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Climate condition affects foliar nutrition in main European tree species

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ABSTRACT

Foliar nutrient concentrations, contents, and ratios are important indicators for the nutritional status of trees. They depend on the availability of nutrients and the uptake capacities of the trees, which are controlled by forest structure, soil and climate condition. Consequently, accounting for climate conditions can aid the interpretation of foliar chemistry measurements.

We applied a moving-window approach to identify the effects of atmospheric temperature and precipitation on tree nutrition at different time intervals based on data collected by institutions of the German Federal States within the ICP Forests Level II network. We studied the main nutrients N, P, K, Ca, and Mg as well as foliar mass for the main temperate tree species (European beech, temperate oaks, Norway spruce, Scots pine).

Results show that foliar traits of all main tree species are affected by either current and/or lagged climate condition. Nutrient concentrations are generally less sensitive to climate condition than foliar mass and nutrient contents. Nutrient contents show the same response direction to climate condition as foliar mass, while nutrient concentrations mostly show an opposite response, potentially indicating the existence of dilution effects. Only Ca content in spruce shows weak effects of climate as changes in foliar mass are entirely counterbalanced by opposing changes in Ca concentrations.

For spruce, pine, and oak significant climate effects on nutrient ratios were found. In general, N:P, N:K, and P:K are less sensitive to climate variations than ratios including Mg or Ca. In beech, all nutrient concentrations show a similar response to climate condition. Nutrient ratios in beech are thus relatively robust against climate condition compared to concentrations and contents.

Our results highlight that intervals of less than three month provide a good indication of the climatic impact on tree nutrition. Longer periods, or means over several years, are less suitable as indicators. Defined periods show, however, a significant role of climate beside soil factors and species on foliar nutrition and should therefore be considered for the interpretation of tree nutrition.

1. Introduction

Foliar chemistry is an important indicator of forest trees' nutritional status. A sufficient and balanced supply of nutrients is important to sustain the growth and vitality of trees (Linder, 1987; Bauer et al., 2000; Lévesque et al., 2016; Rohner et al., 2018) and their resistance and resilience to abiotic and biotic stress factors, including drought and insect calamities (Fangmeier et al., 1994; Flückiger and Braun, 2003; Sardans and Peñuelas, 2012; Pöyry et al., 2017). As nutrients become limiting they constrain the response of forest ecosystems to global change (Rennenberg et al., 2009). Thus, nutrient status is an important tool to evaluate the state of forest ecosystems.

Foliar chemistry is assessed through either foliar nutrient concentrations, ratios (Mellert and Göttlein, 2012), or contents (i.e. the product of nutrient concentrations and the mass of a representative number of needles or leaves) (Jarrell and Beverly, 1981; Mellert et al., 2004). Nutrient contents have been suggested to be more closely related to nutrient availability and growth response of trees than nutrient concentrations (Bauer et al., 1997). At a temporal scale, nutrient contents and concentrations often show opposing long-term trends (Jonard et al., 2015), as the variation in nutrient concentrations can partly be explained by the dilution or concentration effect, suggesting a decrease

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or increase related to the mass of the leaves or needles (Mellert et al., 2004). This interrelation between foliar mass, nutrient content, and nutrient concentrations varies for the respective elements (Reemtsma, 1966). According to their functions in plants, nitrogen and phosphorus, for example, are more closely associated with leaf expansion than potassium, magnesium, and calcium (Larcher, 1994; Peñuelas et al., 2019). Nutrient ratios are more suitable in detecting imbalances as they are not as sensitive to dilution and concentration effects, the effect of ageing, and the foliar concentration of non-structural carbohydrates (Flückiger and Braun, 2003) as nutrient contents and concentrations. Trends in foliar chemistry can be easier to detect in nutrient concentrations than in contents, as the multiplication of two independently measured variables can greatly increase the variability (Jonard et al., 2008) due to the measurement error.

Foliar chemistry is a dynamic measure undergoing seasonal and interannual variations thus only ever representing a single moment in time (Bonneau, 1988; Talkner et al., 2019). The deterioration of tree nutrition observed across Europe since the 1990 s (Jonard et al., 2015) is linked to various environmental factors such as atmospheric CO_2 concentrations, nitrogen deposition rates, and climate (Couture et al., 2014; Günthardt-Goerg and Vollenweider, 2015) as well as evolving stand characteristics such as tree age (DeBell and Radwan, 1984). The role of those different influencing factors can be challenging to disentangle; especially with synchronous change. This includes the attribution of changes to climate conditions, especially when short time series are studied (Heinsdorf and Branse, 2002; Jonard et al., 2009). Further, stand characteristics such as tree species composition and tree age, soil conditions, deposition rates, and climate condition influence foliar chemistry (Vries and Posch, 2011; Talkner et al., 2019).

Increases and decreases in foliar nutrient concentrations due to climatic effects can be linked to the availability of nutrients and their uptake as well as to tree internal cycling (Rennenberg et al., 2006). Decomposition rates of organic matter and nutrient remobilisation, the transport of nutrient to the root surface, as well as the uptake of nutrients by roots are generally favoured by higher temperatures and high water availability. Consequently, warm and wet conditions are considered favourable for tree nutrition (Jonard et al., 2008), whereas droughts can have negative effects (Göttlein et al., 2009). The ranges within which the availability of nutrients varies is controlled by soil properties, atmospheric deposition, stand characteristics, and management (Rennenberg et al., 2006). As a result of different mobility and cycling within the tree and in the environment, favourable climate condition varies between nutrients (Bonneau, 1988; Schleppi et al., 2000). Diagnostics of nutrient status based on a single observation might thus draw attention to particular nutrients.

While nutrient uptake is the main source of nutrients in younger trees, in older trees translocation is more important and potentially leading to a temporal decoupling of nutrient uptake and transport to the foliage (Johnson and Turner, 2019). For example, drought leading to early leaf and needle abscission, affects internal translocation and influences litter properties and decomposition dynamics, causing a potentially long term effect (Göttlein et al., 2009; González de Andrés et al., 2019). Furthermore, allocation of nutrients to different plant organs causes interrelations of foliar nutrition with tree growth, fruiting activity, and crown condition. The climate cues to which these are most sensitive have been identified for various tree species, taking site conditions into consideration (Seidling et al., 2012b; Nussbaumer et al., 2018; Nussbaumer et al., 2020). Previous studies on the effects of temperature and precipitation on foliar chemistry used either annual or vegetation-period means (Evers, 1972; Hippeli and Branse, 1992; Schleppi et al., 2000; Heinsdorf and Branse, 2002). However, climate impacts on foliar chemistry might depend on shorter time intervals, such as periods closely related to the phenological phases or relevant for tree growth.

We use data collected by the German Federal States within the ICP Forests Level II network to study the effect of short-term climatic conditions on the nutritional status of forest trees based on nutrient concentrations, ratios, and contents. Further data from the ICP Forests network allows the comparison of the results to the effects of climate condition on tree growth and phenology. We thereby aim to increase the knowledge on the robustness of single measurements of nutrient concentrations and contents for various research questions.

Specifically, we assessed the relative importance of temporal and spatial variability in five foliar nutrient concentrations and contents and nine foliar nutrient ratios to further identified the climatically most important time periods and assessed their suitability to distinguish favourable from less favourable years. Finally, we discuss the interrelations between foliar mass and nutrient concentrations to elucidate the possible attribution of climate effects to the dilution effect.

2. Materials and methods

2.1. Data preparation

The data set used in this study comprises 97 intensive forest monitoring plots operated as part of the ICP Forests Level II programme by institutions of the German federal states (Fig. 1). The study sites include both homogenous and mixed stands of European beech (36 study sites), sessile and pedunculate oak (combined analysis, 15 study sites), Norway spruce (38 study sites), and Scots pine (21 study sites). Measurements for four to 26 sampling years (covering the time period 1990 to 2017) were available for each study site (average of 11.7 to 15.6 years depending on the tree species). In general, the available data consists of pooled samples of five trees. In cases where separate data was submitted for each tree, arithmetic means were calculated prior to further analysis. Foliar sampling and chemical analyses were carried out according to the ICP Forests Manual (Rautio et al., 2010). The sampling times for each tree species are shown in Figs. 2-5.

Data on atmospheric temperature and precipitation is based on the meteorological measurements at the ICP Forests Level II sites, homogenised by interpolations involving climate data from the German meteorological network (DWD) (Ziche and Seidling, 2010) for the time period between 1990 and 2014. Mean annual temperatures vary between 3.6 and 11.3 °C and mean annual precipitation sums between 560 and 1740 mm. Phenological data, assessed at tree level according to the ICP Forests Manual (Beuker et al., 2010), was available for thirteen beech sites, six oak sites, five for spruce, and ten for pine. For any five day interval, we calculated the percentage of trees with ongoing flushing (all tree species), colour changes and leaf fall (beech and oak only). For these calculations, each available observation was treated as a data point, without taking the specific observation year or study site into consideration. Data on radial stem growth (Beck, 2009; Seidling et al., 2012b) was available for the period between 1990 and 2004. Mean increment growth (INCR) was calculated from measurements on six to 25 individual trees prior to further analysis.

2.2. Statistical analysis

To assess the variability of foliar chemistry, coefficients of variation (CV) were calculated for five macronutrients (N, P, K, Ca, Mg) as well as the most common nutrient ratios in current leaves or needles for the tree species European beech, sessile and pedunculate oak (analysed together), Norway spruce, and Scots pine. Generalized additive models (GAM) from the mgcv package (Pedersen et al., 2019) with the sampling year and the study site as factorial variables were used to identify the proportion of deviance that can be attributed to spatial and temporal variability.

