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   1. Introduction

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

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

11   Since the end of the 1970s, and the impressive episodes of decline in Central European
12   forests, several forest health monitoring networks have been set up. The first in France was
13   set up on a 16x1 km grid, only in the mountains all along the eastern border, where foresters
14   were concerned by a severe health decline in fir.Observations were performed from 1983 to
15   1993 to observe the recovery of coniferous tree health (Barthod, 1994). In 1985, a trans-
16   national network, the International Co-operative Programme on Assessment and Monitoring
17   of Air Pollution Effects on Forests (ICP Forests), was created under the United Nations
18   Economic Commission for Europe (UNECE) (Mueller-Edzards et al., 1997). Forest condition
19   has therefore been monitored since 1986/87 on a large scale, though at a low intensity
20   (Level I), thanks to a systematic network of plots located at the nodes of a 16x16 km grid in
21   all European forests. Annual visual observations of crown condition are carried out for 20
22   trees on these plots according to two criteria: leaf loss compared to a full folied "reference
23   tree" , and abnormal leaf colouration (Eichhorn et al., 2016).

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

33   In Europe, crown condition remains a widely-used forest condition indicator "within Criterion
34   2, 'Forest health and vitality'", one of the six criteria adopted by Forest Europe (formerly the

35   Ministerial Conference on the Protection of Forests in Europe – MCPFE) to provide

36   information for sustainable forest management in Europe[1]"(Michel et al., 2018). ICP technical

37   and executive reports express damage results as the percentage of trees with more than

38   25% defoliation. However, to our knowledge, it has never been properly demonstrated that

39   this threshold is an appropriate breakpoint for deciding whether a tree is in good or poor

40   condition. Assessing the validity of this threshold was one goal of this study.

41   Radial growth, is also a well-established and widely-used indicator of tree health and

42   physiological status (Dobbertin, 2005). Research on the relationship between radial growth

43   and crown condition has shown no clear pattern. Authors discriminate tree populations

44   according to their growth performance and then retrieve characteristic leaf loss thresholds

45   that have a significant effect on radial growth *a posteriori*. However, the thresholds for growth

46   decline are species- and site-dependent (Becker, 1987; Bert et al., 1990).

47   Very few studies have investigated the connection between inter-annual variations in crown

48   condition and radial growth. Dittmar and Elling (2007) showed a decrease in increment with

49   leaf loss but their findings cannot be generalized because their study was restricted to only

50   12 trees. Seidling (2012) found a low correlation between inter-annual beech growth and leaf

51   loss and questioned using leaf loss to explain functional relationships between the two

52   indicators at the plot level. Solberg (1999) also found a weak correlation between tree-

53   specific long-term means for crown condition and growth.

54   This study focuses on common beech, one of the most important and widespread

55   broadleaved trees in France and Europe. In beech, each year, a new shoot grows from a

56   dormant bud at the end of the previous year's shoot. There are two types of shoots:

57   exploratory (long) and exploitation (short) shoots. The long, fast-growing exploratory shoots

58   extend into the space around the tree and are therefore located in the upper periphery of the

59   crown (Teissier Du Cros et al., 1981), where leaf loss is usually assessed. Therefore, leaf

60   loss as compared to a reference tree and assessed on the upper third of the crown, results

61   from abnormal primary development (short elongation, impaired crown development, bud

62   burst deficit), while cambial activity generates the secondary growth responsible for radial

63   increment.

64   There is solid knowledge of radial growth and crown development responses in beech to

65   climate. On one hand, water deficits impair twig elongation (Power, 1994; Stribley and

66   Ashmore, 2002) and reduce the number, rate of expansion and final size of the leaves

67   (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

99 - and more importantly for canopy processes - potential evapotranspiration, are integrated in

100 comprehensive process-based predictors. We can therefore avoid adding monthly

101 precipitation and temperature as done in function response models. Second, to handle the

102 diversity of the potential variables, the presence of nonlinear relationships and the possible

103 correlations among them, we chose to work with a nonparametric variable-selection method,

104 Random Forest (Breiman, 2001). Random Forest models often show a higher predictive

105 ability than classical regression (Muchlinski et al., 2016; Oliveira et al., 2012) and linear

106 response function models (Jevšenak et al., 2018a). Random Forest models are gaining

107 attention in different fields of ecology, including dendrochronology (Cutler et al., 2007;

108 Jevšenak et al., 2018a; Prasad et al., 2006). We emphasize that the objective of this work is

109 to interpret rather than predict results, even though Random Forest has proven to be a very

110 powerful predictive method in many contexts, including tree-ring analysis (Genuer et al.,

111 2015; Jevšenak et al., 2018b). Our aim is to take advantage of this powerful device to

112 disentangle possible non-linear, complex or redundant relationships between variables.

