# Year-to-year crown condition poorly contributes to ring width variations of beech trees in French ICP level I network

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**Title:** Year-to-year crown condition poorly contributes to ring width variations of beech trees in French ICP level I network

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**Abstract:**

Since the 1980-90’s episodes of decline in Central European Forests, forest condition has been surveyed thanks to the trans-national network the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests). It has been traditionally accepted that leaf loss is directly related to impairment of physiological condition of the tree. A few studies tried to correlate crown condition and growth trends while others concentrated on linking annual growth with crown observation at one date clustered into fertility classes. However, none focussed on the high frequency synchronism between leaf loss from annual network observations and annual radial growth issued from dendrochronology. Therefore, we jointly studied annual leaf loss observations and tree-ring width measurements on 715 common beech (*Fagus sylvatica L.*) trees distributed in the French part of the ICP monitoring network. Detrended inter-annual variations of leaf loss and tree-ring width index were used as response variables in the machine-learning algorithm Random Forest to investigate a common response to abiotic (current and lagged) and biotic hazards, to test the extent to which leaf loss helped to predict inter-annual variations in radial growth. Using Random Forest was effective to identify a common sensitivity to soil water deficit at different time lags. Previous-year climatic variables tended to control leaf loss while radial growth was more sensitive to current-year soil water deficit. Late frost damages were observed on crown condition in mountainous regions but no impact was detected on radial growth. Few significant biotic damages were observed on growth or leaf loss. Leaf loss series did not show a clear common signal among trees from a plot as did radial growth and captured fewer pointer years. Radial growth index did not fall below normal until a 20% leaf loss was reached. However, this threshold is driven by a few extreme leaf loss events. As shown by our joint analysis of leaf loss and radial growth pointer years, no relationship occurred in cases of slight or moderate defoliation. Crown condition is a poorer descriptor of tree vitality than radial growth.

**Keywords**: Dendrochronology; climate; drought; leaf loss; Random Forest; *Fagus sylvatica*; forest health monitoring; water balance.

# 1. Introduction

Forests have to cope with a variety of disturbances including acute stressors (climatic events, insect outbreaks or fungal leaf diseases) and chronic pressures (atmospheric pollution, root rots, adverse trends in temperatures) (Seidl et al., 2017). Since the 1980s, forest decline in Europe has triggered a need for robust indicators to help to monitor forest condition.

Diagnosing forest health has mainly been based on descriptive criteria related to primary growth, summarized under the term "crown condition". These descriptors include crown morphology, abnormal leaf discolouration and estimates of leaf deficit relative to a so-called reference tree, later referred to as "leaf loss" (Nageleisen, 2005; Roloff, 1985).

Since the end of the 1970s, and the impressive episodes of decline in Central European forests, several forest health monitoring networks have been set up. The first in France was set up on a 16x1 km grid, only in the mountains all along the eastern border, where foresters were concerned by a severe health decline in fir.Observations were performed from 1983 to 1993 to observe the recovery of coniferous tree health (Barthod, 1994). In 1985, a trans-national network, the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests), was created under the United Nations Economic Commission for Europe (UNECE) (Mueller-Edzards et al., 1997). Forest condition has therefore been monitored since 1986/87 on a large scale, though at a low intensity (Level I), thanks to a systematic network of plots located at the nodes of a 16x16 km grid in all European forests. Annual visual observations of crown condition are carried out for 20 trees on these plots according to two criteria: leaf loss compared to a full folied “reference tree” , and abnormal leaf colouration (Eichhorn et al., 2016).

Visual assessment of crown condition from the ground has historically raised the methodological problem of the experts’ objectivity (Innes et al., 1993). Despite this, many studies have based their analyses on such data and used them to interpret inter-annual variations and trends in crown condition as a function of environmental constraints. Through a cross-sectional approach, van Leuween et al. (2000) proved the limited effect of air pollution on crown condition compared to the effect of tree age and climate. Other studies, based on cross-sectional mean-term and inter-annual resolution approaches, showed the negative impact of drought events on tree crown condition (de Vries et al., 2014; Ferretti et al., 2014; Popa et al., 2017; Seidling, 2007; Solberg, 2004).

In Europe, crown condition remains a widely-used forest condition indicator “within Criterion 2, ‘Forest health and vitality’”, one of the six criteria adopted by Forest Europe (formerly the

Ministerial Conference on the Protection of Forests in Europe – MCPFE) to provide information for sustainable forest management in Europe[1]"(Michel et al., 2018). ICP technical and executive reports express damage results as the percentage of trees with more than 25% defoliation. However, to our knowledge, it has never been properly demonstrated that this threshold is an appropriate breakpoint for deciding whether a tree is in good or poor condition. Assessing the validity of this threshold was one goal of this study.

Radial growth, is also a well-established and widely-used indicator of tree health and physiological status (Dobbertin, 2005). Research on the relationship between radial growth and crown condition has shown no clear pattern. Authors discriminate tree populations according to their growth performance and then retrieve characteristic leaf loss thresholds that have a significant effect on radial growth *a posteriori*. However, the thresholds for growth decline are species- and site-dependent (Becker, 1987; Bert et al., 1990).

Very few studies have investigated the connection between inter-annual variations in crown condition and radial growth. Dittmar and Elling (2007) showed a decrease in increment with leaf loss but their findings cannot be generalized because their study was restricted to only 12 trees. Seidling (2012) found a low correlation between inter-annual beech growth and leaf loss and questioned using leaf loss to explain functional relationships between the two indicators at the plot level. Solberg (1999) also found a weak correlation between tree-specific long-term means for crown condition and growth.

This study focuses on common beech, one of the most important and widespread broadleaved trees in France and Europe. In beech, each year, a new shoot grows from a dormant bud at the end of the previous year's shoot. There are two types of shoots: exploratory (long) and exploitation (short) shoots. The long, fast-growing exploratory shoots extend into the space around the tree and are therefore located in the upper periphery of the crown (Teissier Du Cros et al., 1981), where leaf loss is usually assessed. Therefore, leaf loss as compared to a reference tree and assessed on the upper third of the crown, results from abnormal primary development (short elongation, impaired crown development, bud burst deficit), while cambial activity generates the secondary growth responsible for radial increment.

There is solid knowledge of radial growth and crown development responses in beech to climate. On one hand, water deficits impair twig elongation (Power, 1994; Stribley and Ashmore, 2002) and reduce the number, rate of expansion and final size of the leaves (Zahner, 1968). On the other hand, secondary growth in beech is sensitive to current

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[1] https://www.foresteurope.org/docs/MC/MC_lisbon_resolution_annex1.pdf

summer water shortage as well as the previous year’s climatic conditions. These observations can be explained by the influence of climate on the carbon quantities allocated to growth or storage (Barbaroux and Bréda, 2002) and by a possible trade-off between growth and masting (Genet et al., 2009; Hacket-Pain et al., 2017, 2015). In beech, mild winter temperatures induce the resumption of physiological processes leading to reactivation of cambium and breaking of bud dormancy (Dittmar et al., 2003; Lebourgeois et al., 2005). It has been shown that negative pointer years present in a growth series can be related to late frost events, thus showing a sensitivity of beech to late winter temperatures, especially during the critical stage of leaf unfolding (Dittmar et al., 2006, 2003).

A comprehensive view of the link between primary and secondary growth considers leaf loss as a measure of the mid-term regulation of leaf mass (Bréda, 2008). This leaf loss can impair carbon and water fluxes and, as a consequence, restrict primary and/or secondary radial growth.

The aims of this paper are: 1/ to investigate whether the leaf loss (LL - monitored from 2001 to 2014) and radial growth at permanent plots in the French Level I ICP Forests network respond to common biotic or abiotic hazards; and 2/ to test if annual leaf loss explains part of the annual radial growth.

We compared the impact of climate constraints during the current and previous year on radial growth and leaf loss, and interpreted the results in the light of the current knowledge of beech ecophysiology and development.