To assess the effect of climate condition on foliar chemistry, we used generalized linear mixed models (GLMM) from the nlme package version 3.1–140 (Pinheiro et al., 2020) with study site as a categorical random effect variable and either mean atmospheric temperature or precipitation sums of a given model interval as a fixed effect.

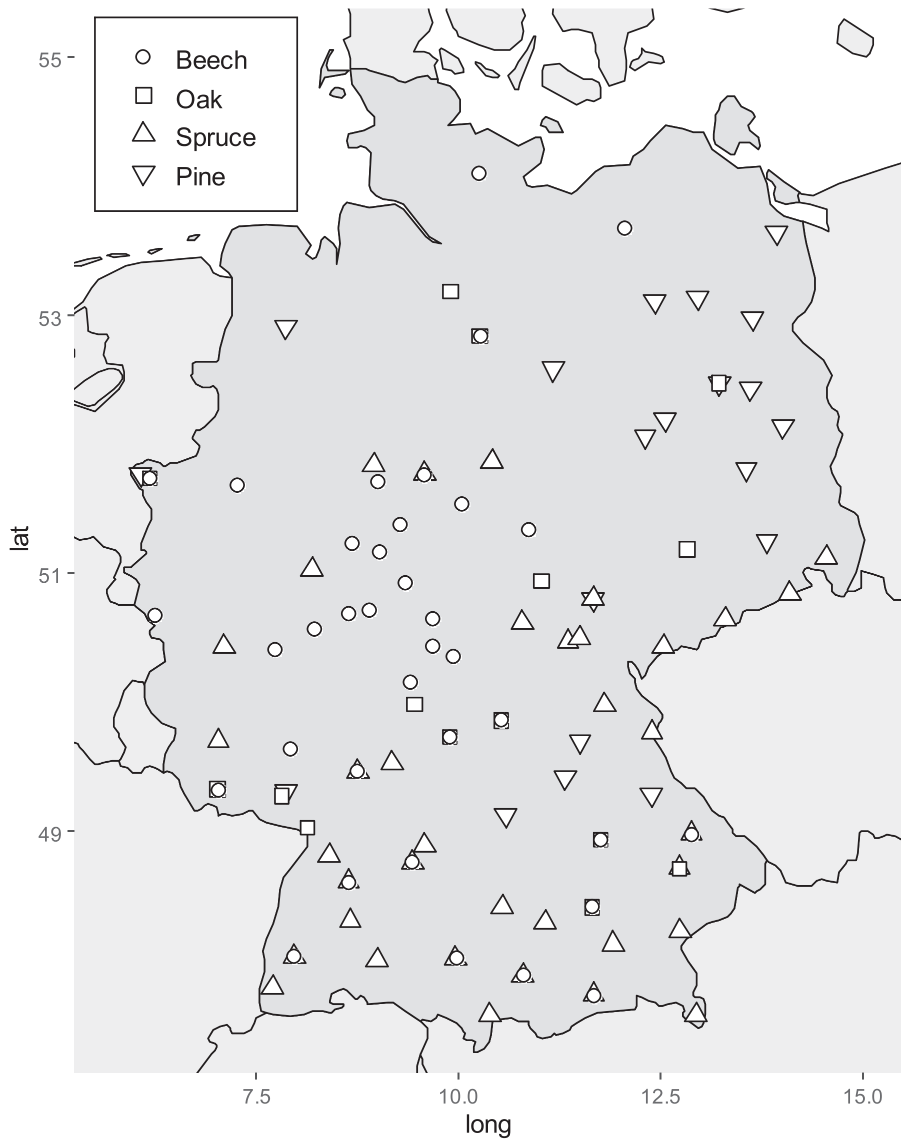

Fig. 1. Map of Germany, showing Level II plots considered in the analysis.

In a moving-window approach, we ran the GLMMs for different time lags and durations of the aggregation period for temperature and precipitation. The model intervals include periods between ten and 550 days, starting from the first day of the year preceding sampling, and moving by five days until the last day of the interval corresponds to the 235th day of the sampling year (August 21th when the observed periods does not include a leap year). This results in a total of 2026 models per combination of response variable and climatic parameter. For each model interval and climate parameter (precipitation sum, mean temperature), a separate GLMM was run. To control for false discovery rates, adjusted p values were calculated using the Benjamini-Hochberg method with the p.adjust function (false discovery rate of 0.05). Adjusted p values < 0.05 were considered significant.

The climatic variables entered the model in a scaled form. First, for each study site and model interval, the mean of atmospheric temperature and precipitation sums were calculated over all sampling years. In the next step, climatic conditions of each sampling year were expressed as deviations from their corresponding long-term means and scaled between -1 and 1 by dividing the deviation by the maximal absolute deviation for any year. The scaling was performed separately for each site and model interval. We then calculated the relative effect of climatic conditions as the ratio of the regression coefficient of the respective climate variable to the intersect (global mean) for each time step. As the climate parameters were scaled between -1 and 1 prior to analysis (see above), the relative effect of any given model interval corresponds to the relative deviation of the respective foliar nutrient value from its mean value expected under the recorded climate extreme for the corresponding interval. We derived four quantities of interest from the GLMMs and corresponding relative effects. Note that these indicators only serve to roughly summarise the results and their absolute values are not directly interpretable. (1) In order to aggregate results and allow a quick identification of climate effects, we calculated a climate sensitivity indicator (CS) corresponding to the sum of the absolute value of the relative effects of significant models divided by 2026 (total number of models). (2) The correlation between the climate effects on foliar mass and nutrient concentrations presents an indicator of the climate driven dilution/concentration (DC) effect. Low values (below zero) point towards dilution/concentration effects. Values close to zero indicate no or low interaction between foliar mass and nutrient concentrations. Positive values indicate that climate affects both foliar concentrations and foliar mass in the same direction. (3) Based on R^2, we then identified the three model intervals for which atmospheric temperature and

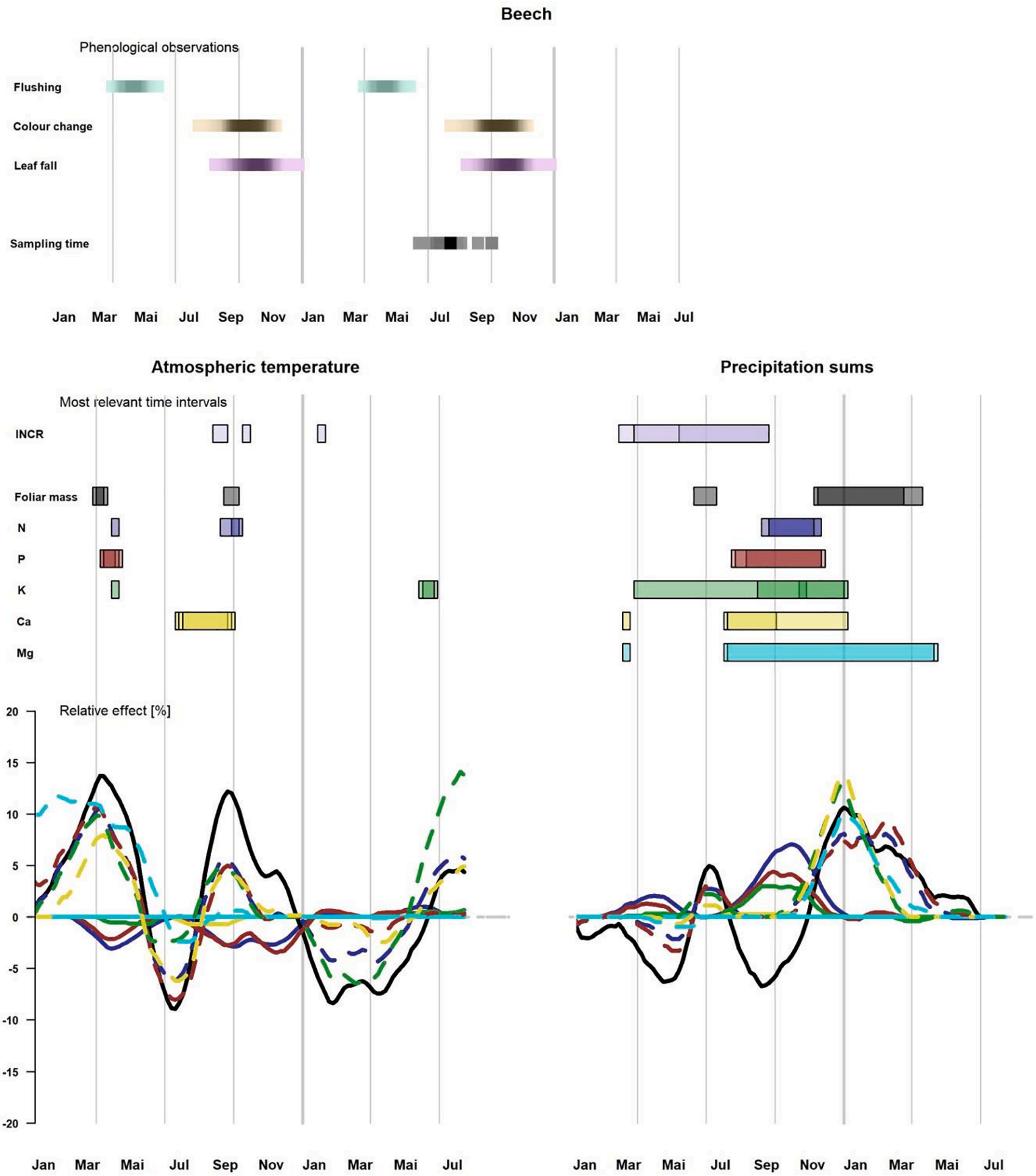

Fig. 2. Graphic summary of the results of the climate sensitivity analysis for beech. Phenological observations: Tints indicate the number of available observations for a period of the year. Most relevant time intervals: up to three time periods for which the corresponding significant models had the highest R^2 for the following parameters: Mean radial stem increment width (INCR) (lilac), foliar mass (black), N concentration (blue), P concentration (red), K concentration (green), Ca concentration (yellow), and Mg concentration (cyan). Relative effect [%]: relative effect of models with model intervals between 30 and 90 days for foliar mass, nutrient concentrations (straight lines – colours correspond to those above), and nutrient contents (dashed lines – colours correspond to those of nutrient concentrations).