113 2. Materials and methods

114   2.1. Sampled plots

115 The French part of the ICP Forests "Level I" transnational monitoring network includes 112

116 plots with at least one common beech (*Fagus sylvatica* L.) tree. For this study, 97 plots, with

117 a total of 715 beech trees, were selected based on three criteria: 1/ the plot contained at

118 least five beech trees, 2/ crown condition observations were available from 1989 to 2014,

119 and 3/ the plots were distributed as widely as possible within the beech distribution range in

120 France. The French national territory is divided into eight ecological regions, referred to as

121 GRECOs ('Large Ecological Regions'), with similar bio-climates, bedrock formations and

122 topography, as defined by the French NFI (National Forest Inventory). The eight GRECOs

123 are as follows: three lowland regions in the west, north and east; three mid-mountain areas in

124 the Massif Central, Vosges and Jura; and two high-mountain regions in the Pyrenees and

125 Alps. For statistical reasons, and based on climatic similarities, we grouped together the plots

126 in the western and northern regions (Northern lowlands), and the plots in the Jura and

127 Vosges (Vosges-Jura) mountains, for a total of six ecological regions.

128   2.2. Crown condition data

129 Assessing crown condition is central to monitoring in the ICP Forests. The currently used

130 assessment methods were developed in the mid-1980s. Crown condition is evaluated by

131 visually assessing leaf loss (LL) from the ground and a standardised method presented in a

132 manual for crown condition assessment is followed (Eichhorn et al., 2016). Every year from

133 July 1st to August 31st, trained observers assess LL in 5% incremental steps on 20

134 numbered, dominant or co-dominant trees. Leaf loss in the crown of the sampled trees is

135 visually compared to a virtual local "reference tree". This reference is a conceptual tree,

136 optimally foliated under the specific local site conditions and of a similar age and social

137 status to the average tree in the stand. Leaf loss series are available from 1989 to the

138 present.

139 Age is known to be the factor most correlated to crown condition (Seidling and Mues, 2005).

140 Because we wanted to identify signals in relation to climate, we needed to remove any trends

141 caused by other factors. Furthermore, we hoped to explain the inter-annual variations in leaf

142 loss and to keep only high-frequency inter-annual signals. We therefore standardized leaf-

143 loss series at the tree level to create two indices. For the first leaf-loss series index (LLd1),

144 we fitted the long-term trend with a linear regression of time for a given tree, then, for each

145 year, used the ratio method to compute a de-trended signal (Cook et al., 1990; Douglass,

146 1936; Dyer and Fritts, 1978).

147   2.3. Radial growth data

148 Each assessed tree was cored to the pith at breast height for dendrochronological analysis.

149 We measured tree-ring from the bark to the pith to the nearest 1/100 mm with a microscope

150 connected to a computer running the SAISIE program (Bert et al., 1990). Ring-reading

151 mistakes were checked for and corrected by cross-dating the tree ring series, according to

152   the procedure described in Becker et al. (1994). During the cross-dating step, each individual

153   chronology was compared to an average chronology for the corresponding ecological region

154   to identify regional pointer years. Then, each ring-series was checked for erroneous dating

155   with the INTERDAT computer program (Becker and Dupouey, unpublished). This program

156   depends on pointer years calculated with the method proposed by Becker (1989): a year is

157   considered characteristic when at least 75% of the trees in a stand have the same sign for

158   change in growth with an absolute variation in growth of at least 10% from the previous year.

159   Plots were chosen according to a systematic grid. Therefore, trees of different ages, social

160   status and stand management were cored to the pith. To investigate year-to-year tree-ring

161   variations, we removed non-climatic signals (trends related to age, competition, stand

162   management, long term trend due to climate change): each individual tree-ring series was

163   transformed into a growth index which kept only the annual growth signal, i.e. inter-annual

164   climatic variations and annual pest and disease damage (Fig. 1b). We used the statistical

165   freeware R (R Core Team, 2016) with the "dplR" package (Bunn, 2008) to standardize each

166   individual tree-ring series and to isolate the inter-annual signal thanks to a smoothing spline

167   with a frequency response of 50% at 30 years (Cook and Peters, 1981), thus yielding

168   dimensionless de-trended ring widths (rwi). With this de-trending method, we kept high

169   frequency variations, the signals that we sought to interpret. In addition, because we were

170   interested in the relation between leaf loss and tree-ring increment, we did not remove the

171   autocorrelation. Indeed, both leaf loss and tree-ring increment can have legacy effects from

172   the previous year through amounts of non-structural carbohydrates or bud preformation.

173   2.4. Predictors

174   In order to characterize inter-annual variations in growth and in leaf loss, the selected

175   predictors were related to plot (mainly climatic) or individual tree characteristics (annual leaf

176   damage). For each plot, daily climatic variables were extracted from the mesoscale SAFRAN

177   reanalysis, which covers France with an 8 km x 8 km grid (Quintana-Seguí et al., 2008).

