul 3 – Jul 30 [y-1]	0.8	0.14	–0.73
M_A	May 22 – Jun 18 [y-1]	0.8	0.12	–0.56
M_B	May 22 – Jun 18 [y-1]	0.9	0.23	–0.13
M_C	May 22 – Jun 18 [y-1]	0.9	0.26	–0.04
T_O	Jul 2 – Jul 29	0.3	0.17	–1.28
T_A	Jan 16 – Feb 12 [y-1]	0.9	0.34	–0.68
T_B	Jan 16 – Feb 12 [y-1]	0.9	0.43	–0.07
T_C	Jan 2 – Jan 29 [y-1]	0.8	0.3	–0.37
NEE	Apr 9 – May 6	1	0.38	0.2
TER	Aug 13 – Sep 9	0.6	0.25	–0.98
GPP	Apr 9 – May 6	1	0.42	0.26
ET	Jan 2 – Jan 29 [y-1]	0.6	0.12	–1.45
H	Jan 2 – Jan 29 [y-1]	0.9	0.39	–0.06
VPD	May 22 – Jun 18 [y-1]	0.4	0.16	–1.23
SW	Nov 20 – Dec 17 [y-1]	0.6	0.3	–1.33
SW_R	Apr 23 – May 20	1	0.4	0
PAR	May 22 – Jun 18 [y-1]	0.8	0.22	–0.66
PAR_R	Aug 28 – Sep 24 [y-1]	0.8	0.26	–0.96
UVA	Nov 20 – Dec 17 [y-1]	0.7	0.28	–0.93
UVB	Nov 20 – Dec 17 [y-1]	0.4	0.26	–1.31
d_{snow}	Apr 24 – May 21 [y-1]	0.8	0.24	–5.28
Snow	Apr 24 – May 21 [y-1]	0.7	0.15	–3.77
WS	Apr 9 – May 6	0.6	0.2	–1.29
WD_{EW}	Jun 5 – Jul 2 [y-1]	0.9	0.18	–1.74
WD_{NS}	Sep 25 – Oct 22 [y-1]	0.9	0.09	–1.22

Table 2b. Predictive accuracies of explanatory variables for height growth indices. Columns as in Table 2a.

Feature	Best time	Cons.	R^2 *fit*	R^2 *test*
Prec.	Jan 16 – Feb 12 [y-1]	0.8	0.25	–1.24
T	Jul 3 – Jul 30 [y-1]	0.4	0.26	–2.19
P	Feb 12 – Mar 11	0.4	0.32	–0.66
RH	Jun 4 – Jul 1	0.9	0.36	–0.84
CO_2	Aug 13 – Sep 9	0.5	0.01	–0.92
H_2O	Apr 23 – May 20	0.9	0.3	–0.82
M_O	Jun 4 – Jul 1	0.6	0.14	–1.19
M_A	Jun 4 – Jul 1	0.3	0.12	–1.32
M_B	May 8 – Jun 4 [y-1]	0.4	0.17	–1.15
M_C	May 22 – Jun 18 [y-1]	0.8	0.13	–1.2
T_O	Jan 16 – Feb 12 [y-1]	0.9	0.29	–0.84
T_A	Jan 2 – Jan 29 [y-1]	0.8	0.25	–1.21
T_B	Jan 2 – Jan 29 [y-1]	0.9	0.22	–0.62
T_C	Nov 20 – Dec 17 [y-1]	0.3	0.08	–1.2
NEE	Jul 31 – Aug 27 [y-1]	0.9	0.42	0.14
TER	Mar 26 – Apr 22	0.6	0.29	–0.83
GPP	Jul 31 – Aug 27 [y–1]	0.9	0.38	–0.27
ET	Jun 18 – Jul 15	0.8	0.22	–0.71
H	Jan 2 – Jan 29 [y-1]	0.8	0.34	–0.76
VPD	Jun 4 – Jul 1	0.7	0.4	–0.78
SW	Jul 31 – Aug 27 [y-1]	0.7	0.31	–0.78
SW_R	Sep 25 – Oct 22 [y-1]	0.6	0.31	–1.59
PAR	Jul 3 – Jul 30 [y-1]	0.9	0.39	–0.14
PAR_R	Nov 20 – Dec 17 [y-1]	0.9	0.46	–0.09
UVA	Jan 29 – Feb 25	0.9	0.43	–0.79
UVB	Apr 10 – May 7 [y-1]	1	0.51	0.31
d_{snow}	Nov 6 – Dec 3 [y-1]	0.4	0.17	–5.13
Snow	Apr 9 – May 6	0.9	0.38	–0.6
WS	Mar 12 – Arp 8	0.6	0.21	–1.02
WD_{EW}	Sep 25 – Oct 22 [y-1]	0.8	0.29	–0.2
WD_{NS}	Jun 19 – Jul 16 [y-1]	0.9	0.28	–0.34