precipitation were most informative for each nutrient concentration as well as for foliar mass and INCR. Only models for intervals with an adjusted $p < 0.05$ were considered. (4) Finally, we identified mean relative effects of climatic conditions on each foliar parameter for each time step prior to foliar sampling (five days as defined by the moving window, visualized in Figs. 2-5). Calculated relative effects were averaged across all (significant and non-significant) models per climate variable and foliar parameter by dividing the sum of the relative effects by the number of models overlapping with the considered time step. To reduce inhomogeneity in the number of available model intervals between time steps, the averaging includes results from models based on model intervals between 30 and 90 days only and does thus not include all models considered in the CS.

3. Results

Results show that foliar traits of all main tree species are affected by either current and/or lagged climatic conditions while the influence

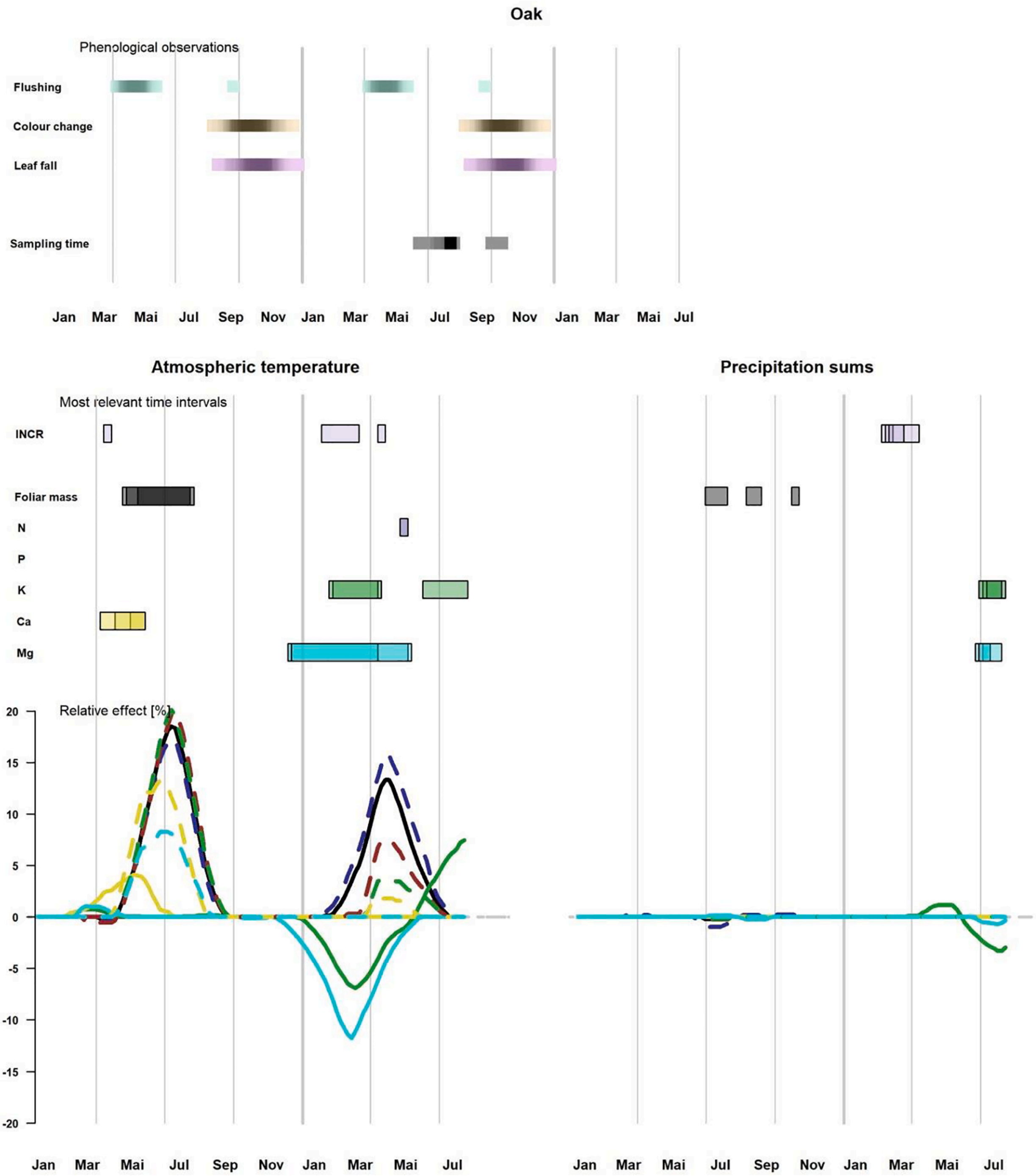

Fig. 3. Graphic summary of the results of the climate sensitivity analysis for oak. Phenological observations: Tints indicate the number of available observations for a period of the year. Most relevant time intervals: up to three time periods for which the corresponding significant models had the highest R^2 for the following parameters: Mean radial stem increment width (INCR) (lilac), foliar mass (black), N concentration (blue), P concentration (red), K concentration (green), Ca concentration (yellow), and Mg concentration (cyan). Relative effect [%]: relative effect of models with averaging periods between 30 and 90 days for foliar mass, nutrient concentrations (straight lines – colours correspond to those above), and nutrient contents (dashed lines – colours correspond to those of nutrient concentrations).

varies between nutrients. To highlight the differences, ranges and mean values of foliar mass, nutrient concentrations, nutrient contents, and nutrient ratios are given in Table 1 (beech and oak) and Table 2 (spruce and pine).

Variability is lowest for N, followed by K and P, consecutively by Ca or Mg for all tree species. Nutrient contents show higher variability than nutrient concentrations. Variability in foliar mass tends to be in a similar range as in nutrient contents. Deviance explained by study site and sampling year depends on tree species. In beech, the deviance explained by the sampling year is higher than the deviance explained by the study site for N, P, K and foliar mass, whereas the opposite applies for Ca and Mg (Fig. 6). In oak, a higher percentage of the deviance in all measures of foliar chemistry is explained by study site rather than by sampling year. K content is the only nutrient content for which no significant effect of sampling year is found (Fig. 7). In spruce, study site explains some of the deviance in nutrient concentrations and contents while sampling