The originality of our approach is twofold. First, typical dendrochronological analyses rely on a bootstrapped response function requiring monthly climatic values as input (Biondi and Waikul, 2004) and not considering any time-related cumulative impact. Such results are not suited for a functional interpretation because the variables are disconnected from the underlying gaseous exchanges and the growth and carbon-allocation processes. In contrast, based on our knowledge of ecophysiology, we assume a posture that differs from classical dendrochronology. We computed several drought indices retrospectively with the process-based model Biljou©. The daily time resolution in Biljou© allowed us to take into account changes in canopy conductance in response to soil water deficit. A daily calculation makes it possible to integrate key phenological periods for beech water balance or carbon assimilation and allocation. Through soil water balance modelling, responses to temperature, precipitation

- and more importantly for canopy processes - potential evapotranspiration, are integrated in comprehensive process-based predictors. We can therefore avoid adding monthly precipitation and temperature as done in function response models. Second, to handle the diversity of the potential variables, the presence of nonlinear relationships and the possible correlations among them, we chose to work with a nonparametric variable-selection method, Random Forest (Breiman, 2001). Random Forest models often show a higher predictive ability than classical regression (Muchlinski et al., 2016; Oliveira et al., 2012) and linear response function models (Jevšenak et al., 2018a). Random Forest models are gaining attention in different fields of ecology, including dendrochronology (Cutler et al., 2007; Jevšenak et al., 2018a; Prasad et al., 2006). We emphasize that the objective of this work is to interpret rather than predict results, even though Random Forest has proven to be a very powerful predictive method in many contexts, including tree-ring analysis (Genuer et al., 2015; Jevšenak et al., 2018b). Our aim is to take advantage of this powerful device to disentangle possible non-linear, complex or redundant relationships between variables.

## 2. Materials and methods

### 2.1. Sampled plots

The French part of the ICP Forests “Level I” transnational monitoring network includes 112 plots with at least one common beech (*Fagus sylvatica* L.) tree. For this study, 97 plots, with a total of 715 beech trees, were selected based on three criteria: 1/ the plot contained at least five beech trees, 2/ crown condition observations were available from 1989 to 2014, and 3/ the plots were distributed as widely as possible within the beech distribution range in France. The French national territory is divided into eight ecological regions, referred to as GRECOs (‘Large Ecological Regions’), with similar bio-climates, bedrock formations and topography, as defined by the French NFI (National Forest Inventory). The eight GRECOs are as follows: three lowland regions in the west, north and east; three mid-mountain areas in the Massif Central, Vosges and Jura; and two high-mountain regions in the Pyrenees and Alps. For statistical reasons, and based on climatic similarities, we grouped together the plots in the western and northern regions (Northern lowlands), and the plots in the Jura and Vosges (Vosges-Jura) mountains, for a total of six ecological regions.

### 2.2. Crown condition data

Assessing crown condition is central to monitoring in the ICP Forests. The currently used assessment methods were developed in the mid-1980s. Crown condition is evaluated by visually assessing leaf loss (LL) from the ground and a standardised method presented in a manual for crown condition assessment is followed (Eichhorn et al., 2016). Every year from July 1st to August 31st, trained observers assess LL in 5% incremental steps on 20 numbered, dominant or co-dominant trees. Leaf loss in the crown of the sampled trees is visually compared to a virtual local “reference tree”. This reference is a conceptual tree, optimally foliated under the specific local site conditions and of a similar age and social status to the average tree in the stand. Leaf loss series are available from 1989 to the present.

Age is known to be the factor most correlated to crown condition (Seidling and Mues, 2005). Because we wanted to identify signals in relation to climate, we needed to remove any trends caused by other factors. Furthermore, we hoped to explain the inter-annual variations in leaf loss and to keep only high-frequency inter-annual signals. We therefore standardized leaf-loss series at the tree level to create two indices. For the first leaf-loss series index (LLd1), we fitted the long-term trend with a linear regression of time for a given tree, then, for each year, used the ratio method to compute a de-trended signal (Cook et al., 1990; Douglass, 1936; Dyer and Fritts, 1978).

### 2.3. Radial growth data

Each assessed tree was cored to the pith at breast height for dendrochronological analysis. We measured tree-ring from the bark to the pith to the nearest 1/100 mm with a microscope connected to a computer running the SAISIE program (Bert et al., 1990). Ring-reading mistakes were checked for and corrected by cross-dating the tree ring series, according to the procedure described in Becker et al. (1994). During the cross-dating step, each individual chronology was compared to an average chronology for the corresponding ecological region to identify regional pointer years. Then, each ring-series was checked for erroneous dating with the INTERDAT computer program (Becker and Dupouey, unpublished). This program depends on pointer years calculated with the method proposed by Becker (1989): a year is considered characteristic when at least 75% of the trees in a stand have the same sign for change in growth with an absolute variation in growth of at least 10% from the previous year.

Plots were chosen according to a systematic grid. Therefore, trees of different ages, social status and stand management were cored to the pith. To investigate year-to-year tree-ring variations, we removed non-climatic signals (trends related to age, competition, stand management, long term trend due to climate change): each individual tree-ring series was transformed into a growth index which kept only the annual growth signal, i.e. inter-annual climatic variations and annual pest and disease damage (Fig. 1b). We used the statistical freeware R (R Core Team, 2016) with the “dplR” package (Bunn, 2008) to standardize each individual tree-ring series and to isolate the inter-annual signal thanks to a smoothing spline with a frequency response of 50% at 30 years (Cook and Peters, 1981), thus yielding dimensionless de-trended ring widths (rwi). With this de-trending method, we kept high frequency variations, the signals that we sought to interpret. In addition, because we were interested in the relation between leaf loss and tree-ring increment, we did not remove the autocorrelation. Indeed, both leaf loss and tree-ring increment can have legacy effects from the previous year through amounts of non-structural carbohydrates or bud preformation.

### 2.4. Predictors

In order to characterize inter-annual variations in growth and in leaf loss, the selected predictors were related to plot (mainly climatic) or individual tree characteristics (annual leaf damage). For each plot, daily climatic variables were extracted from the mesoscale SAFRAN reanalysis, which covers France with an 8 km x 8 km grid (Quintana-Seguí et al., 2008). These climatic variables were then summarized into seasonal variables known to influence crown condition and/or growth (Nevalainen et al., 2010; Seidling, 2007; Seidling et al., 2012) over the reference period 2001-2014. Based on temperature functions, the budburst date (BBD) was also modelled for each plot (Dufrêne et al., 2005). As beech is a diffuse-porous species, its radial growth starts just after budburst and ends sometime in August (Barbaroux and Bréda, 2002; Michelot et al., 2012). For this reason, we used the modelled budburst date to define the start of the growing season for all our plots (Table 1) and we aggregated mean temperatures from April to August (TM.AA).

One-year-lagged climatic variables were also computed as potential predictors. However, no significant trends were observed on the series.