3.1.3 Traditional combination of temperature and precipitation

The model for RWI with the two traditionally used explanatory variables (precipitation and air temperature) fitted reasonable well (R^2 *fit* = 0.62) and the generalization was decent (R^2 *test* = 0.27) when periods were as in Table 2a, i.e. precipitation in previous December and air temperature in January (y-1). However, the generalization performance was worse than it would be using only precipitation as a single variable (Table 2a). For HII, the best periods for precipitation and air temperature were in winter and summer in the previous year (Table 2b), respectively. As these were combined, the model fit was low (R^2 *fit* = 0.38) and it failed at generalization i.e. R^2 *test* was lower than the baseline.

Table 3. Predictive accuracy of selected models with 1–4 predictors for the ring width and height growth indices by the greedy approach. The abbreviations are introduced in Table 1. The used periods are as in Table 2 a and b.

	Predictor				R^2 *fit*	R^2 *test*
	1	2	3	4		
Ring width	Prec.	M_C	GPP	H	0.81	0.52
	H_2O	M_C	T_B	NEE	0.92	0.48
	Prec.	T_B	T_C	ET	0.70	0.41
	T	M_B	M_C	SW_R	0.75	0.38
	H_2O	H	SW_R	-	0.67	0.36
	Prec.	NEE	-	-	0.59	0.35
	H_2O	M_B	T_C	GPP	0.28	0.84
	M_O	T_B	SW_R	-	0.17	0.57
Height growth	PAR_R	UVB	d_{snow}	Snow	0.81	0.63
	M_A	GPP	H	UVB	0.89	0.60
	H_2O	T_B	NEE	PAR	0.74	0.46
	Prec.	RH	TER	UVB	0.84	0.38
	PAR	UVB	-	-	0.63	0.33
	H_2O	GPP	SW_R	PAR_R	0.77	0.31
	M_B	T_A	NEE	H	0.17	0.79
	NEE	PAR_R	WD	-	0.15	0.64

3.1.4 Greedy models with 2–4 predictors

Explanatory factors in the RWI models by the greedy approach were mostly related to water (precipitation, soil water, water vapour, evapotranspiration), soil temperature and CO_2 uptake (GPP) (Table 3). For HII, explanatory factors related to radiation (PAR, UVB), but also to water (soil water, water vapour, precipitation, snow depth) and CO_2 exchange (GPP, NEE), appeared several times (Table 3). The used time periods for the variables were the same as indicated in Table 2ab. For few combinations, the resulting R^2 *fit* and *test* values were reasonably high in comparison with the models with a single predictor.