178   These climatic variables were then summarized into seasonal variables known to influence

179   crown condition and/or growth (Nevalainen et al., 2010; Seidling, 2007; Seidling et al., 2012)

180   over the reference period 2001-2014. Based on temperature functions, the budburst date

181   (BBD) was also modelled for each plot (Dufrêne et al., 2005). As beech is a diffuse-porous

182   species, its radial growth starts just after budburst and ends sometime in August (Barbaroux

183   and Bréda, 2002; Michelot et al., 2012). For this reason, we used the modelled budburst date

184   to define the start of the growing season for all our plots (Table 1) and we aggregated mean

185   temperatures from April to August (TM.AA).

186   One-year-lagged climatic variables were also computed as potential predictors. However, no

187   significant trends were observed on the series.

188

189   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

190

191 The ICP Forests network underwent two soil surveys during the study period. A soil

192 description (soil type, depth, root distribution) took place between 1994 and 1995

193 (Vanmechelen et al., 1997) and soil properties (bulk density, texture, carbon content) were

194 measured between 2005 and 2008 through the BioSoil-Biodiversity project (Lacarce et al.,

195 2009). These soil data were used to compute soil extractable water (in mm) for each plot.

196 For each plot, ecophysiologically-based drought indices were computed thanks to the forest

197 water balance model Biljou © (Granier et al., 1999). The model simulates the water fluxes

198 between the atmosphere, the canopy and the soil for a given plot. The soil water content is

199 computed daily as a function of precipitation, rainfall interception, tree transpiration, soil

200 evaporation and drainage. The model represents the regulation of canopy gaseous

201 exchanges when the soil water deficit drops below a threshold of 0.4, which induces stomatal

202 closure (Granier et al., 1999, Bréda and Granier, 1996). Below this threshold, canopy

203 conductance and GPP (gross primary production) decreases, as we demonstrated in beech

204 stands (Granier et al., 2007). The calculation of potential evapotranspiration integrates

205 elementary variables into radiative and convective components, which are the drivers for

206 canopy exchanges with the atmosphere. The daily meteorological variables required are

207 rainfall, air temperature and humidity, global radiation and wind speed. Soil descriptions and

208 properties at each plot (rooting pattern, extractable water, soil bulk density) were used to

209 calculate water balance. The output variable characterizing drought events was soil water

210 deficit intensity from June to July (maximum growth rate, Michelot et al., 2012) or from

211 budburst to leaf fall (Table 1).

212 Since 2000, in addition to rating leaf loss, the ICP reports have required annual descriptions

213 of damaging agents for each sampled tree. Damage assessment consists of describing the

214 symptoms and determining the cause, if possible. A symptom is defined as an indicator of

215 the presence of harmful agents having had a significant impact on any part of the tree

216 (Eichhorn et al., 2016). Only the symptoms observed on leaves were kept in our analysis.

217 The symptom variable indicates the presence or absence of a symptom on the leaves. The

218 symptom variable is declined into different categories identifying the symptom observed on

219 the leaves.

220   2.5. Data sets

221 Our objective was to work on continuous leaf-loss series that were homogeneous in quality

222 while maximizing the number of trees for analysis. To avoid (1) biases due to the change in

223 the leaf loss assessment protocol that occurred between 1994 and 1996 (Landmann et al.,

224 1999, 1998) and (2) the disturbances related to the 1999 storms (Lothar and Martin,

225 depending on the region), we selected homogeneous leaf-loss series starting in 2001. Due to

226 the joint analysis of leaf loss and radial growth series, the end of the study period was the

227 year of the last available tree-ring width data, i.e. 2014. Therefore, we worked over the
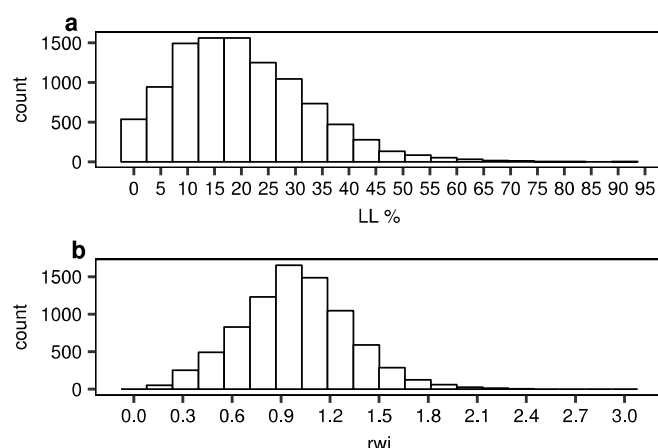
228 common period 2001 to 2014.

229

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)

244

245 Our second objective was to analyse the influence of leaf loss on radial growth. We therefore

246 created a second data set of 583 trees with a continuous series for leaf loss and growth

247 index from 2001 to 2014 (Fig. 1, Table 2). The response variable was the annual ring-width

248 index (rwi) and the same predictors were used as in the previously described analyses (i.e.