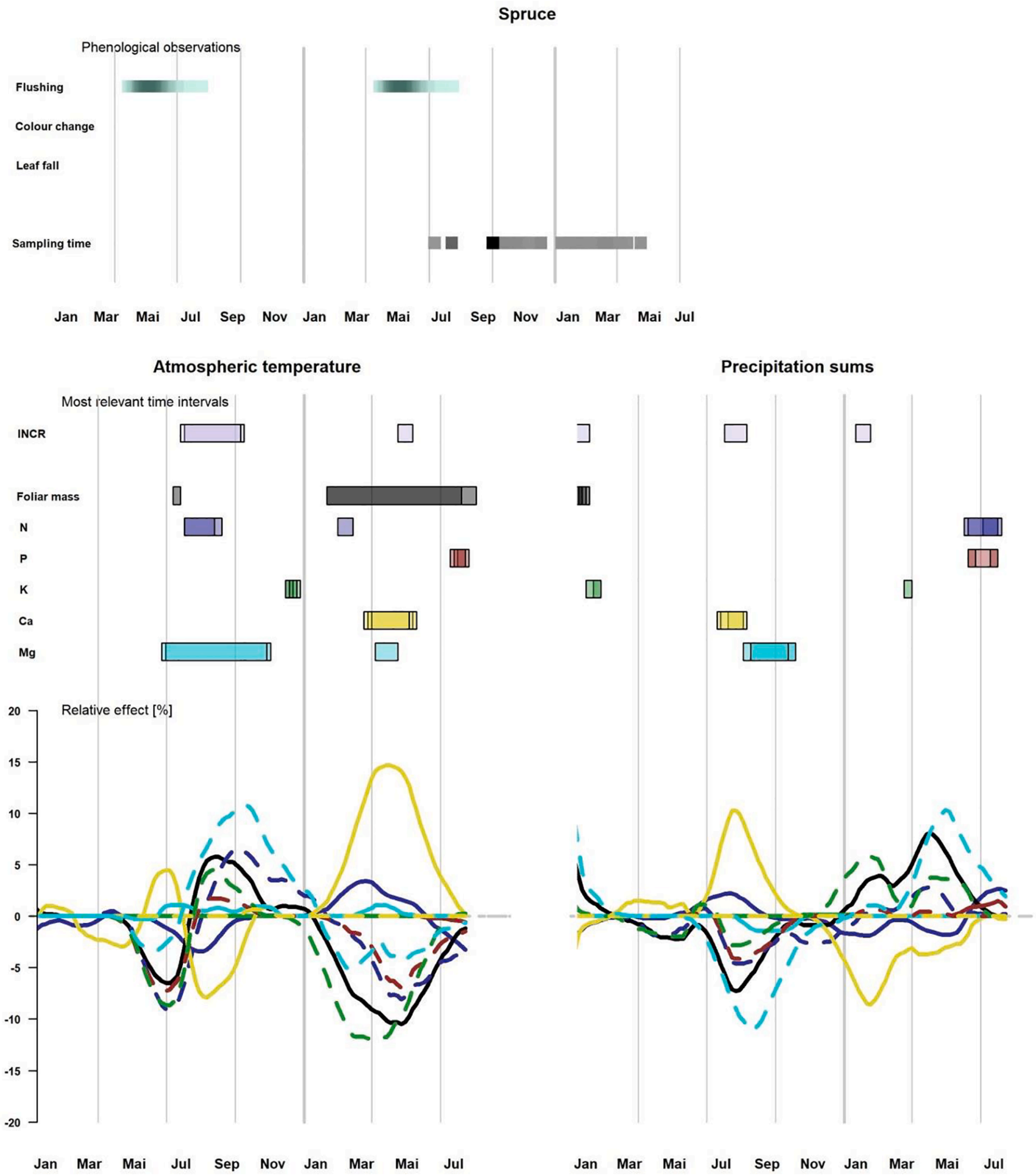

Fig. 4. Graphic summary of the results of the climate sensitivity analysis for spruce. Phenological observations: Tints indicate the number of available observations for a period of the year. Most relevant time intervals: up to three time periods for which the corresponding significant models had the highest R^2 for the following parameters: Mean radial stem increment width (INCR) (lilac), foliar mass (black), N concentration (blue), P concentration (red), K concentration (green), Ca concentration (yellow), and Mg concentration (cyan). Relative effect [%]: relative effect of models with averaging periods between 30 and 90 days for foliar mass, nutrient concentrations (straight lines – colours correspond to those above), and nutrient contents (dashed lines – colours correspond to those of nutrient concentrations).

year explains only a lower percentage of the deviance (Fig. 8). In pine, sampling year explains a higher percentage of deviance in all nutrient concentrations and contents than study site (Fig. 9). Whereas deviance explained by sampling year for nutrient concentrations and contents are similar, deviance explained by study site is higher for nutrient concentrations than for nutrient contents.

For all tree species, the analyses (GLMMs) show that climatic conditions have significant effects on foliar chemistry for all tree species (Table 3). The climate sensitivity indicator (CS) of nutrient contents is generally higher than climate sensitivity of nutrient concentrations (Table 3). With the exception of beech, CS of atmospheric temperature tends to be slightly higher than CS of precipitation for nutrient contents, whereas it is on average slightly lower for nutrient concentrations. Overall, the lowest CS of all parameters are found for the N:P ratio (Table 4). When climate effects on nutrient concentrations are significant, they are in most cases negatively correlated with foliar mass

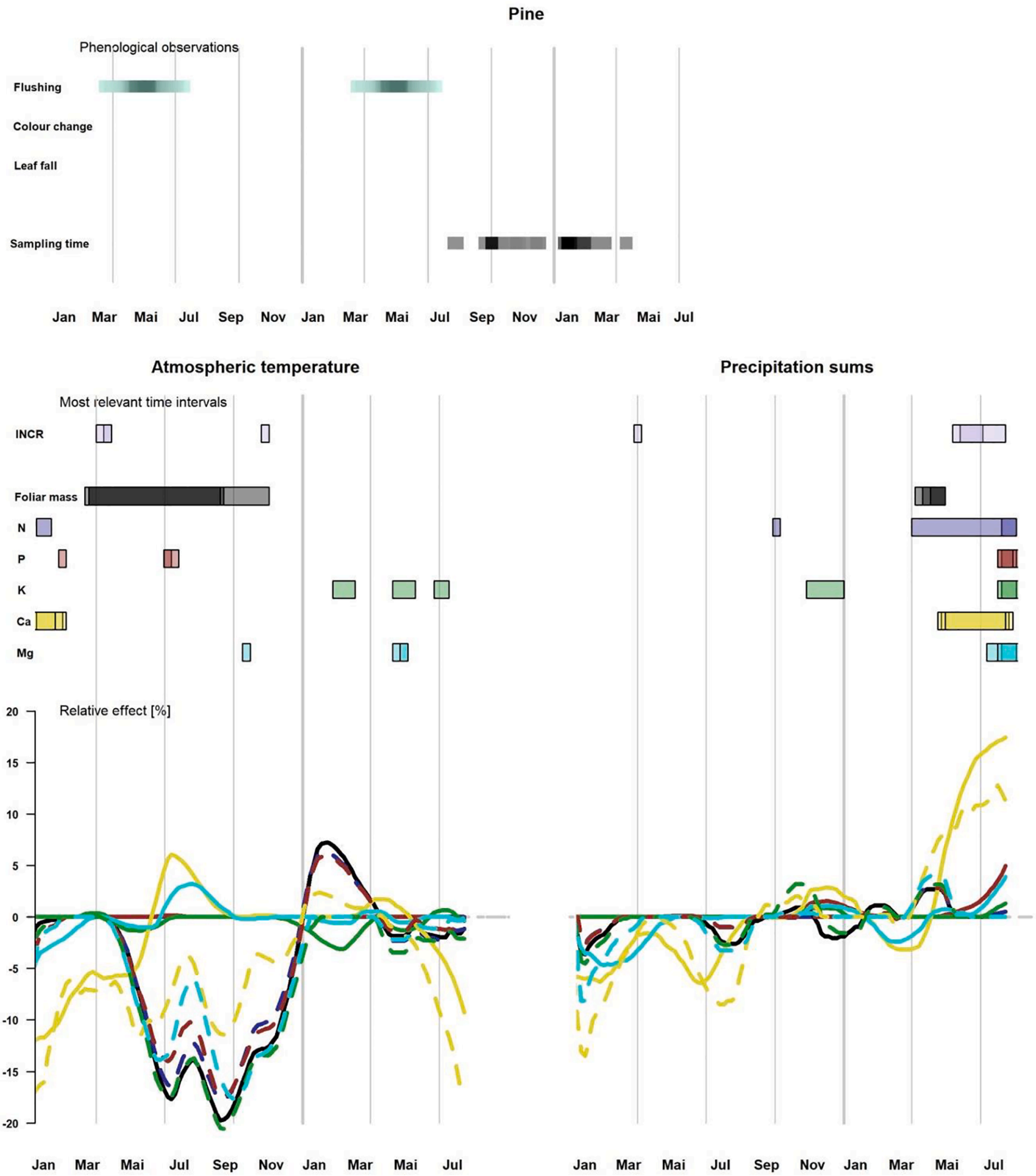

Fig. 5. Graphic summary of the results of the climate sensitivity analysis for pine. Phenological observations: Tints indicate the number of available observations for a period of the year. Most relevant time intervals: up to three time periods for which the corresponding significant models had the highest R^2 for the following parameters: Mean radial stem increment width (INCR) (lilac), foliar mass (black), N concentration (blue), P concentration (red), K concentration (green), Ca concentration (yellow), and Mg concentration (cyan). Relative effect [%]: relative effect of models with averaging periods between 30 and 90 days for foliar mass, nutrient concentrations (straight lines – colours correspond to those above), and nutrient contents (dashed lines – colours correspond to those of nutrient concentrations).

(Table 5). Dilution/concentration effect (DC) is strongest for Ca in spruce as the value is lowest (-0.93 and −0.85 for atmospheric temperature and precipitation respectively). Further, strong DC effects are found for N in beech and spruce, whereas for pine and oak DC is close to zero (Table 5).

In beech, CS of precipitation sums are generally higher than CS of atmospheric temperature (Table 3). The most informative model intervals, with an R^2 of up to 0.09 (atmospheric temperature) and 0.18 (precipitation sums), are generally shorter for atmospheric temperature (10–70 days) than for precipitation sums (up to 280 days). If a significant relationship with atmospheric temperature or precipitation sums for short averaging periods (10–90 days) exists, we also find significant relationships for medium (90–180 days) or long (over 180 days) periods (data not shown). No significant effect of climatic conditions on the considered nutrient ratios is found (Table 4). The effects of atmospheric temperature and precipitation on foliar mass, nutrient concentrations

Table 1
Minimum, mean, maximum values as well as coefficients of variation (%) for foliar mass (g 100 leaves or 1000 needles), nutrient concentrations (mg per g) (CN) and nutrient contents (mg per 100 leaves or 1000 needles) (CT), and nutrient ratios for beech and oak.