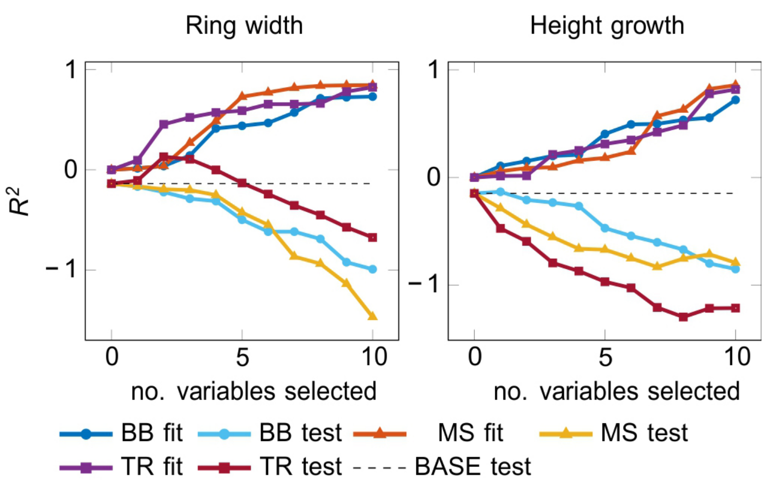

Fig. 3. Accuracy of fit and test models by LARS (see 2.4.2) as a function of the number of included variables.

3.2 Variable time models

The fit and the test accuracies for Black-Box (BB), manual selection (MS), and traditional (TR) models are reported in Fig. 3. Many test results for the ring width modelling were negative, but TR models with 2–4 selected variables (i.e. periods) performed reasonably well (Fig. 3). The height growth models had a fair fitting performance, but the generalization was generally poor, except for BB approach with one selected variable producing a positive R^2 *test*. The variable was UVB during proceeding April–May (y-1), which also performed well in one-variable models (Table 2b).