249 current- and previous-year annual climatic variables, water balance variables and presence

250 of damage symptoms).

251 Because we expected the average level of leaf loss to influence inter-annual variations in

252 radial growth, we calculated a second index, LLd2.

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

$$LLd2_{iy} = LLd1_{iy} \times \overline{LL_\iota}$$

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

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

257 percentage.

258 In the second objective, the de-trended leaf loss (LLd2) of the previous and current year was

259 introduced as an additional predictor of radial growth.

260   2.6. Statistics

261 To provide deeper understanding of the relationship between leaf loss and tree-ring width,

262 pointer years were detected on raw tree-ring and leaf-loss series. Analysing pointer years is

263 typical in dendrochronological studies (Becker et al., 1994; Schweingruber et al., 1990).

264   Pointer years represent a growth reaction to abrupt changes in environmental conditions and

265   are usually expressed as a relative change in growth, in percentage. Usually, pointer years

266   correspond to a calendar year when, at least, 75% of the trees have the same sign of change

267   with rings at least 10% narrower, or wider, than the previous year (Becker et al., 1994). By

268   testing different thresholds, it is possible to distinguish very characteristic years from less

269   characteristic years. We transposed this technique to our leaf-loss series. However, because

270   no pointer years were detected with the above-mentioned thresholds, we defined pointer

271   years for radial growth and leaf loss as years when at least 60% of the trees shared a

272   variation of at least 10% with the previous year (Becker et al., 1994; Mérian and

273   Lebourgeois, 2011).

274   We calculated the Gini coefficient (GINI) of the de-trended leaf loss (LLd1) and growth index

275   (rwi) series to compare growth sensitivity to climate. GINI is a relative index, quantifying

276   sensitivity scaled by mean and sample size (Biondi and Qeadan, 2008). We calculated GINI

277   for each tree and then averaged the GINI values in a second step. We used the

278   Gleichläufigkeit index (GLK) (Schweingruber, 1987) to check for a similarity in signal

279   between the series, in other words, their synchronization.

280   We chose to apply the machine-learning algorithm Random Forest (RF) (Breiman, 2001), a

281   nonparametric technique for classification or regression. RF is based on the Classification

282   And Regression Tree (CART) algorithm (Breiman et al., 1984). CART builds a decision tree

283   by finding the dichotomy at each iteration that minimizes a goodness-of-fit criterion among all

284   predictors. CART is known to be very sensitive to small changes in the data set (Genuer and

285   Poggi, 2019). RF is a tree-based ensemble method, which overcomes these limitations by

286   averaging regression over a great number of randomized variants of the decision trees

287   obtained with CART. The number of trees, *ntree*, is usually set between 500 and 2000.

288   Variants are obtained from bootstrap samples of the learning set (*the bagging*) and random

289   subsets of variables. Breiman (2001) showed, both theoretically and empirically, that these

290   averaged trees have fewer expected errors than do single trees. Because random subsets of

291 variables are selected at each node (control parameter *mtry*), the collinearity of the predictors

292 is reduced.

293 RF therefore has two interesting features: it is able to model nonlinear relationships and it

294 can handle redundancy in the variables. RF has proven to be a very efficient method, usually

295 ranked among the most efficient machine-learning methods (Genuer et al., 2015), both for

296 classification and for regression.

297 In addition to these advantages over regressions, RF makes it possible to rank the

298 importance of the predictor variables and to evaluate their marginal effect on the response

299 variable, without any a priori assumptions. The bagging process makes it possible to predict

300 the "out-of-bag" (OOB) samples from the "in-the-bag" ones. The importance of the variables

301 is then measured as the averaged increase of squared OOB residuals when the predictor is

302 permuted (Genuer et al., 2015).

303 Variable importance provides a measure to compare predictors within a dataset but does not

304 provide a threshold to select the most relevant ones. The R package "VSURF" (Genuer et

305 al., 2015) selects variables in two ways: for interpretative purposes, it can select all the

306 relevant predictors related to the variable under study (there can be redundancies); and, for

307 predictive purposes, it can select the smallest set of predictors that explains most of the

308 variability for the variable. Since we wanted to select predictors for functional interpretation

309 and not for prediction, we will only discuss the first type of selection in this paper. As a first

310 step, VSURF eliminated certain predictors based on the standard deviation of the variable's

311 importance (averaged over 50 runs of RF). The remaining variables were used to construct

312 nested RFs starting with the single most important variable and finishing with all the

313 important predictors. The predictors leading to the smallest OOB error were kept. After some

314 exploratory analysis (not reported here), VSURF was implemented with *ntree*= 2000 and

315 *mtry*=p/3 (p, being the number of variables involved in the model). Most of the time, the

316 cross-validated optimised parameters were very close to these values; and even when they

317 were not, predictions were not significantly different from those obtained with the above

318   setting. We randomly sampled 70% of the data set to train the RF and kept the remaining

319   30% to test prediction-error. For each model, the pseudo-R^2 predictive accuracy metric was

320   computed on the test set as calculated in the "randomForest" package (Liaw and Wiener,

321   2002). This metric is defined as the proportion of total variation in the outcome explained by

322   the model (or forest); values range between 0 and 1.