Table 1. Target and explanatory variables

| Variables | Code | Description | Type | Min | Median | Max |
|---|---|---|---|---|---|---|
| Target variables | | | | | | |
| Defoliation | LL | Raw leaf loss (5% steps) | numeric | 0 | 20 | 95 |
| | LLd1 | De-trended leaf loss (indices around 1) | numeric | 0 | 0.9 | 8 |
| | LLd2 | De-trended leaf loss index centred on the mean (% of leaf loss) | numeric | 0 | 22.54 | 95.17 |
| Growth | rwl | Raw ring-width (1/100 mm) | numeric | 6 | 124 | 894 |
| | rwi | Growth index | numeric | 0.10 | 0.98 | 2.62 |
| Explanatory variables | | | | | | |
| Climate | TM.AA | Mean temperature from April to August | numeric | 5.79 | 14.5 | 19.42 |
| | late.chill | Sum of maximum temperatures < 0°C from March to May | numeric | -116.50 | 0 | 0 |
| | chill | Sum of maximum temperatures < 0°C from previous-year October to current February | numeric | -352.40 | -25.80 | 0 |
| | BBD | Bud burst day modelled according to Dufrêne et al.(2005) | numeric | 96 | 114 | 154 |
| Water balance | DI | Soil water deficit intensity from budburst to leaf-fall | numeric | 0 | 30 | 120 |
| | DI.JJ | Soil water deficit intensity from June to July | numeric | 0 | 7.58 | 58.76 |
| Leaf symptoms | symptom | Identification of leaf damage according to: | Categorical | | | |
| | WHITE | Whitish coloration | | | | |

| | |
|---|---|
| BRON | Bronze coloration |
| CONS | Consumption |
| COLOR | Coloration |
| ENTO | Insects present |
| DEFORM | Deformation |
| FRUC | Fructification |
| YELLOW | Light green to yellow coloration |
| MISS | Missing without any trace of consumption |
| MICR | Microphylly |
| MORT | Mortality |
| MYCO | Fungus |
| NECR | Necrosis |
| RED | Reddening to browning |

The ICP Forests network underwent two soil surveys during the study period. A soil description (soil type, depth, root distribution) took place between 1994 and 1995 (Vanmechelen et al., 1997) and soil properties (bulk density, texture, carbon content) were measured between 2005 and 2008 through the BioSoil-Biodiversity project (Lacarce et al., 2009). These soil data were used to compute soil extractable water (in mm) for each plot.

For each plot, ecophysiologically-based drought indices were computed thanks to the forest water balance model Biljou © (Granier et al., 1999). The model simulates the water fluxes between the atmosphere, the canopy and the soil for a given plot. The soil water content is computed daily as a function of precipitation, rainfall interception, tree transpiration, soil evaporation and drainage. The model represents the regulation of canopy gaseous exchanges when the soil water deficit drops below a threshold of 0.4, which induces stomatal closure (Granier et al., 1999, Bréda and Granier, 1996). Below this threshold, canopy conductance and GPP (gross primary production) decreases, as we demonstrated in beech stands (Granier et al., 2007). The calculation of potential evapotranspiration integrates elementary variables into radiative and convective components, which are the drivers for canopy exchanges with the atmosphere. The daily meteorological variables required are rainfall, air temperature and humidity, global radiation and wind speed. Soil descriptions and properties at each plot (rooting pattern, extractable water, soil bulk density) were used to calculate water balance. The output variable characterizing drought events was soil water deficit intensity from June to July (maximum growth rate, Michelot et al., 2012) or from budburst to leaf fall (Table 1).

Since 2000, in addition to rating leaf loss, the ICP reports have required annual descriptions of damaging agents for each sampled tree. Damage assessment consists of describing the symptoms and determining the cause, if possible. A symptom is defined as an indicator of the presence of harmful agents having had a significant impact on any part of the tree (Eichhorn et al., 2016). Only the symptoms observed on leaves were kept in our analysis. The symptom variable indicates the presence or absence of a symptom on the leaves. The symptom variable is declined into different categories identifying the symptom observed on the leaves.

### 2.5. Data sets

Our objective was to work on continuous leaf-loss series that were homogeneous in quality while maximizing the number of trees for analysis. To avoid (1) biases due to the change in the leaf loss assessment protocol that occurred between 1994 and 1996 (Landmann et al., 1999, 1998) and (2) the disturbances related to the 1999 storms (Lothar and Martin, depending on the region), we selected homogeneous leaf-loss series starting in 2001. Due to the joint analysis of leaf loss and radial growth series, the end of the study period was the year of the last available tree-ring width data, i.e. 2014. Therefore, we worked over the common period 2001 to 2014.

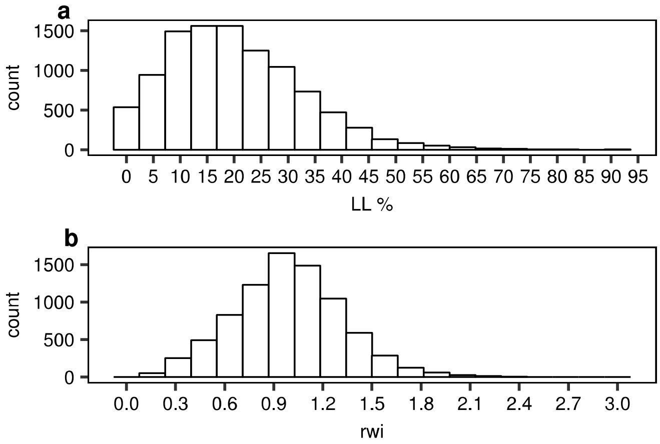


Figure 1. Distribution of (a) leaf loss according to 5% classes (LL) and (b) tree-ring width index (rwi) over the period 2001-2014.

Two different data sets were created for the analyses, according to their objectives.

Our first objective was to analyse inter-annual variations in leaf loss, observed in July or August. The response variable was the de-trended annual leaf loss (LLd1) of each tree covering the period from 2001 to 2014 (Fig. 1, Table 2). The predictors used were current- and previous-year annual climatic variables, water balance variables and the presence of damage symptoms. Current-year soil water deficit from budburst to leaf fall and water deficit duration were eliminated because these variables aggregate events that may have happened after the observation of leaf loss (in July-August) and may therefore have had no influence on current-year crown condition estimates. Two symptoms with a possible delayed impact on leaf loss were introduced with a one-year lag: fructification and microphylly.

Table 2. Number of sampled trees and plots (in brackets) composing each data set by ecological region.

| Ecological regions | Site code | Radial growth | Leaf loss | Common samples |
|---|---|---|---|---|
| Alps | ALPS | 107 (14) | 103 (14) | 103 (14) |
| Northern lowlands | CNO | 92 (18) | 81 (17) | 70 (17) |
| Eastern lowlands | EAST | 147 (23) | 103 (20) | 66 (15) |

| | | | | |
|---|---|---|---|---|
| Massif central | MC | 142 (16) | 135 (16) | 135 (16) |
| Vosges-Jura mountains | VJ | 134(18) | 126 (18) | 121 (18) |
| Pyrenees | PYR | 94 (8) | 93 (8) | 88 (8) |
| National | NAT | 716 (97) | 641 (93) | 583 (88) |

Our second objective was to analyse the influence of leaf loss on radial growth. We therefore created a second data set of 583 trees with a continuous series for leaf loss and growth index from 2001 to 2014 (Fig. 1, Table 2). The response variable was the annual ring-width index (rwi) and the same predictors were used as in the previously described analyses (i.e. current- and previous-year annual climatic variables, water balance variables and presence of damage symptoms).

Because we expected the average level of leaf loss to influence inter-annual variations in radial growth, we calculated a second index, LLd2.

For a given tree, *i* in year *y,* the new index $LLd2_{iy}$ was:

$$LLd2_{iy} = LLd1_{iy} \times \overline{LL_i}$$

where $\overline{LL_i}$ is the average leaf loss for tree *i* for the period 2001-2014.

The index LLd2 is centred on the average leaf loss of the tree and is expressed as a percentage.

In the second objective, the de-trended leaf loss (LLd2) of the previous and current year was introduced as an additional predictor of radial growth.

### 2.6. Statistics

To provide deeper understanding of the relationship between leaf loss and tree-ring width, pointer years were detected on raw tree-ring and leaf-loss series. Analysing pointer years is typical in dendrochronological studies (Becker et al., 1994; Schweingruber et al., 1990).

Pointer years represent a growth reaction to abrupt changes in environmental conditions and are usually expressed as a relative change in growth, in percentage. Usually, pointer years correspond to a calendar year when, at least, 75% of the trees have the same sign of change with rings at least 10% narrower, or wider, than the previous year (Becker et al., 1994). By testing different thresholds, it is possible to distinguish very characteristic years from less characteristic years. We transposed this technique to our leaf-loss series. However, because no pointer years were detected with the above-mentioned thresholds, we defined pointer years for radial growth and leaf loss as years when at least 60% of the trees shared a variation of at least 10% with the previous year (Becker et al., 1994; Mérian and Lebourgeois, 2011).