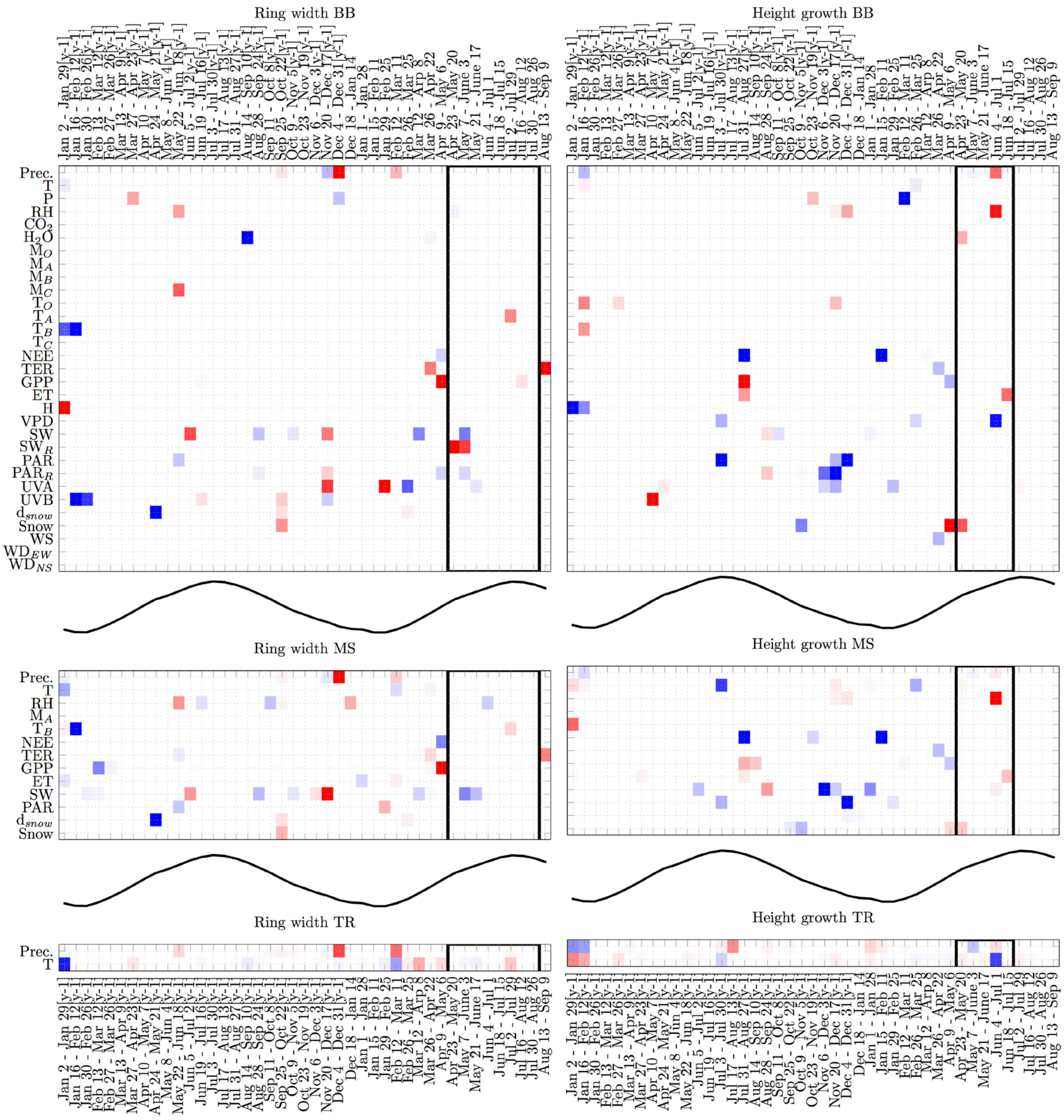

Fig. 4. Analysis of variable selection by LARS in three types of any-time models with different number of candidate predictors (BB, MS and TR). The vertical axis lists variables and the horizontal axis times of year. Black-lined rectangles indicate the most probable actual growing period (Schiestl-Aalto et al. 2015). For time reference, the mean temperature over time is plotted in the middle of the models. Each square is an average over 15–16 models obtained using leave-one-out cross-validation procedure. Blue squares indicate negative relations, and red squares indicate positive relations. Darker colours encode more stable (consistent) performance over multiple trials. Abbreviations are introduced in Table 1.

Generally, the models with fewer input variables did not perform any better than the models with all available input.

LARS analysis focused on predictors that appear most often and most consistently in terms of their relation with the target variables. The Black-box model (BB) and the manual selection model (MS) showed similar relations between RWI and weather events (Fig. 4). The remarkable common negative relations were with GPP in the early phase of a growing period, with global radiation during the growing period and snow depth in the previous spring (y-1). Common positive relations rose with global radiation in previous spring. Both models showed mixed relations with precipitation in winter. In addition, BB model indicated negative relation with water vapour concentration in the previous summer (y-1) and UVA in the winter, positive ones with UVA in the spring and reflected radiation during the growth. On the other hand, only MS indicated negative relations with RH in summer and positive ones in winter. The traditional model (TR) with two variables showed mainly positive relation with precipitation in the winter and negative with air temperature in early spring but during the actual growing period all relations were very weak.

BB and MS models showed some similar relations between HII and weather events as well (Fig. 4). The common positive relations were with RH during growth and GPP during previous summer. Common negative relations were NEE during previous summer and early year, and PAR in previous winter and summer. In addition, BB showed negative relations with reflected PAR in winter, air pressure in late winter and VPD during the growing period. Positive relations only by BB were UVB in previous spring (y-1) and snow presence in the early phase of growing season. On the other hand, only MS showed negative relations with temperature during previous summer and global radiation in the winter. The relations between HII and air temperature during previous summer and during the timing of actual growth were negative with TR model.

4 Discussion

4.1 Performance of data-driven models

We investigated which environmental variables sampled at which time periods of the years had the strongest relation to the annual radial and height increment indices. The task setting was non-trivial because there were only a small number of observations of the dependent variables (15–16) for the time when SMEAR data was available, while there were a large number of independent variables from different time periods within the study years. Selected greedy models with fixed time periods demonstrated the best performance whereas several single variables gave positive R^2 test values, but their overall performance was not up to scale to predict annual growth variation.