		Beech				Oak			
		Min	Mean	Max	CV	Min	Mean	Max	CV
Foliar mass		4	12	20.4	25.2	9.0	26.4	60.0	35.2
N	CN	18.5	23.7	32.0	9.5	19.3	25.9	31.8	10.3
	CT	107.2	283.1	515.7	25.7	188.1	677.6	1582.8	35.4
P	CN	0.7	1.2	2.0	17.2	0.4	1.5	2.3	21.0
	CT	6.2	14.8	34.2	28.0	11.3	39.7	102.6	39.2
K	CN	3.5	7.0	14.5	21.1	5.5	8.3	13.4	16.8
	CT	27.1	84.5	212.4	33.2	66.4	219.1	454.2	35.9
Ca	CN	2.0	7.0	15.9	38.6	3.1	6.5	16.8	36.9
	CT	21.4	84.1	264.5	44.8	49.9	163.6	365.0	35.6
Mg	CN	0.5	1.3	4.0	45.8	0.6	1.6	4.0	32.4
	CT	5	15.6	44.1	46.0	10.6	41.3	96.3	33.7
N:P		10.7	19.6	33.4	17.2	11.3	17.7	59.2	25.6
N:K		1.7	3.5	6.6	22.3	2.0	3.2	5.2	18.4
N:Ca		1.3	4.0	11.5	46.8	1.6	4.4	9.3	30.9
N:Mg		5.8	21.7	48.2	41.0	6.9	17.0	41.6	26.2
Ca:P		1.3	5.8	15.7	42.1	2.2	4.4	18.9	47.2
K:Ca		0.4	1.2	3.5	47.7	0.4	1.4	2.6	29.5
K:Mg		1.4	6.5	18.0	47.3	1.5	5.4	12.2	26.8
P:K		0.1	0.2	0.4	26.4	0.1	0.2	0.3	18.1
Ca:Mg		2.4	5.8	16.6	41.6	2.0	4.0	7.9	26.4

Table 2
Minimum, mean, maximum values as well as coefficients of variation (%) for foliar mass, nutrient concentrations (CN) and nutrient contents (CT), and nutrient ratios for spruce and pine.

		Spruce				Pine			
		Min	Mean	Max	CV	Min	Mean	Max	CV
Foliar mass		1.8	5.1	9.8	22.0	1.7	20.6	59.0	39.1
N	CN	9.9	14.5	19.4	10.3	12.2	16.0	21.8	10.2
	CT	25.4	73.2	150.3	22.0	27.4	332.7	882.6	42.2
P	CN	0.8	1.5	2.5	19.8	0.8	1.5	2.2	13.6
	CT	1.7	7.7	24.4	30.2	2.5	30.3	77.4	41.1
K	CN	2.2	4.9	8.4	22.8	3.0	5.3	8.1	13.5
	CT	6.2	24.9	43.3	28.8	8.6	109.1	293.8	42.3
Ca	CN	1.1	3.4	10.1	46.0	1.7	3.0	5.8	22.4
	CT	5.0	16.8	60.7	51.2	3.9	61.0	182.9	44.8
Mg	CN	0.3	1.0	2.0	29.6	0.2	0.8	1.4	19.6
	CT	0.8	5.2	15.4	39.5	1.4	17.2	44.1	42.8
N:P		5.9	9.9	16.1	16.4	6.5	11.1	20.1	16.1
N:K		1.7	3.1	6.4	25.0	2.1	3.1	4.5	13.9
N:Ca		1.2	5.2	14.1	47.5	2.8	5.7	9.8	22.4
N:Mg		6.5	15.6	64.0	36.1	11.1	19.9	67.6	25.6
Ca:P		0.6	2.4	11.5	58.3	1.0	2.0	3.2	20.7
K:Ca		0.3	1.8	5.7	55.3	0.9	1.9	3.1	23.5
K:Mg		1.5	5.4	17.8	42.7	3.6	6.5	19.7	26.0
P:K		0.2	0.3	0.7	26.1	0.2	0.3	0.5	16.0
Ca:Mg		1.0	3.4	11.8	43.7	2.1	3.6	8.3	24.7

and nutrient contents can be either positive or negative depending on the time period (Fig. 2). The effect of atmospheric temperature on N and P concentration closely mirrors the effect on foliar mass. N, P, and K concentrations all show a significant negative effect of lagged spring temperature, a time period corresponding to the flushing of previous leaves. Foliar mass and nitrogen concentrations both show a significant effect of lagged autumn temperature for a time period that roughly coincides with the beginning of colour change. A positive effect of lagged autumn precipitation on all nutrient concentrations also corresponds with this time period. Significant effects of atmospheric temperature (R^2 of up to 0.16) and precipitation sums (R^2 of up to 0.12) are found for INCR. Lagged autumn temperatures, early spring temperatures, and lagged spring precipitation are most significant (Fig. 2). The durations of phenological periods (flushing, colour change, and leaf fall) are shown in Fig. 2. Flushing starts between the 96th and the 136th day of the year, colour change between the 165th and the 289th day of the year, and leaf fall starts between the 239th and the 305th day of the year.

In oak, significant effects of atmospheric temperature (R^2 values of up to 0.19) and precipitation sums (R^2 values of up to 0.15) are found for fewer measures of foliar chemistry. The strongest effect of climate is a negative influence of early spring temperature on K and Mg concentrations. For K, a positive effect of summer temperature and a negative effect of summer precipitation are also found (Fig. 3). The most informative periods of temperature effect on N and Ca concentrations roughly correspond to the periods of flushing of the sampling and the preceding year respectively (Fig. 3). Lagged spring and summer temperature as well as spring and summer temperature of the sampling year have a positive effect on foliar mass. To some degree, foliar contents of all nutrients show similar patterns as foliar mass, although spring temperature of the sampling year has no significant effect on foliar Mg content. While significant effects can be found for both short and medium time periods (up to 180 days), models with yearly average atmospheric temperatures give few significant results. In contrast to beech, significant effects of either temperature or precipitation are identified

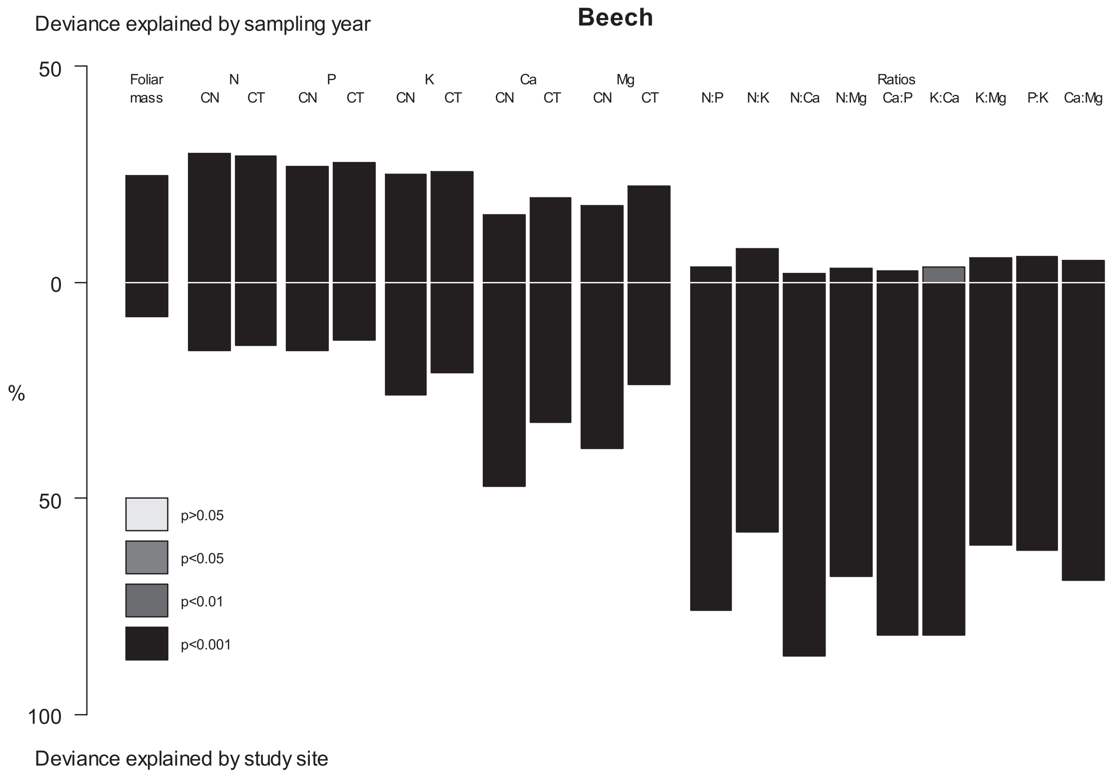

Fig. 6. Deviance explained by sampling year and study site in % for beech.