We calculated the Gini coefficient (GINI) of the de-trended leaf loss (LLd1) and growth index (rwi) series to compare growth sensitivity to climate. GINI is a relative index, quantifying sensitivity scaled by mean and sample size (Biondi and Qeadan, 2008). We calculated GINI for each tree and then averaged the GINI values in a second step. We used the Gleichläufigkeit index (GLK) (Schweingruber, 1987) to check for a similarity in signal between the series, in other words, their synchronization.

We chose to apply the machine-learning algorithm Random Forest (RF) (Breiman, 2001), a nonparametric technique for classification or regression. RF is based on the Classification And Regression Tree (CART) algorithm (Breiman et al., 1984). CART builds a decision tree by finding the dichotomy at each iteration that minimizes a goodness-of-fit criterion among all predictors. CART is known to be very sensitive to small changes in the data set (Genuer and Poggi, 2019). RF is a tree-based ensemble method, which overcomes these limitations by averaging regression over a great number of randomized variants of the decision trees obtained with CART. The number of trees, *ntree*, is usually set between 500 and 2000. Variants are obtained from bootstrap samples of the learning set (*the bagging*) and random subsets of variables. Breiman (2001) showed, both theoretically and empirically, that these averaged trees have fewer expected errors than do single trees. Because random subsets of variables are selected at each node (control parameter *mtry*), the collinearity of the predictors is reduced.

RF therefore has two interesting features: it is able to model nonlinear relationships and it can handle redundancy in the variables. RF has proven to be a very efficient method, usually ranked among the most efficient machine-learning methods (Genuer et al., 2015), both for classification and for regression.

In addition to these advantages over regressions, RF makes it possible to rank the importance of the predictor variables and to evaluate their marginal effect on the response variable, without any a priori assumptions. The bagging process makes it possible to predict the “out-of-bag” (OOB) samples from the “in-the-bag” ones. The importance of the variables is then measured as the averaged increase of squared OOB residuals when the predictor is permuted (Genuer et al., 2015).

Variable importance provides a measure to compare predictors within a dataset but does not provide a threshold to select the most relevant ones. The R package “VSURF” (Genuer et al., 2015) selects variables in two ways: for interpretative purposes, it can select all the relevant predictors related to the variable under study (there can be redundancies); and, for predictive purposes, it can select the smallest set of predictors that explains most of the variability for the variable. Since we wanted to select predictors for functional interpretation and not for prediction, we will only discuss the first type of selection in this paper. As a first step, VSURF eliminated certain predictors based on the standard deviation of the variable’s importance (averaged over 50 runs of RF). The remaining variables were used to construct nested RFs starting with the single most important variable and finishing with all the important predictors. The predictors leading to the smallest OOB error were kept. After some exploratory analysis (not reported here), VSURF was implemented with *ntree*= 2000 and *mtry*=p/3 (p, being the number of variables involved in the model). Most of the time, the cross-validated optimised parameters were very close to these values; and even when they were not, predictions were not significantly different from those obtained with the above setting. We randomly sampled 70% of the data set to train the RF and kept the remaining 30% to test prediction-error. For each model, the pseudo-$R^2$ predictive accuracy metric was computed on the test set as calculated in the “randomForest” package (Liaw and Wiener, 2002). This metric is defined as the proportion of total variation in the outcome explained by the model (or forest); values range between 0 and 1.

Strobl et al. (2008) report that variable importance metrics can be biased towards correlated variables in some situations and propose an improved method in order to take this into account. The method requires implementing a conditional permutation scheme within a group that can potentially contain large sets of covariables. Genuer et al. (2010) specifically studied RF variable importance in the presence of groups of highly correlated explanatory variables. They did not diagnose any such bias for variable selection. In our case, we performed preliminary exploratory analyses with the “party” package (Strobl et al., 2009). We consistently obtained extremely low importance scores for all variables (results not reported here), making it completely impossible to come up with any interpretation. Strobl et al. (2008) and Genuer et al. (2010) agree on the fact that, despite possible overestimation of the importance score, the order of the variables is usually preserved.

We used the “PDP” package (Greenwell, 2017) to describe the relationships between the selected predictors and the variables of interest and illustrated the results with partial dependence plots. A partial dependence plot (PDP) shows if the relationship between the response and the predictor is linear, monotonous or more complex. For a given predictor value, the PDP tells what the average marginal effect on the prediction is. We used the R 3.3.2 statistical software for all of our statistical analyses.

# 3. Results

## 3.1. Leaf-loss and radial-growth series

On the overall period (2001-2014), beech presented a mean defoliation of 24% (median=20%). We calculated the Gini (GINI) and the “Gleichlaufigkeit” (GLK) coefficients to compare the year-to-year variability and the strength of the common signal between the trees (Table A.1). The GINI coefficient was higher for LLd1 (0.22) than for rwi (0.18), and quantified a wider year-to-year variability for leaf loss. Inversely, the GLK coefficients were weaker for LLd1 (0.52) than for rwi (0.58), suggesting a weaker common signal for leaf loss, as shown in Fig.2.

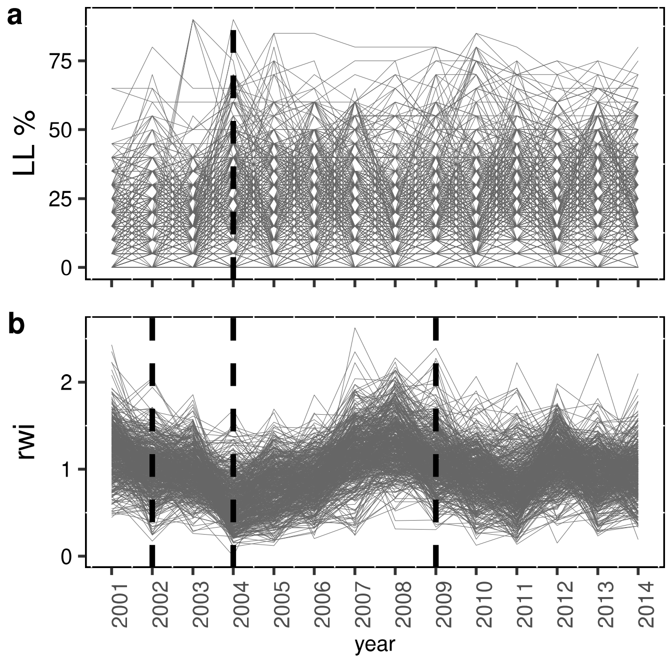


Figure 2: Mean yearly a) leaf loss (LL) and b) tree-ring width index (rwi) for each plot from 2001 to 2014 with dashed lines representing positive or negative pointer years.

In order to check if the high year-to-year variability in LL among trees could be attributed to the quality of the visual assessment, we took into account the changes in observers at a given plot during the observation period (information available in the ICP database). There was no clear continuous pattern between the GINI coefficient and the number of pairs of LL observers. The GINI coefficient did increase when there was more than one pair of observers during the visual assessment period; however, it did not increase with increasing numbers of pairs (Fig. 3).

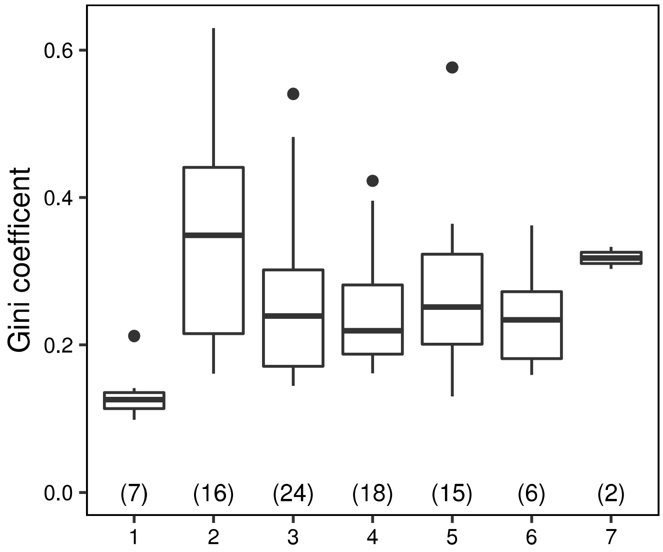


Figure 3: Boxplots of the relationship between the GINI coefficients calculated on the de-trended leaf-loss series (LLd1) for the period 2001-2014 and the number of pairs of observers on the same period. In brackets, the number of observations.