323   Strobl et al. (2008) report that variable importance metrics can be biased towards correlated

324   variables in some situations and propose an improved method in order to take this into

325   account. The method requires implementing a conditional permutation scheme within a

326   group that can potentially contain large sets of covariables. Genuer et al. (2010) specifically

327   studied RF variable importance in the presence of groups of highly correlated explanatory

328   variables. They did not diagnose any such bias for variable selection. In our case, we

329   performed preliminary exploratory analyses with the "party" package (Strobl et al., 2009). We

330   consistently obtained extremely low importance scores for all variables (results not reported

331   here), making it completely impossible to come up with any interpretation. Strobl et al. (2008)

332   and Genuer et al. (2010) agree on the fact that, despite possible overestimation of the

333   importance score, the order of the variables is usually preserved.

334   We used the "PDP" package (Greenwell, 2017) to describe the relationships between the

335   selected predictors and the variables of interest and illustrated the results with partial

336   dependence plots. A partial dependence plot (PDP) shows if the relationship between the

337   response and the predictor is linear, monotonous or more complex. For a given predictor

338   value, the PDP tells what the average marginal effect on the prediction is. We used the R

339   3.3.2 statistical software for all of our statistical analyses.

340   3. Results

341   3.1. Leaf-loss and radial-growth series

342   On the overall period (2001-2014), beech presented a mean defoliation of 24%

343   (median=20%). We calculated the Gini (GINI) and the "Gleichlaufigkeit" (GLK) coefficients to

344 compare the year-to-year variability and the strength of the common signal between the trees

345 (Table A.1). The GINI coefficient was higher for LLd1 (0.22) than for rwi (0.18), and

346 quantified a wider year-to-year variability for leaf loss. Inversely, the GLK coefficients were

347 weaker for LLd1 (0.52) than for rwi (0.58), suggesting a weaker common signal for leaf loss,
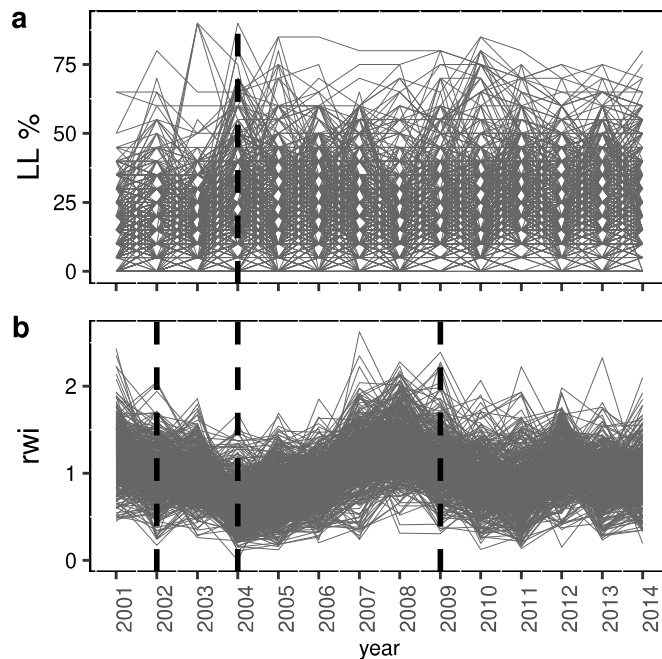
348 as shown in Fig.2.

349

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

352 In order to check if the high year-to-year variability in LL among trees could be attributed to

353 the quality of the visual assessment, we took into account the changes in observers at a

354 given plot during the observation period (information available in the ICP database). There

355 was no clear continuous pattern between the GINI coefficient and the number of pairs of LL

356 observers. The GINI coefficient did increase when there was more than one pair of observers

357 during the visual assessment period; however, it did not increase with increasing numbers of