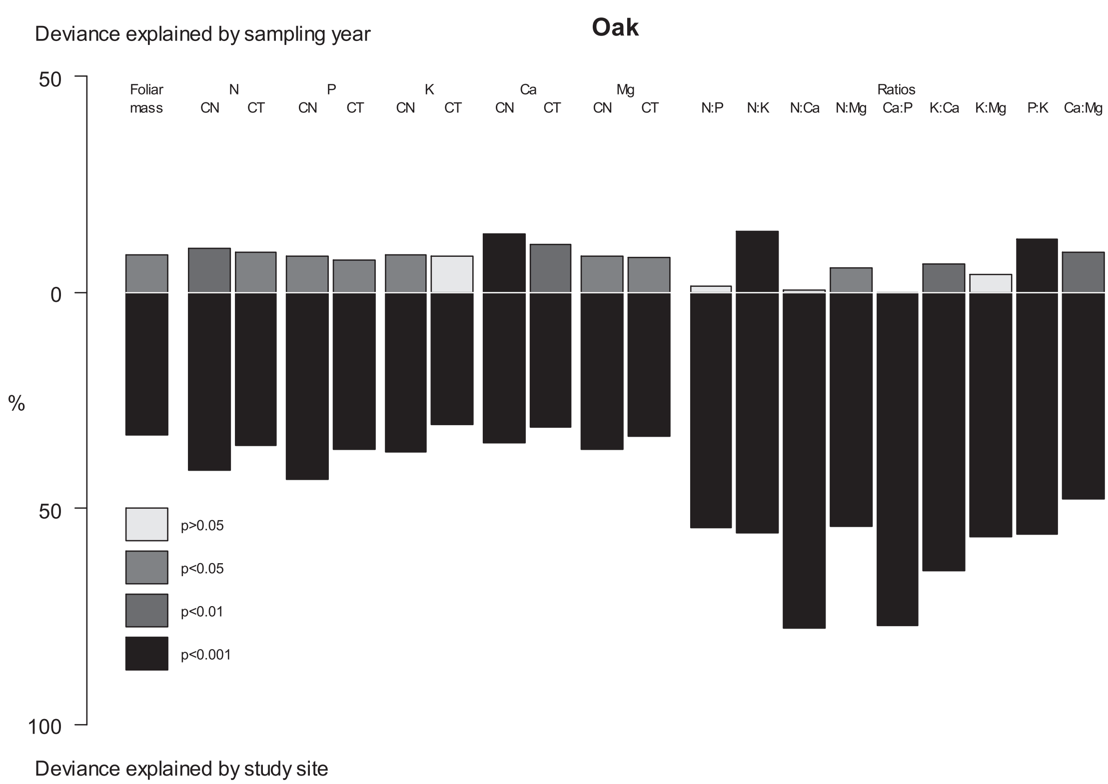

Fig. 7. Deviance explained by sampling year and study site in % for oak.

for all nutrient ratios but Ca:P (Table 4). Especially the Ca:Mg, the N:K, and the N:Mg ratio are influenced by climatic conditions. In accordance to the most informative time periods for nutrient concentrations, spring temperatures have the most significant influence on nutrient concentrations. Although short model intervals with up to 90 days have higher R^2 values (up to 0.18), significant effects are found for periods with more than 180 days also (R^2 up to 0.09). INCR is significantly influenced by atmospheric temperature and precipitation (R^2 up to 0.10

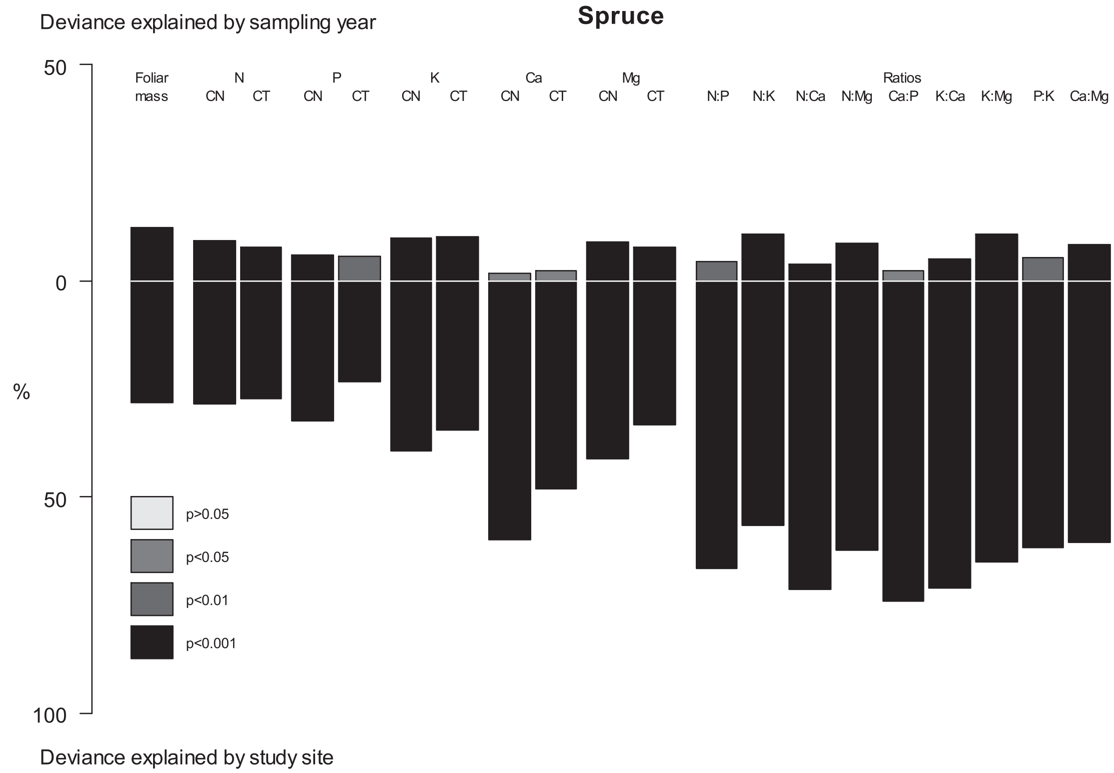

Fig. 8. Deviance explained by sampling year and study site in % for spruce.

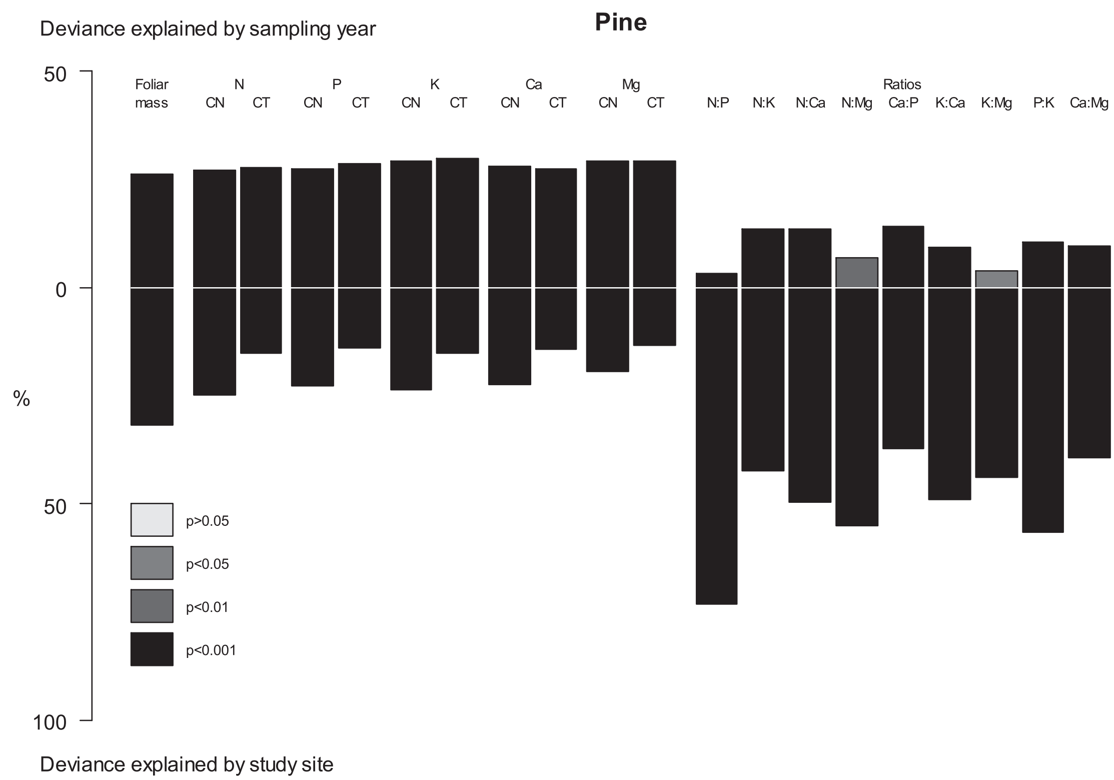

Fig. 9. Deviance explained by sampling year and study site in % for pine.

and 0.13 respectively). Climatic conditions in spring of the current year are most important for INCR (Fig. 3). In oak, flushing starts between the 96th and the 127th day of the year, colour changes starts between the 101st and 291st day of the year, and leaf fall starts between the 243rd and 333rd day of the year (Fig. 3).

In spruce, effects of either atmospheric temperature as well as precipitation sums have R^2 values of up to 0.11. Ca has the highest CS among nutrient concentrations but the lowest among nutrient contents.

Table 3
Summary of results for climate sensitivity (CS) for foliar mass, nutrient concentrations (CN), and nutrient contents (CT). CS of 0.00 indicates that no model gave significant results.

—	—	Atmospheric temperature				Precipitation sum			
		Beech	Oak	Spruce	Pine	Beech	Oak	Spruce	Pine
Foliar mass		3.04	4.06	1.59	8.47	2.78	0.01	2.62	0.19
N	CN	0.51	<0.01	0.53	<0.01	3.96	0.00	0.59	0.04
	CT	1.47	6.03	1.32	6.53	6.04	0.02	2.49	0.11
P	CN	0.48	0.00	0.01	0.01	3.10	0.00	0.04	1.05
	CT	1.11	0.76	0.99	6.61	5.67	<0.01	1.26	0.11
K	CN	0.06	0.70	1.84	0.83	4.49	0.08	0.03	0.14
	CT	1.31	1.14	4.75	12.55	6.49	<0.01	1.21	0.24
Ca	CN	0.01	0.15	4.58	1.37	3.30	0.00	2.66	3.39
	CT	0.53	0.74	0.01	7.70	7.87	0.00	0.00	3.31
Mg	CN	0.00	5.62	1.71	0.19	0.04	0.03	0.05	0.35
	CT	3.03	0.21	1.37	10.57	6.30	0.00	3.40	0.30

Table 4
Summary of results for climate sensitivity (CS) for nine nutrient ratios. CS of 0.00 indicates that no model gave significant results.