Since annual tree growth is a complex process, consisting of cumulative responses to several simultaneous and fluctuating internal and external factors, it is challenging to model the annual growth variation using a temporally averaged period in a single or in a few environmental factors. This approach may yield more consistent results if longer time series were available, but even the exploration over 16 years is an interesting step forward, as this is the first time when so wide a variety of measurements at so high a resolution have been related to tree growth using data mining techniques.

Modelling using the traditional combination of air temperature and precipitation was not sufficient to predict the tree growth since the used periods, selected only by the correlation analysis, may be not the most effective ones for growth. Combining one to four of any single variables on their best times resulted in better test performances but most of the combinations were not consistent with respect to earlier findings and knowledge of the growth process. The Black Box models were clearly too flexible and resulted in overfitting i.e. they achieved in a good model fit but the generalization performance was poor. Even the decrease in the number of variables did not increase the predictive accuracy. The introduced models may have captured some essential factors, but they would require more evaluation and iterative validation to achieve credibility for example as a mixture of data-driven and first principle modeling approaches. Removing the effects of known affecting factors by traditional methods and mining the residuals, for example, could be one step forward.

Nevertheless, the visual examination of the consistent correlations (Fig. 2) over the high-frequency dataset provided new insights even when the build models were not very powerful. The analysis revealed numerous and, in some cases, lagged correlations with both height and diameter growth of trees. Some of the correlations likely result from the short time series in combination with high dimensional dataset, but there also seems to be a consistent pattern in them. Height and diameter growth correlated partially to different factors with very different delays and often respond in an opposite manner to the same factors.

4.2 Height increment

The buds of Scots pine are formed in July–August, whereas the actual elongation takes place in the following year. Therefore, the conditions during the bud formation are influential for the height increment (Salminen and Jalkanen 2007; Schiestl-Aalto et al. 2013). The consistent correlations found in this study suggest that high GPP together with high soil water content and low water demand for transpiration (high RH, low VPD, and low air temperature) during the bud forming period are favourable for height increment during the following summer. High water content in air and soil maintains tree water potential and turgor pressure needed in forming new cells (Pantin et al. 2012). GPP on the other hand promotes material for new cells but also for turgor maintenance (Pantin et al. 2012).

Against earlier findings from Northern latitudes (Salminen and Jalkanen 2007), this study indicated a negative correlation between air temperature during the bud forming period and height increment. This could indicate that high temperature increases transpirational demand which reduces the water potential of the tree and also may decrease the net carbon uptake and the capability to invest in buds. In addition, a decrease in soil water potential may lead apart from low shoot turgor pressure, also to decreased shoot:root ratio (Brunner et al. 2016), causing a competing sink for the assimilates.

During the period when the actual growth takes place, circumstances supporting the high water potential of the tree (soil moisture, RH, precipitation, water vapour concentration) are beneficial for the height increment, whereas circumstances lowering the water potential (high air temperature and VPD) effect negatively. Also the positive correlations with springtime RH and negative correlations with radiation, VPD and air temperature indicate that circumstances accompanied with low transpirational demand favouring high turgor pressure in the early spring are beneficial for the height growth.

UVB radiation in the preceding spring (y-1) unexpectedly showed a strong positive correlation with the height increment in all analyses. Ren et al. (2006) studied *Populus* species and found that UVB radiation significantly decreased height growth. High UVB may point to high radiation in general that in combination with low temperatures are harmful for needles in spring (Öquist and Huner 2003; Ensminger et al. 2004; Porcar-Castell et al. 2008) and thus, cause growth losses to be compensated in the following year.

The individual correlations and coefficients, such as the positive correlations or coefficients between the height increment and temperatures, water vapour concentration, evapotranspiration and carbon fluxes accompanied with negative correlations with snow and radiation during the dormant period more than one year earlier (y-1) are difficult to explain. They could result from the whole tree level structural changes reflecting changes in allocation or alterations, e.g., in hormonal control or some other, unknown reason. It cannot be ruled out that some of the correlations are due to coincidences in a relatively short time series. The low overall predictive power of individual explanatory variables and the models by the greedy approach indicates that not all found correlations are meaningful. For example, the sensible heat flux that is roughly the incoming radiation minus evapotranspiration appears as predictor in the regression models for height and diameter growth. The sensible heat flux depends on radiation, moisture conditions, biological activity etc. hardly having by its own a causal relation to growth.