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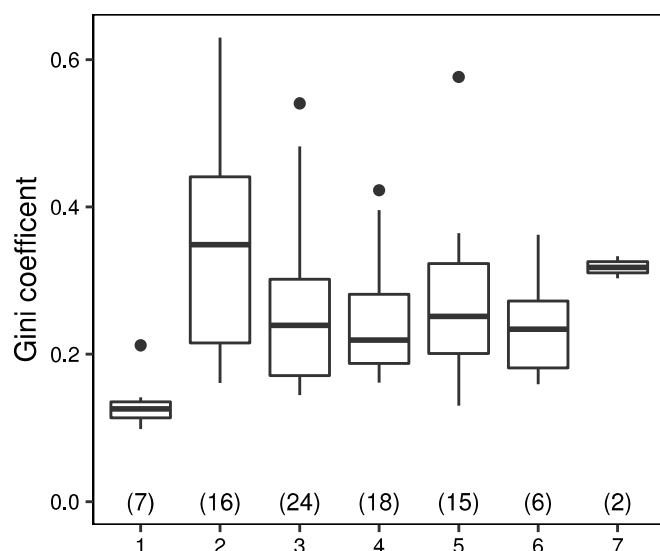
Figure 3: Boxplots of the relationship between the GINI coefficients calculated on the de-trended leaf-loss series (LLd1) for the period 2001-2014 and the number of pairs of observers on the same period. In brackets, the number of observations.

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

378

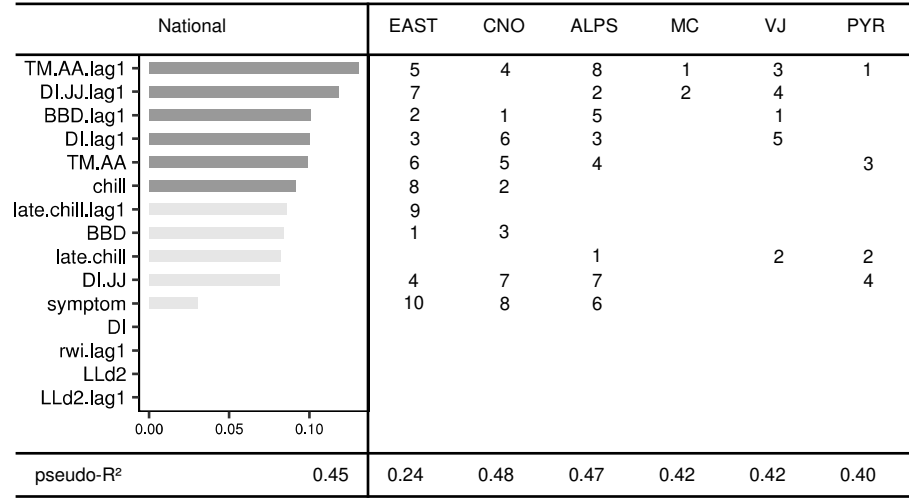### 3.2. Common explanatory variables of the inter-annual variations in leaf loss and radial growth

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-R²	0.45	0.24	0.48	0.47	0.42	0.42	0.40

386

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

398 From partial dependence plots (PDPs) and the importance of the selected variables shown in

399 Fig. 4 and Fig.5, we can describe the relationship between rwi or LLd1 and the predictors. A

400 PDP helps visualize the relationship between a predictor and the response variable of

401 interest, by keeping the other predictors constant. PDPs highlight the existence of non-linear

402 relationships between predictors and the variables of interest rwi and LLd1 (Fig.B.1 and

403 Fig.B.2).

404 The Random Forest model explained 47% of the growth index. For the period 2001-2014,

405 both the current and previous years' climatic variables controlled the tree-ring width index

406 (Fig. 5). For LLd1, the Random Forest model explained 45% of the inter-annual variability in

407 leaf loss. The inter-annual variations in LLd1 were mainly predicted by the previous year's

408 climatic variables (Fig. 4). Seven of the explanatory variables selected for the interpretation

409 of the inter-annual variations were common to LLd1 and rwi. The ranking of the variables

410 shown in Fig. 4 and 5 is independent of whether they are common or not, meaning that the

411 most important explanatory variable for leaf loss could be the least important one for radial

412 growth.

413 For LLd1, lagged climatic variables had a major impact (Fig. 4). LLd1 mainly responded to

414 summer soil water deficit and temperature surplus with a 1-year lag. Leaf loss increased with

415 the previous year's soil water deficit. LLd1 also responded to temperature variables (bud

416 burst date, chill, TM.AA). An early budburst in the year before crown condition assessment

417 sometimes resulted in reduced leaf loss (i.e. a better crown condition). LLd1 tended to

418 increase with the accumulation of negative maximum temperatures during the winter (from

419 October of the previous year to February of the current year) and with mean temperatures
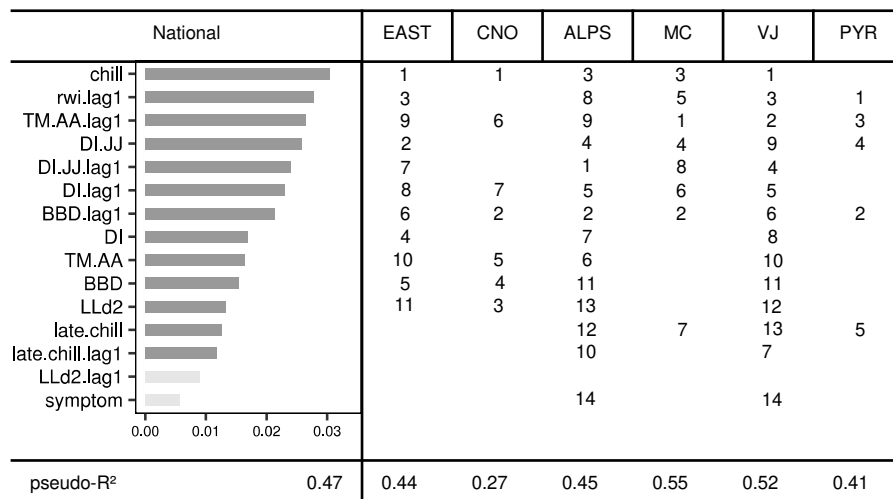
420 above 18°C during the growing season (TM.AA).