Looking only at positive pointer years for leaf loss (i.e. significant increase in leaf loss) and negative pointer years for radial growth (i.e. significant decrease in radial growth) for the period 2001-2014, pointer years were less frequent for leaf loss than for radial growth, confirming the lower sensitivity of leaf loss to climatic events.

At the national scale, we detected only one pointer year (2004) common to both high leaf loss and low radial growth, while two other national-scale negative pointer years for radial growth were observed in 2002 and 2009 (Table 3). At this scale, no negative pointer year was detected for LL (i.e. a significant decrease in leaf loss), while radial growth had two positive pointer years (i.e. significant increase in radial growth) in 2007 and 2012 (Table 3). At the ecological-region scale, each positive pointer year found for the leaf loss series corresponded to a negative pointer year for radial growth, in 2004 and 2011 (Table A.2).

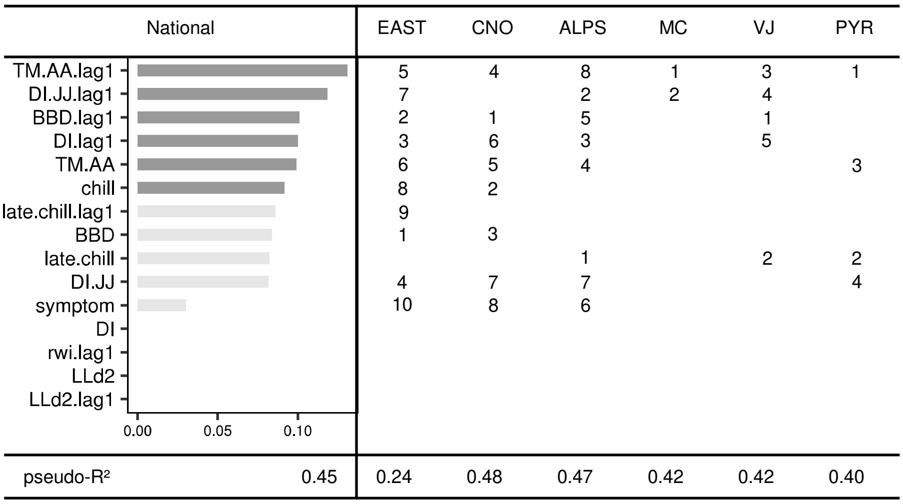
Table 3. Negative and positive pointer years (PY) for radial growth and positive pointer years for leaf loss at the national scale, with their relative variation (LL_RV and RWI_RV, respectively) and abnormal climatic events that might be related.

| PY | LL_RV | RWI_RV | Abnormal climatic events |
|---|---|---|---|

| | | | |
|---|---|---|---|
| 2002 | | -14.99 | |
| 2004 | 122.63 | -32.15 | lag effects from the extreme summer drought and heat wave in 2003 |
| 2007 | | 45.3 | High precipitation distributed equally over the vegetation period |
| 2009 | | -15.38 | Hot, dry summer and August 2008 drought with a lag effect |
| 2012 | | 55.94 | Autumn precipitation |

## 3.2. Common explanatory variables of the inter-annual variations in leaf loss and radial growth

We selected variables with an important relation to LLd1 or rwi for interpretative, not predictive, purposes; consequently, our selected variables present redundancies. The interpretation of the selection should not be seen as an additive model but rather as a list of the most important variables to select when modelling inter-annual variability in leaf loss and radial growth.



| | National | EAST | CNO | ALPS | MC | VJ | PYR |
|---|---|---|---|---|---|---|---|
| TM.AA.lag1 | | 5 | 4 | 8 | 1 | 3 | 1 |
| DI.JJ.lag1 | | 7 | | 2 | 2 | 4 | |
| BBD.lag1 | | 2 | 1 | 5 | | 1 | |
| DI.lag1 | | 3 | 6 | 3 | | 5 | |
| TM.AA | | 6 | 5 | 4 | | | 3 |
| chill | | 8 | 2 | | | | |
| late.chill.lag1 | | 9 | | | | | |
| BBD | | 1 | 3 | | | | |
| late.chill | | | | 1 | | 2 | 2 |
| DI.JJ | | 4 | 7 | 7 | | | 4 |
| symptom | | 10 | 8 | 6 | | | |
| DI | | | | | | | |
| rwi.lag1 | | | | | | | |
| LLd2 | | | | | | | |
| LLd2.lag1 | | | | | | | |
| pseudo-$R^2$ | 0.45 | 0.24 | 0.48 | 0.47 | 0.42 | 0.42 | 0.40 |

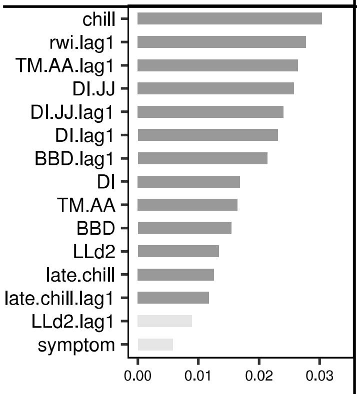
Figure 4: Variable importance plot generated by the Random Forest (VSURF) algorithm for inter-annual variations in de-trended leaf-loss series (LLd1, 2001-2016) at the national scale, and the ranking of the six ecological regions: East, North (CNO), Alps, Massif Central (MC), Vosges-Jura mountains (VJ) and Pyrenees (PYR). The predictors are ranked by the variable's importance measured as the average increase in squared OOB residuals when the predictor was permuted (Genuer et al., 2015). The coloured variables were selected from the interpretation step of VSURF procedure. For each model, the variance explained is computed as pseudo R-squared: 1 - mse / Var(y). For the retained predictors: mean temperature from April to August (TM.AA), sum of maximum temperatures < 0°C from March to May (late.chill), sum of maximum temperatures < 0°C from previous-year October to current February (chill), modelled bud burst day (BBD), soil water deficit intensity from budburst to

leaf-fall (DI), soil water deficit intensity from June to July (DI.JJ), leaf damage assessment (symptom), de-trended leaf loss index centred on the mean LLd2). Lag.1= previous year.

From partial dependence plots (PDPs) and the importance of the selected variables shown in Fig. 4 and Fig.5, we can describe the relationship between rwi or LLd1 and the predictors. A PDP helps visualize the relationship between a predictor and the response variable of interest, by keeping the other predictors constant. PDPs highlight the existence of non-linear relationships between predictors and the variables of interest rwi and LLd1 (Fig.B.1 and Fig.B.2).

The Random Forest model explained 47% of the growth index. For the period 2001-2014, both the current and previous years' climatic variables controlled the tree-ring width index (Fig. 5). For LLd1, the Random Forest model explained 45% of the inter-annual variability in leaf loss. The inter-annual variations in LLd1 were mainly predicted by the previous year's climatic variables (Fig. 4). Seven of the explanatory variables selected for the interpretation of the inter-annual variations were common to LLd1 and rwi. The ranking of the variables shown in Fig. 4 and 5 is independent of whether they are common or not, meaning that the most important explanatory variable for leaf loss could be the least important one for radial growth.