4.3 Ring width

There were no consistent correlations between the meteorological conditions and ring width during the supposed cambial growth period. Only air humidity and atmospheric water vapour concentration showed slightly negative correlations and VPD slightly positive correlation to ring width indicating, that unlike with height growth, diameter growth was favoured by dry weather during the growing period. This could reflect the fact that growth at the lower part of a stem is not critically limited by air humidity conditions and the level of water potential, which is always higher at the lower part of a stem than at shoots (Zimmermann 1983). Also this combination of conditions is normally favourable for photosynthetic production (Chan et al. 2015).

Summer temperature often correlates with ring width (Mäkinen et al. 2001; Korpela et al. 2011; Grudd 2008; Seo et al. 2011), but our results do not support this indicating again that air temperature during the growing period does not limit the growth in the studied site. Our results are, however, similar with those of Hordo et al. (2011) who found that the temperature in current year March–April correlated positively with Scots pine radial growth in southern Finland and Estonia. Warm spring may also favour the recovery of xylem and phloem transport capacity after winter (Vanhatalo et al. 2015) and for certain extend the growing season that reflects as larger accumulated growth at certain fixed time points.

Our analyses also indicate that high GPP at the beginning of the growing season promotes radial growth supporting the findings of Schiestl-Aalto et al. (2015), Chan et al. (2015) and Babst et al. (2014). The role of early carbon gain can be seen also in the negative correlation with NEE, whose negative values indicate carbon uptake as opposed to GPP. In the spring, high GPP may act as a trigger for the onset of cell division or give compensation for the off-season respiratory losses and thus positively affect tree carbon balance. Alternatively, high GPP in the early spring may indicate earlier onset for the growing season. Rossi et al. (2006) suggested that in cold environments, conifers synchronize the maximum growth rate of tree-ring formation with day length. If the growth were culminated by day length, the early onset would simply increase the annual ring width. On the other hand, Chan et al. (2015) showed that a large amount of recently photosynthesized carbon increased daily growth in spring, so perhaps GPP in the early season stands out in the correlations since sugars have an important role both as a growth resource for cell differentiation and as a factor behind sufficient cell turgor together with water availability.

5 Conclusion

The models produced by the data-driven approaches lacked predictive power to firmly identify strong drivers for growth variation at our study site in southern Finland. The accuracy of the prediction did not increase even if the number of candidate explanatory variables was manually decreased in the massive dataset. However, the approach highlighted several interesting aspects on the annual variation in the height and diameter growth of Scots pine: the growth of the Scots pine trees was not promoted by high temperatures during the growing or bud forming periods. Instead, height growth was favoured by a weather that supported high water potential and carbon gain during the bud forming period, and by circumstances maintaining high water potential during the elongation period. A winter with high precipitation and a long-lasting snow cover and a spring with high photosynthetic production indicated promoted diameter growth during the oncoming summer.

Acknowledgements

This study was supported by the Academy of Finland (257641, 277623) and the Academy of Finland Finnish Centre of Excellence Program (272041). We thank Janne Levula for the increment core measurements.

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Total of 66 references.

Supplementary files

1: Figure_S1-2.pdf

- Figure S1. Measured tree wing widths (black line) and the fitted trends (orange line) in 28 trees over 31 years (1984–2014).
- Figure S2. Measured height increments (black line) and fitted trends (orange line) in 7 trees over 31 years (1982–2012).

2: Figure_S3.pdf

- Figure S3. Intercorrelations of the detrended and averaged indices with individual trees.

available at http://dx.doi.org/10.14214/sf.1680