Nutrient ratio	Atmospheric temperature				Precipitation sum			
	Beech	Oak	Spruce	Pine	Beech	Oak	Spruce	Pine
N:P	0.00	0.02	0.00	<0.01	0.00	<0.01	<0.01	0.90
N:K	0.00	1.41	3.06	2.23	0.00	0.14	1.93	0.01
N:Ca	0.00	0.21	1.87	1.05	0.00	0.07	0.92	2.89
N:Mg	0.00	5.07	0.40	0.02	0.00	0.05	0.29	0.01
Ca:P	0.00	0.36	4.85	0.87	0.00	0.02	1.67	3.26
K:Ca	0.00	0.01	7.51	2.98	0.00	<0.01	2.31	2.26
K:Mg	0.00	0.00	7.19	0.02	0.00	<0.01	0.30	0.01
P:K	0.00	0.78	0.33	2.60	0.00	0.05	0.26	0.01
Ca:Mg	0.00	6.06	2.38	0.35	0.00	0.00	2.83	1.80

Table 5
Summary of the strength of dilution/concentration effects (DC) related to climatic effects.

Nutrient concentration	Atmospheric temperature				Precipitation sum			
	Beech	Oak	Spruce	Pine	Beech	Oak	Spruce	Pine
N	−0.75	0.00	−0.65	0.00	−0.50	0.00	−0.72	0.03
P	−0.68	0.00	0.04	−0.41	−0.55	0.00	0.10	−0.18
K	−0.27	−0.19	0.00	−0.48	−0.53	−0.03	−0.02	−0.19
Ca	−0.19	0.05	−0.93	−0.48	−0.42	0.00	−0.85	0.11
Mg	0.00	−0.07	−0.02	−0.55	0.00	−0.32	0.38	−0.06

The period for which effects are significant for Ca content is relatively short: significant effects are found for lagged autumn and spring temperatures of the current year. By contrast, the other nutrient contents follow the effects of foliar mass at least partially throughout the observed period (Fig. 4). A positive effect of spring temperatures on nutrient concentrations is found for N and Mg, whereas summer precipitation has a positive effect on N and P concentrations (Fig. 4). The most informative model intervals depend on the nutrient, indicating that different mechanism control nutrients to a different degree. Significant effects of atmospheric temperature and precipitation sums are found for all nutrient ratios. While the relative effect for the N:P ratio is low, the CS of K:Ca, K:Mg, and Ca:Mg ratios are higher (Table 4). The effect of precipitation sums on nutrient ratios is smaller than that of atmospheric temperature, especially during spring. Significant effects of atmospheric temperature (R^2 of up to 0.13) and precipitation sums (R^2 of up to 0.10) for INCR. The most important climate parameters include lagged summer temperatures, spring temperatures, lagged winter precipitation, lagged summer precipitation, and precipitation during current winter (Fig. 4). Flushing of spruce needles starts between the 110th and the 153rd day of the year (Fig. 4).

In pine, models including precipitation sums generally have higher R^2 values (0.04–0.18 depending on the nutrient concentration) than models including atmospheric temperature (0.03–0.12 depending on the nutrient concentration). CS is smallest for N concentration and highest for Ca concentrations. The model intervals during which precipitation sums have significant positive effects is relatively short, starting around the beginning of May for all nutrient concentrations (Fig. 5). When longer model intervals of at least 180 days are observed, significant effects of precipitation are found for P, K and Ca concentrations only. Foliar mass, and by consequence foliar nutrient content, is, on the other hand, more strongly influenced by atmospheric temperature than by precipitation. INCR is significantly influenced by atmospheric temperature and precipitation (R^2 up to 0.16 and 0.12). Early summer precipitation, lagged autumn temperatures, and climate condition in early spring of the previous year influence INCR the most (Fig. 5). Flushing of pine needles starts between the 79th and the 147th day of the year (Fig. 5).

4. Discussion

4.1. Variability in foliar chemistry

The total variability in foliar chemistry is affected by aspects such as spatial and temporal variability, as well as variability due to the methodology, such as precision of laboratory analysis, variability due to the sampling position within the tree, and tree-to-tree variability (Yang et al., 2015). The Expert Panel “Foliage and Litterfall” of ICP Forests adopted a tolerable deviation of ± 10% in ring tests for the elements considered in this study (Fürst, 2020). We consider mixed samples from a minimum of five trees (Rautio et al., 2010) and consequently do not assess tree-to-tree or within tree variability in this study. Year-to-year variability and site-to-site variability both explain significant percentages of the deviance in all assessed foliar chemistry parameters and show clear differences between the tree species.

For nutrient concentrations and contents, temporal variability is of similar importance compared to spatial variability in beech and pine, whereas for oak and spruce, temporal variability is much less important. This might be caused by greater variability in site conditions an inclusion of plots in mountains areas (spruce) and the pooled treatment of pedunculated and sessile oak as well as higher within tree nutrient buffering in oaks (Thomas and Schafellner, 1999; Parelle et al., 2006; Beck, 2009; Millard and Grelet, 2010; Mijnsbrugge et al., 2017). In addition to the variation between tree species, the relative importance of spatial and temporal variability also differs between nutrients. These differences were in accordance with previous findings (Duquesnay et al., 2000; Yang et al., 2015). To a certain extent, this pattern reflects the increasing importance of geological processes compared to biological processes of the element cycles (Lukac et al., 2010). In beech, our results correspond to findings by (Bauer et al., 1997) demonstrating that N concentrations are relatively constant at the spatial scale, whereas Ca and Mg are most likely to be influenced by site conditions. Further, they also show a higher sensitivity of nutrient concentrations compared to nutrient contents. We find that spatial variability outweighs temporal variability in all nutrient ratios and tree species. Comparison of the variability of nutrient concentrations and nutrient contents indicate stoichiometric flexibility of foliage and hint towards interrelations in nutrient concentrations and foliar mass. For instance, the variability in foliar N content is close to the variability in foliar mass, in line with observations by (Reemtsma, 1966) that the availability of N to the plant directly affects leaf expansion.

Several other factors on different spatial and temporal scales likely have affected our results to different extents. These factors include spatial gradients of air pollution (atmospheric deposition), pedological and climatological conditions (Seidling et al., 2012a) as well as differences in the mycorrhizal association of trees (van der Linde et al., 2018), an increasing in atmospheric CO_2 concentrations and decrease nitrogen deposition rates over time (Peñuelas et al., 2017), tree age effects on foliar nutrition (Netzer et al., 2017; Braun et al., 2020) and local extreme climate events, insect calamities, or management measures. Differences in stand characteristics are integrated in the variability between study sites. The ICP Forests Level II network includes sites along deposition gradients as well as different pedological and climatological conditions (Seidling et al., 2012a). Across Europe, the time period assessed in this study was characterized by a deterioration of foliar nutrition (Jonard et al., 2015; Penuelas et al., 2020) related to environmental change at different scales. At the global scale, increasing atmospheric CO_2 concentrations and decreasing nitrogen deposition rates (Peñuelas et al., 2017) impact foliar nutrition (Jonard et al., 2015; Sardans et al., 2017). Interrelations with temperature and precipitation have been shown to modulate the long-term trends in foliar nutrition at the continental scale (Penuelas et al., 2020). Changes in mycorrhizal association of trees can affect nutrient uptake capacity (van der Linde et al., 2018). At the site level, increasing tree age might also contribute to decreasing nutrient concentrations (Netzer et al., 2017; Braun et al., 2020). Consistent large-scale temporal effects can be covered by including the sampling year in the analyses, whereas many further sources of year-to-year variability, such as extreme climate events, insect calamities, or management measures, can be restricted to individual sites. Nutrient availability modulates the effects of environmental conditions. For instance, beech shows differences in tree internal P cycling strategies depending on nutrient availability and tree age (Lang et al., 2017).

4.2. Climate effects on foliar chemistry

We found significant effects of atmospheric temperature and precipitation on most studied parameters. The magnitude of effects was relatively small, ranging between ± 20% of the respective mean level for the most extreme climatic conditions observed. It should be noted that this refers to site-specific variations in climatic conditions, excluding climatic differences between study sites. Results show differentiated response patterns to climate effects between nutrients and tree species hinting at differences in nutrient availability, nutrient demands, and nutrient cycling strategies (Miller, 1966). It has long been known that due to differences in mobility and physiological role, within-tree cycling and seasonal fluctuations of nutrients in the foliage can differ considerably (Guha and Mitchell, 1966).