421

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?

448   Working on smaller ecological regions highlighted specific responses of leaf loss and radial

449   growth (Fig.4 and 5). As opposed to other regions, the northern lowlands and the Pyrenean

450   mountains were more sensitive to temperatures than to previous year's soil water deficit.

451   Leaf loss increased with the accumulation of cold temperatures between March and May of

452   the current year in three regions: the Alps, Vosges-Jura mountains and the Pyrenees.

453   Except in the Alps, northern lowlands and Eastern ecological regions, no observed

454   symptoms of leaf damage induced a significant increase in leaf loss, nor did fructification

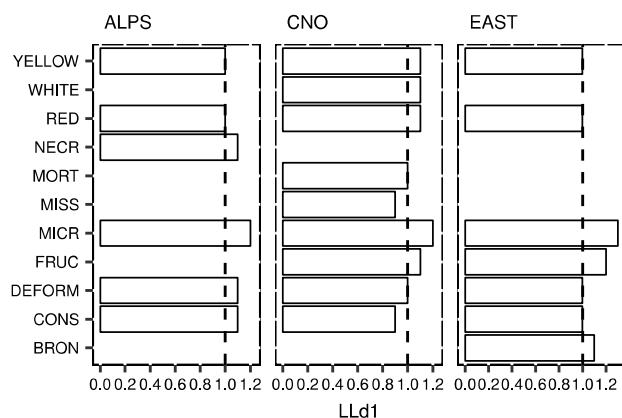455   (Fig. 4).

456

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

460   The same three regions presented high enough microphylly to increase LLd1. Leaf loss also

461   increased with high fructification in the Eastern and northern lowlands. Necrosis symptoms

462   were only found in the Alps (insect consumption and leaf deformation - (Fig. 6)). Leaves in

463   the northern plains presented colouring symptoms (yellowing, reddening, whitish coloration).

464   The northern lowlands stands out as the only case in the models where LLd2 was a relatively

465   important variable contributing to radial growth, ranking third (Fig. 5). Otherwise, like results

466   at the national scale, LLd2 was the least important variable explaining radial growth

467   variations in three other regions (East, Vosges-Jura, Alps). In the Massif Central and the

468   Pyrenees (Fig. 5), LLd2 did not influence growth.

469   3.4. Leaf-loss as a predictor of inter-annual variability in radial growth

470 Leaf loss (LLd2) appeared to be the least important variable predicting tree-ring width

471 variations at the national and regional scale, except in the northern lowlands (CNO) where

472 LLd2 was in third position (Fig. 5). However, the partial dependence plots seem to show a

473 decrease in rwi with increasing LL (Fig. 7). When analysing the residuals of the models, we

474 identified two years, corresponding to the two pointer years, with extreme leaf loss in the

475 northern lowlands (2004 and 2011), one year (2004) in the Vosges-Jura mountains, and four

476 years (2002, 2004, 2011 and 2014) in the Eastern lowlands. Removing these points

477 decreased LLd2 importance as well as the slope of the partial dependence plots (Fig. 7). The

478 tree-ring width index reached a value below 1 for leaf loss with a range of 9-34 %.