For LLd1, lagged climatic variables had a major impact (Fig. 4). LLd1 mainly responded to summer soil water deficit and temperature surplus with a 1-year lag. Leaf loss increased with the previous year's soil water deficit. LLd1 also responded to temperature variables (bud burst date, chill, TM.AA). An early budburst in the year before crown condition assessment sometimes resulted in reduced leaf loss (i.e. a better crown condition). LLd1 tended to increase with the accumulation of negative maximum temperatures during the winter (from October of the previous year to February of the current year) and with mean temperatures above 18°C during the growing season (TM.AA).



| National | EAST | CNO | ALPS | MC | VJ | PYR |
|---|---|---|---|---|---|---|
| chill | 1 | 1 | 3 | 3 | 1 | |
| rwi.lag1 | 3 | | 8 | 5 | 3 | 1 |
| TM.AA.lag1 | 9 | 6 | 9 | 1 | 2 | 3 |
| DI.JJ | 2 | | 4 | 4 | 9 | 4 |
| DI.JJ.lag1 | 7 | | 1 | 8 | 4 | |
| DI.lag1 | 8 | 7 | 5 | 6 | 5 | |
| BBD.lag1 | 6 | 2 | 2 | 2 | 6 | 2 |
| DI | 4 | | 7 | | 8 | |
| TM.AA | 10 | 5 | 6 | | 10 | |
| BBD | 5 | 4 | 11 | | 11 | |
| LLd2 | 11 | 3 | 13 | | 12 | |
| late.chill | | | 12 | 7 | 13 | 5 |
| late.chill.lag1 | | | 10 | | 7 | |
| LLd2.lag1 | | | | | | |
| symptom | | | 14 | | 14 | |
| pseudo-R² 0.47 | 0.44 | 0.27 | 0.45 | 0.55 | 0.52 | 0.41 |

Figure 5: Variable importance plot generated by the Random Forest (VSURF) algorithm for inter-annual variations of tree-ring width index (rwi, 2001-2014) at the national scale, and the ranking of the six ecological regions East, North (CNO), Alps, Massif Central, Vosges-Jura mountains and Pyrenees. The predictor is ranked by the variable's importance measured as the average increase in squared OOB residuals when the predictor was permuted (Genuer et al., 2015). The variables are identified in Tab.1. The coloured variables were selected from the interpretation step of the VSURF procedure. For each model, the variance explained is computed as pseudo R-squared: 1 - mse / Var(y). For the retained predictors: mean temperature from April to August (TM.AA), sum of maximum temperatures < 0°C from March to May (late.chill), sum of maximum temperatures < 0°C from previous-year October to current February (chill), modelled bud burst day (BBD), soil water deficit intensity from budburst to leaf-fall (DI), soil water deficit intensity from June to July (DI.JJ), leaf damage assessment (symptom), de-trended leaf loss index centred on the mean LLd2). Lag.1= previous year.

The accumulation of cold temperatures from the previous October to the current February seems to be a particularly important predictor, with a negative impact on radial growth (Fig. 5), meaning that a cold winter inhibits radial growth. The second most important explanatory variable for the tree-ring index (rwi) is the previous year's growth index, known as a first-order autocorrelation in dendrochronology, which was not removed with the de-trending method we applied. Soil water deficit reduces tree-ring width since summer drought affects the current year's growth and a long and/or severe drought event impairs next year's growth. In addition to the influence of water deficit on radial growth, the model highlights the negative impact on rwi of increasing April-to-August temperatures between the previous and current year. The model also suggests that the date of bud burst, modelled as a temperature function, influences radial growth in two possible ways: an early bud burst will benefit next year's growth; however, it can reduce current year's radial growth.

### 3.3. Are the variables controlling inter-annual variations in leaf loss and tree-ring index constant across ecological regions?

Working on smaller ecological regions highlighted specific responses of leaf loss and radial growth (Fig.4 and 5). As opposed to other regions, the northern lowlands and the Pyrenean mountains were more sensitive to temperatures than to previous year’s soil water deficit. Leaf loss increased with the accumulation of cold temperatures between March and May of the current year in three regions: the Alps, Vosges-Jura mountains and the Pyrenees.

Except in the Alps, northern lowlands and Eastern ecological regions, no observed symptoms of leaf damage induced a significant increase in leaf loss, nor did fructification (Fig. 4).

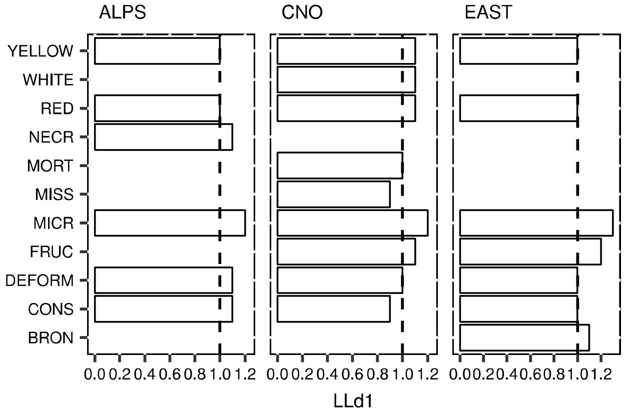


Figure 6: Partial dependence plots for the observed symptoms on leaves (categorical variable) and fructification, showing the marginal effect on the de-trended leaf-loss series (LLd1, 2001-2014) for the three affected ecological regions. The black dashed line represents a threshold above which the observed damage increased leaf loss.

The same three regions presented high enough microphylly to increase LLd1. Leaf loss also increased with high fructification in the Eastern and northern lowlands. Necrosis symptoms were only found in the Alps (insect consumption and leaf deformation - (Fig. 6)). Leaves in the northern plains presented colouring symptoms (yellowing, reddening, whitish coloration).

The northern lowlands stands out as the only case in the models where LLd2 was a relatively important variable contributing to radial growth, ranking third (Fig. 5). Otherwise, like results at the national scale, LLd2 was the least important variable explaining radial growth variations in three other regions (East, Vosges-Jura, Alps). In the Massif Central and the Pyrenees (Fig. 5), LLd2 did not influence growth.

### 3.4. Leaf-loss as a predictor of inter-annual variability in radial growth

Leaf loss (LLd2) appeared to be the least important variable predicting tree-ring width variations at the national and regional scale, except in the northern lowlands (CNO) where LLd2 was in third position (Fig. 5). However, the partial dependence plots seem to show a decrease in rwi with increasing LL (Fig. 7). When analysing the residuals of the models, we identified two years, corresponding to the two pointer years, with extreme leaf loss in the northern lowlands (2004 and 2011), one year (2004) in the Vosges-Jura mountains, and four years (2002, 2004, 2011 and 2014) in the Eastern lowlands. Removing these points decreased LLd2 importance as well as the slope of the partial dependence plots (Fig. 7). The tree-ring width index reached a value below 1 for leaf loss with a range of 9-34 %.