4.2.1. Nutrient concentrations and contents - deciduous species

Our result show that nutrient concentrations in beech and oak have different responses to variations in climate: whereas oak show stronger reactions to temperature compared to precipitation (for K, Ca, Mg), the opposite is true for beech (N, P, K, Ca). Further while Mg concentrations show the greatest response to climate condition in oak, the effects on Mg concentration in beech are lower than those of other nutrient concentrations. The only nutrient that is sensitive to both atmospheric temperature and precipitation sums in both tree species is K. K concentrations in leaves have a high seasonal variability caused by mechanisms to avoid water stress (Sardans and Peñuelas, 2015). Trees adapt their K allocation to leaves to optimize vital functions according to climate condition (Sardans et al., 2012; Sardans and Peñuelas, 2015). Additionally, as K occurs exclusively in soluble form and has the highest mobility of the main nutrients, it is most susceptible to being leached by precipitation (Jonard et al., 2008), explaining the slightly negative effect of summer precipitation on K concentrations in oak. For beech and oak, a strong dependance of tree internal nutrient storage on nutrient allocation and growth has been demonstrated (Dyckmans and Flessa, 2001; Vizoso et al., 2008). In line with this finding, we found lagged climate condition to have effects of similar magnitude compared to climatic conditions in the respective sampling year in multiple cases. In beech, foliar mass and nitrogen concentrations both show a significant effect of lagged autumn temperature for a time of the year that roughly coincides with the beginning of colour change. A positive effect of lagged autumn precipitation on all nutrient concentrations also corresponds with that time of the year, pointing towards an effect of nutrient resorption. Drought conditions in late summer can result in early leaf senescence which in turn leads to a lower nutrient resorption (Estiarte and Peñuelas, 2015).

As yearly measurements of foliar chemistry are not available over the whole study period, we did not test for autocorrelation within the time series (Jonard et al., 2008). Our results do nonetheless clearly indicate that lagged climate condition influence foliar nutrient concentrations and contents, suggesting that climate condition of the previous year need to be taken into account when assessing the favourability of particular sampling years. While the results suggest that climatic conditions during relatively short periods appear to control – in a direct or indirect way – foliar chemistry, meteorological observations over longer periods are also suitable to assess the favourability of a given year for tree nutrition.

4.2.2. Nutrient concentrations and contents - coniferous species

The effect of lagged atmospheric temperature on foliar mass in pine, and by consequence all nutrient contents, stands out as the effect with the highest CS values of all tested parameters. Temperature variation between May and November of the year preceeding the foliar sampling seem to trigger a reaction of foliar mass and nutrient contents in the opposite direction (i.e. high summer temperatures are related to a low foliar mass in the next year and vice versa). (Kouki and Hokkanen, 1992) noted that summer temperatures are positively correlated with the amount of litterfall, which could impact the substrates available for growth in the following year. (Kivimäenpää et al., 2017) report that warming led to bigger needles under experimental conditions. The differences in response compared to our findings might be explained by the different aspects of temperature effects studied (isolated effect of a moderate temperature increase applied to seedlings vs. effects of temperature variations on mature trees potentially correlated with other phenomena, e.g. drought). Interestingly, our results show that nutrient concentrations in spruce are only very weakly affected by atmospheric temperature, which is in strong contrast to foliar mass and nutrient contents.

For nutrient concentrations, our results indicate more influence of climate condition of the current year. The evergreen character of coniferous tree species with needle leaf spans of several years means that more nutrients are stored within the green biomass than in the wood (Weis et al., 2009; Göttlein et al., 2012). While re-translocation of nutrients from older to new needles does not appear to be significant (Manghabati et al., 2019), mechanisms such as needle retention time could modulate nutrient cycling in coniferous tree species (Johnson and Turner, 2019). In pine, precipitation of the current year is shown to have a notable effect on nutrient concentrations. The positive effect of precipitation on nutrient uptake through the roots is frequently discussed in relation to the effects of climate condition on foliar chemistry (Tian et al., 2018; Mani and Cao, 2019). In general, higher precipitation are expected to result in higher nutrient concentrations in the needles (Jonard et al., 2008). The period during which precipitation sums had significant positive effects is relatively short, starting around the beginning of May for all nutrient concentrations. When longer periods of at least 180 days are observed, significant effects of precipitation are found for P, K and Ca concentrations only. This indicates that for most measures, precipitation sums over the entire vegetation period or whole year are not suitable to assess the favourability for tree nutrition for a sampling time. Positive effects of precipitation during the vegetation period and the whole year on nutrient concentrations have been described for pine stands in Brandenburg, Germany (Hippeli and Branse, 1992). The study notes that the effect of precipitation depends on site conditions and that the interrelations between nutrient concentrations tend to have more effects than precipitation.

4.2.3. Nutrient ratios

Significant effects of either temperature or precipitation were identified for all nutrient ratios in oak, pine, and spruce. Meanwhile in beech, no significant effect of climate condition on nutrient ratios was found for any of the considered ratios. This indicates that favourability of climate condition for tree nutrition is not consistent between nutrients and that an assessment based on a single sampling could yield misleading information on nutrient imbalances (Bonneau, 1988). Our results indicate that this especially concerns ratios that include Mg or Ca for oak and spruce. Differences in sensitivity to climate parameters could lead to a further decoupling of nutrient stoichiometry under changing climate condition (Tan et al., 2018). Nonetheless, N and P generally show similar patterns and reactions to climatic conditions and relative effects on the N:P ratio are relatively small, especially in oak and spruce. Our results show that N:P ratios can be considered robust against climate conditions and is thus more suitable for site-to-site comparisons in cases of inhomogeneity between sampling conditions. Similarly, nutrient ratios generally show relatively lower deviance explained by sampling year than nutrient contents or nutrient concentrations, whereas deviance explained by study site is higher.

4.2.4. Dilution and concentration effects

In general our result show tendencies of negative correlation between nutrient concentrations and foliar mass (Table 5). This hints at dillution/concentration (DC) effects (Jonard et al., 2015). As noted by (Jarrell and Beverly, 1981), DC effects can occur in two variants: In a "strong" form, nutrient contents react opposite to foliar mass. In the "weaker" form, nutrient contents react with the same tendency as foliar mass, but with a smaller magnitude. We mostly observe the latter variant (Figs. 2-5). Dilution/concentration effects often occur in cases of latent nutrient deficiency when non-nutrient resources become more optimal (Isaac and Kimaro, 2011). However, they can also occur, when nutrient availability is sufficient (Jarrell and Beverly, 1981). In our study, the strongest DC effects do not reflect nutrient limitations based on critical limits, underlying the complexity of interrelations of nutrient cycles in forest ecosystems. For example, in oak, Mg content does not show a significant reaction to current year's spring temperature in contrast to all other nutrients. At the same time, Mg concentrations drops as foliar mass increases with spring temperature. A comparison of nutrient concentrations to critical limits (Mellert and Göttlein, 2012) shows that 18% of oak samples are below the critical limit for Mg, which is less than the number of observations showing deficiencies for Ca, P, and K (40, 39, and 24% respectively). In spruce, patterns in Ca concentrations and content could indicate a dilution effect. Although Ca deficiency in spruce is rare in Germany (Göttlein, 2020), critical limits (Mellert and Göttlein, 2012) indicate latent Ca deficiency for over half the spruce samples (57%). In mineral deficient trees, Ca concentrations are an indication for transpiration intensity (Heinze, 1973; Achat et al., 2018), which matches the observed positive effects of spring temperature and lagged summer precipitation and the negative effect of precipitation during the sampling on Ca concentration.

Comparisons of effects of climate conditions on tree nutrition and tree growth did not give conclusive results. In beech, nutrient and carbon limitations, reflected in foliar chemistry and mass, can lead to a decrease in the current year's growth (Linder, 1987). Lagged autumn temperatures have been shown to be negatively correlated with tree growth (Scharnweber et al., 2011), thus showing a similar trend as nutrient concentrations and an opposite trend to foliar mass. (Seidling et al., 2012b) found positive relationships for growth with temperature of lagged early summer precipitation that are consistent with effects on foliar mass. However early spring temperature had a positive effect on growth, whereas in our study, a warmer early spring resulted in a lower foliar mass. In spruce, (Seidling et al., 2012b) identified negative relationships between increment growth and temperatures in early summer of the current and previous year as well as with precipitation of the previous summer. These time periods do not correspond to the most informative model intervals identified by our statistical approach, although matching effects of climate conditions on foliar mass were found. In pine, (Seidling et al., 2012b) identified a positive effect of temperature in early spring on growth. In our study, a positive effect of atmospheric temperature on foliar mass was identified for the same time of the year as well as a negative effect of temperature on K concentrations. According to the statistical approach used in this study, atmospheric temperatures in the previous year were more informative for increment growth and foliar mass than temperatures during the sampling year itself.

5. Conclusions

Foliar traits of all main tree species are affected by either current and/or lagged climate condition. Nutrient concentrations are generally less sensitive to atmospheric temperature and precipitation than nutrient contents and foliar mass. Climate effects on nutrient contents are more strongly coupled with those on foliar mass than those on the corresponding nutrient concentration. The effect of climate condition on the N:P ratio were weakest of the studied parameters, making it the most robust indicator in studies comparing samples taken in years with different climatic conditions. Observed individually, effects on P and N concentrations are lowest, followed by Mg and K and then Ca.

No universal period of favourable climate condition could be found for the investigated species and nutrients. Rather, climatic conditions affect all tree species differently, reflecting different nutrient cycling strategies, possible nutrient limitations, as well as general sensitivity to climatic conditions. The most informative averaging periods of atmospheric temperature and precipitation are generally short (three months or less). For beech and oak, means over longer averaging periods yield comparable effects. For spruce and pine, significant climatic effects are no longer detectable when using half yearly or longer aggregation periods. In most cases, climatic conditions during the year preceding sampling can have a stronger or comparable effect on foliar chemistry as climate condition during the sampling year itself, and should thus be taken into consideration when interpreting foliar data.

CRediT authorship contribution statement

Inken Krüger: Conceptualization, Formal analysis, Software, Writing – original draft. **Andreas Schmitz:** Conceptualization, Validation, Writing – review & editing. **Tanja Sanders:** Conceptualization, Project administration, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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