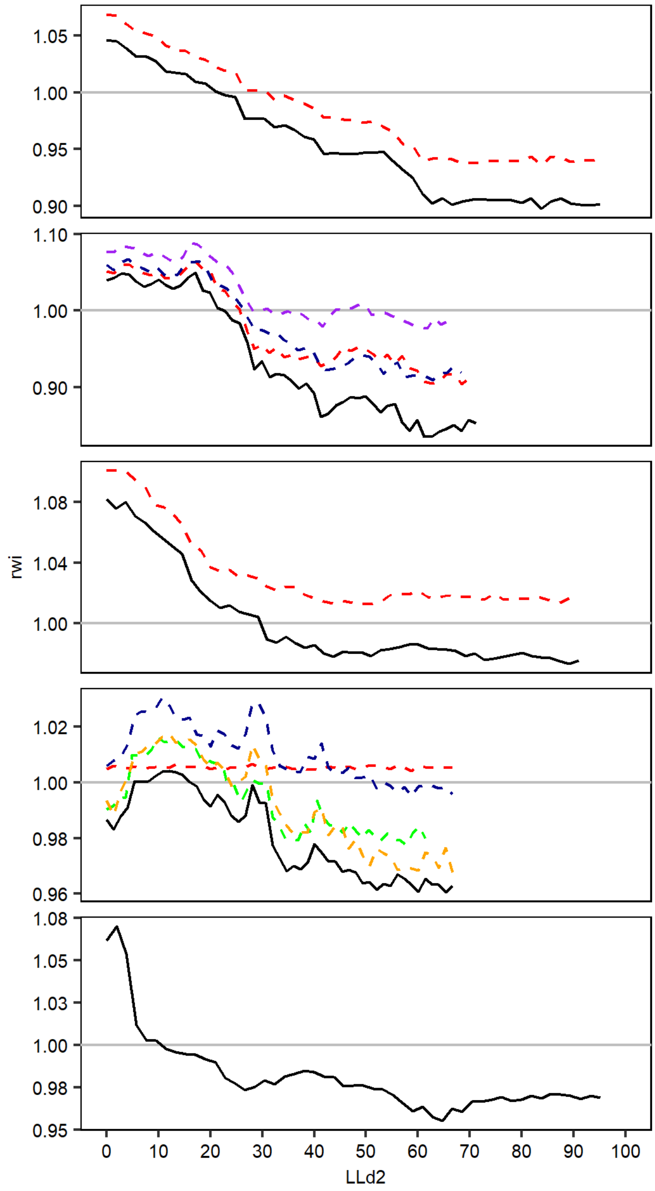


Figure 7 : Partial dependence plots showing the marginal effect of de-trended leaf loss indices centred on the average (LLd2) on modelled common-beech tree-ring indices (rwi, 2001-2014) using all combinations of the other predictor variables for all regression trees in the forest. The plain black line shows the relationship between rwi and LLd2, and the dotted line shows the relationship between rwi and LLd2 without leaf-loss positive pointer years. At the national scale (a), in the northern lowlands, (b) in the Vosges-Jura mountains (c), in the Eastern lowlands and (d) in the Alps. Coloured lines show the relation without the positive pointer year 2004 (red), 2011 (blue), 2004 and 2011 (purple), 2002 (green) and 2014 (orange).

# 4. Discussion

## 4.1. Beech health status in the French network and in Europe as a whole

From 2001 to 2014, beech trees in the French part of the ICP network showed slightly higher leaf loss than all the ICP European beech trees (average defoliation of 26.5% in France compared to 20.39% in Europe). During the same period, according to the ICP Forests defoliation classes (Eichhorn et al., 2016), 23% of French beech trees presented no defoliation (class 0), 39% slight defoliation (class 1), 35 % moderate defoliation (class 2), only 2 % presented severe defoliation (class 3) and none were observed with 100% leaf loss. According to the European criteria, French beech forests overall were in good condition.

### 4.2. Are inter-annual variations in leaf-loss and radial growth controlled by the same climatic variables?

The systematic forest health monitoring network allowed us to work on a set of plots representative of the species in the regions or on the whole territory. The various growing conditions and ecological sites were taken into account through the calculation of specific bio- and pedo-climatic variables for each plot. Our approach resulted in a robust growth and leaf loss signal for each region.

Over the period 2001-2014, we observed that several variables had an effect on both radial growth and crown condition. Most of these variables likely reflect ecophysiological processes. Previous year's (n-1) climatic variables mainly control LL inter-annual variations, whereas radial growth is more sensitive to the climatic parameters of the current year (n). This observation is in line with previous studies on crown development, radial growth and their relationships with climate (Power, 1994; Thabeet et al., 2009) and confirm our hypothesis that climatic factors during the previous year control inter-annual variations in leaf loss.

Whether the effect of soil water deficit occurs on primary or secondary growth depends mostly on when the stress occurs (Power, 1994).

Soil water deficit in the **previous** year increases leaf loss. This a consequence of the climatic constraints on leaf preformation during the previous year. Cochard et al. (2005) suggest a correlation between primary growth and secondary growth through xylem hydraulic conductance. The shoots developing in year n depend on the number of leaf primordia in the bud, which themselves depend on the outermost tree-ring of year n-1. Finally, the soil water deficit of the previous year may increase the number of short shoots. In England (Stribley and Ashmore, 2002), the annual growth of both the leader, or primary, shoots and the lateral, or secondary, shoots were suppressed in drought years. A one-year delayed response of crown condition to soil water deficit is a common observation throughout Europe (Bréda and Badeau, 2008; Power, 1994; Seidling, 2007; Seidling et al., 2012; Wilson et al., 2008; Zierl, 2004).

Previous- and current-year soil water deficit controls tree-ring width.

In our study, tree-ring width decreased with increasing **current** summer (June-July) soil water deficit (SWD). High evaporative demand and low precipitation during summer increase soil water deficit, reducing canopy conductance (Lemoine et al., 2002) and gross primary production (GPP) in beech stands (Granier et al., 2008, 2007). Ultimately, this can affect carbon storage and lead to dieback (Bréda et al., 2006). GPP depends on 1/ the duration and intensity of the water deficit cumulated over the growing season, and 2/ the growing season length, i.e. the period of carbon uptake by the stand (Granier et al., 2008).

The negative effect of the previous year’s water deficit can be explained by a dysfunction in carbon storage. Skomarkova et al. (2006) showed that 20% of the ring-width in corresponds to carbon stored during the previous year. The previous year's level of growth may therefore explain part of the ongoing year's growth. However, in addition to a delayed effect of the non-structural carbohydrate amount on radial growth, beech trees may sacrifice growth to sustain allocation to carbon storage. In young beech trees that had been submitted to an extremely long and intense drought period, Chuste et al. (2019) observed that carbon was allocated in storage at the expense of primary and secondary growth, that were severely reduced.

The sensitivity of both LL and rwi to soil water deficit and mean April-to-August temperature could be a result of carbon partitioning among secondary and primary growth and reproduction (Drobyshev et al., 2010; Innes, 1994; Mund et al., 2010; Seidling, 2007).

Leaf and flower production depend on carbon concentrations during the previous year (Cochard et al., 2005; Hoch et al., 2013; Miyazaki, 2013). Several authors show that after a hot dry summer, beeches can sometimes produce a large number of flowers (Etzold et al., 2016; Hacket-Pain et al., 2017; Nussbaumer et al., 2018; Piovesan and Adams, 2002; Vacchiano et al., 2018). This may lead to a trade-off between leaf production and reproduction. In addition, heavy fruit production can also decrease the number of leaves per ground area because primordial leaf buds are replaced by flower buds (Müller-Haubold et al., 2015). Microphylly can also lead to an abnormally high assessment of leaf loss. The observer may confuse leaf loss and a more transparent crown with smaller leaves.

Fruit development depends on newly assimilated carbon and this can lead to a competition for carbon between growth and reproduction (Hacket-Pain et al., 2017; Hoch, 2005; Hoch et al., 2013; Miyazaki, 2013). In our study, however, when we added the presence or absence of fructification, we found no relationship between reproduction and radial growth. However, fructification, the product of flowering, did significantly increase leaf loss (i.e. primary growth and leaf mass) in two ecological regions (Northern and Eastern lowlands). However, the fact that fructification observations were not mandatory or systematic for the ICP Network data we used may have caused an underestimation of the effect of fructification on growth and/or leaf loss in our study.

Both rwi and LL responded to current- and previous-year bud burst date (estimated through modelling). While an earlier bud burst date induces cambium activation and lengthens the growing season (Davi et al., 2006), it also exposes the tree to a higher risk of late frost damage in April. In our study, an early leaf unfolding in the previous year appeared to be an advantage for both secondary and primary growth. Granier et al. (2008) observed that canopy photosynthesis (GPP) depended on growing season length, i.e. the period of carbon uptake. A high assimilation rate increases C storage, allows wider tree rings in twigs, and enables buds to preformat a large number of leaf primordia. Indeed, the width of the outermost ring is positively correlated to xylem conductance to the buds (Cochard et al., 2005). For beech, radial growth initiation is synchronous with leaf unfolding (Barbaroux and Bréda, 2002) and is closely dependent on leaf photosynthesis (Granier et al., 2008, Michelot et al., 2012). If previous-year leaf unfolding occurs early and there is no late frost damage, the growing season is longer and there is therefore more assimilated carbon available for the preformation of next year's leaves and tree growth. For the current year, an early bud burst reduces radial growth without any deleterious effects to crown condition. However, we observed an effect of late frost on crown condition in mountainous regions. This agrees with other studies of frost damage on current growth and leaf loss (Dittmar et al., 2006; Menzel et al., 2015; Nolè et al., 2018; Príncipe et al., 2017); the intensity and frequency of late frosts increase with altitude (Cailleret and Davi, 2011). The newly formed leaves are damaged and the tree needs to mobilize more stored carbohydrates to create new foliation. The second foliation is nitrogen-depleted and therefore less efficient; furthermore, there is less carbon available to preform next year's leaves (Augspurger, 2009; Awaya et al., 2009; Bascietto et al., 2018).

As opposed to previous findings, we observed that the accumulation of negative daily maximum temperatures during winter impaired radial growth. As mentioned earlier, a reduction in growth is usually interpreted as the result of damage to buds or young leaves after a late frost. Oddly, the negative influence we observed on beech occurred for cold temperatures accumulated during the dormancy period. Indeed, the reduction in growth with winter temperatures cannot be attributed to bud damage. Winter buds have a high tolerance to cold temperatures, though this tolerance decreases as budburst approaches (Gömöry and Paule, 2011; Menzel et al., 2015). Lenz et al. (2016) demonstrated high frost resistance in the upper parts of the tree, with temperatures of -40°C damaging only 50% of the buds. However, as in previous, more local dendrochronological studies (Di Filippo et al., 2007; Dittmar et al., 2003; Weigel et al., 2018), we observed a relationship between winter temperatures and growth at national and regional scales. Power (1994) reported a significant impact of winter temperatures from December to February on apical growth, i.e. primary growth, on twigs of declining beech trees. This negative impact could lead to increased leaf loss the following summer.

A deficiency in the frost hardening process is one possible explanation for beech growth sensitivity to negative temperatures during winter. Converting starch to soluble sugars is essential for hardening; this is observed through a decrease in starch and an increase in soluble sugar content during winter (Barbaroux and Bréda, 2002; Charra-Vaskou et al., 2012). If a harsh winter is preceded by a summer drought or any event that could impair carbon storage, reserves may not be fully restored by the time hardening begins, thus leading to less efficient protection against freezing temperatures. These observations encourage us to deepen our understanding of the processes responsible for this result at different compartmental levels (crown, trunk, roots).

Thanks to data provided by the French Forest Health Department (DSF) on the causes of observed leaf symptoms, we were able to explain most of the significant symptoms we found on beech leaves in our study. In the Northern region, leaf loss increased with leaf coloration (yellow, red), and a high proportion of abnormal leaf coloration occurred in the years following the exceptionally early drought in 2011. Constantly increasing leaf consumption by phyllophagous insects in the Alps has been observed since 2005 (data not shown here), thus explaining the increase in leaf loss. Unfortunately, the insects causing the consumption have not been clearly identified. Beech weevils have been recorded since 2011; however, their impact remains unknown. Finally, the leaf necrosis we observed was the result of a frost in 2012.

## 4.3. Assessment of the relationship between rwi and LL

### 4.3.1. Leaf loss is a poor predictor of radial growth inter-annual variability

At the national scale and in the different ecological regions, there was a slight though continuous decrease in radial growth with leaf loss. The typical vertical canopy profile and differentiated leaves of the beech tree can explain our result. Leaf area is mostly distributed in the upper and middle part of the crown (Holdaway et al., 2008) with small, thick sun-exposed leaves at the top, and thinner larger leaves in the middle and at the bottom of the canopy (Hagemeier and Leuschner, 2019). The sun-exposed leaves have higher photosynthetic rates (higher maximum $CO_2$ assimilation rates, maximum stomatal conductance) than do the shaded leaves (Scartazza et al., 2016; Urban et al., 2007). Only the upper third of the crown is assessed (Eichhorn et al., 2016) where the photosynthesis rate is maximum. Therefore, annual recorded leaf loss corresponds to a potential decrease in carbon assimilation rate. However, leaf loss in the sun-exposed upper crown also induces a reduction in transpiration. Thanks to a trade-off between transpiration and assimilation, leaf loss should therefore have a limited impact on radial growth thanks to a more limited soil water shortage.

However, even though we observed slowed radial growth starting from 5% leaf loss, values did not fall below normal (rwi=1) until a 20% leaf loss was reached. This threshold must be interpreted with precaution. While we did find a relationship between LL and rwi, LL ranked low. This is because the correlation between growth and leaf loss only occurs in case of extreme events, as shown by our joint analysis of leaf loss and radial growth pointer years; no relationship occurs in cases of slight or moderate defoliation. Almost all of the pointer years were due to climatic factors accounting for both the small radial increment and high leaf loss (Table A.2). Often, severe soil water deficits were involved (lag effects form 2003's extreme summer drought and heat wave, a direct impact of the early drought event in spring of 2011). In fact, in the regions where LL appeared to predict radial growth, removing the common pointer years for the two indicators decreased the ability of LL to explain the variation in radial growth (rwi above 1). Drobyshev et al.'s (2007) and Sánchez-Salguero et al.'s (2013) results are in complete accordance with our findings. In their study, more significant differences in increment were observed between healthy crowns (class 1, < 25 %) and heavily declining crowns (class 3, > 60 %) than between other crown classes. Therefore, leaf loss is a good indicator of growth potential only in case of extreme events and when leaf loss is high. As supported by Seidling et al. (2012), leaf loss and radial growth are only weakly correlated.

### 4.3.2. Crown condition, a poorer descriptor of tree vitality than radial growth

Leaf loss showed fewer significant relationships with the selected climate variables than did radial growth. The LL series of common beech did not show as clear a common signal as did rwi, as indicated by high between-tree variability in the leaf loss series and by a smaller “Gleichläufigkeit” coefficient (year-to-year agreement between the series). In accordance with earlier studies, we confirm that tree-ring series reflect exogenous signals more clearly for common beech (Dittmar et al., 2003).

Describing crown condition and morphology enables forest managers to detect severe tree dysfunction through discoloration, abnormal leaf loss or branch mortality (Innes, 1998; Ling et al., 1993; Power, 1994). However, the multiple factors influencing inter-annual variations in leaf deficiency are challenging to disentangle (Innes et al., 1993). Our surprisingly strong GINI results for leaf loss, indicating a higher year-to-year variability than for growth, first led us to question the reliability of the observations made by the pairs of operators. We investigated this issue but found no clear relationship imputable to operator inconsistency. Nevertheless, the GINI coefficient clearly increased when more than one pair of operators assessed a given plot. Even though overall assessment quality has recently improved (Ferretti et al., 2014; Meining et al., 2016), it is important to keep in mind that one of the main weaknesses in the ICP monitoring network is operator subjectivity, which can lead to inconsistency among assessments related to different sky conditions, observation years and countries.

## 5. Conclusions

Using the machine-learning algorithm Random Forest to identify the response of inter-annual leaf loss or radial growth to biotic and abiotic constraints proved to be effective. The climatic drivers of radial growth we found through this approach are in accordance with previous studies. Several have an effect on both radial growth and crown condition, though previous-year climatic variables tend to control leaf loss while radial growth is more sensitive to current-year climate. There is a common sensitivity to soil water deficit but with different time lags. Primary and secondary growth are related to each other through hydraulic structure or resource partitioning. With regard to its use as an indicator of tree health, leaf loss captured fewer pointer years than did radial growth. Leaf loss only explained a reduction in radial growth in the case of extreme leaf loss events. Furthermore, radial growth, unlike leaf loss, presented a strong common signal among trees, allowing us to study tree response to abiotic factors with more assurance. Radial growth also allowed us to carry out a retrospective analysis of living conditions thanks to more reliable measurements. A rigorous dendrochronological approach including coring to the pith can help to accurately measure the effect of age and is possibly more cost-effective than estimating a poor quality indicator like leaf loss every year. A study comparing our results on beech with other species, including coniferous trees, is underway in order to conclusively assess the performance of annual visual estimations of leaf loss.

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