479
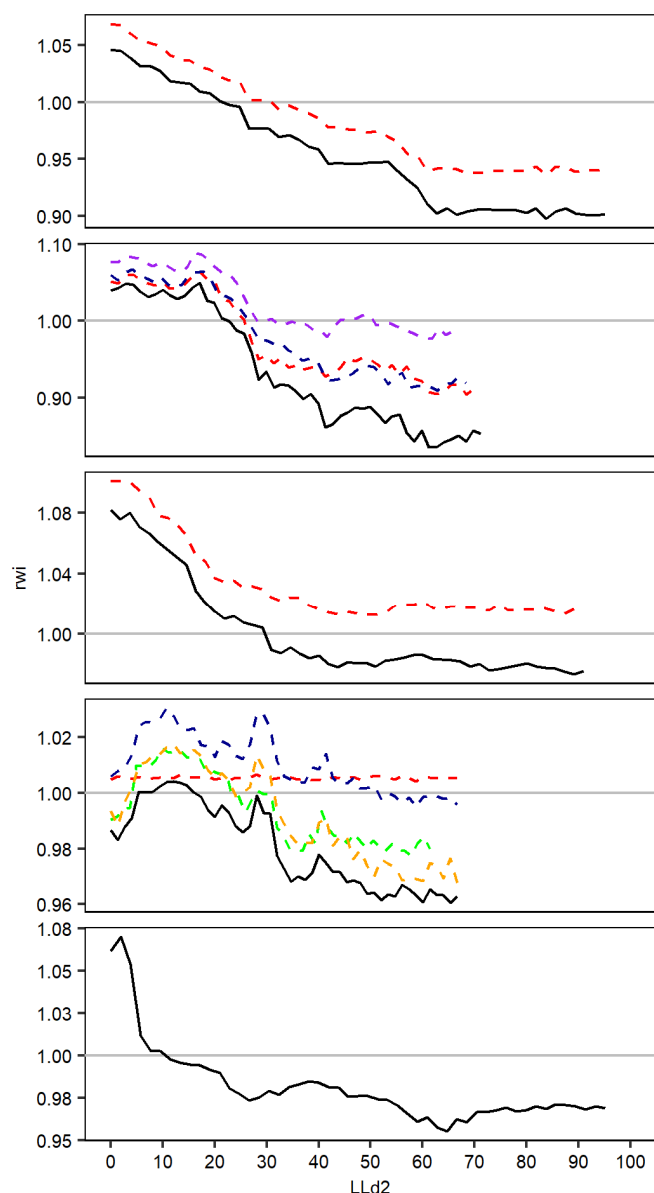
Figure 7 : Partial dependence plots showing the marginal effect of de-trended leaf loss indices centred on the average (LLd2) on modelled common-beech tree-ring indices (rwi, 2001-2014) using all combinations of the other predictor variables for all regression trees in the forest. The plain black line 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).

487   4. Discussion

488   4.1. Beech health status in the French network and in Europe as a whole

489   From 2001 to 2014, beech trees in the French part of the ICP network showed slightly higher

490   leaf loss than all the ICP European beech trees (average defoliation of 26.5% in France

491   compared to 20.39% in Europe). During the same period, according to the ICP Forests

492   defoliation classes (Eichhorn et al., 2016), 23% of French beech trees presented no

493   defoliation (class 0), 39% slight defoliation (class 1), 35 % moderate defoliation (class 2),

494   only 2 % presented severe defoliation (class 3) and none were observed with 100% leaf loss.

495   According to the European criteria, French beech forests overall were in good condition.

496   4.2. Are inter-annual variations in leaf-loss and radial growth controlled by the same

497   climatic variables?

498   The systematic forest health monitoring network allowed us to work on a set of plots

499   representative of the species in the regions or on the whole territory. The various growing

500   conditions and ecological sites were taken into account through the calculation of specific

501   bio- and pedo-climatic variables for each plot. Our approach resulted in a robust growth and

502   leaf loss signal for each region.

503   Over the period 2001-2014, we observed that several variables had an effect on both radial

504   growth and crown condition. Most of these variables likely reflect ecophysiological

505   processes. Previous year's (n-1) climatic variables mainly control LL inter-annual variations,

506   whereas radial growth is more sensitive to the climatic parameters of the current year (n).

507   This observation is in line with previous studies on crown development, radial growth and

508   their relationships with climate (Power, 1994; Thabeet et al., 2009) and confirm our

509   hypothesis that climatic factors during the previous year control inter-annual variations in leaf

510   loss.

511   Whether the effect of soil water deficit occurs on primary or secondary growth depends

512   mostly on when the stress occurs (Power, 1994).

513   Soil water deficit in the **previous** year increases leaf loss. This a consequence of the climatic

514   constraints on leaf preformation during the previous year. Cochard et al. (2005) suggest a

515   correlation between primary growth and secondary growth through xylem hydraulic

516   conductance. The shoots developing in year n depend on the number of leaf primordia in the

517   bud, which themselves depend on the outermost tree-ring of year n-1. Finally, the soil water

518   deficit of the previous year may increase the number of short shoots. In England (Stribley

519   and Ashmore, 2002), the annual growth of both the leader, or primary, shoots and the lateral,

520   or secondary, shoots were suppressed in drought years. A one-year delayed response of

521   crown condition to soil water deficit is a common observation throughout Europe (Bréda and

522   Badeau, 2008; Power, 1994; Seidling, 2007; Seidling et al., 2012; Wilson et al., 2008; Zierl,

523   2004).

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

525   In our study, tree-ring width decreased with increasing **current** summer (June-July) soil

526   water deficit (SWD). High evaporative demand and low precipitation during summer increase

527   soil water deficit, reducing canopy conductance (Lemoine et al., 2002) and gross primary

528   production (GPP) in beech stands (Granier et al., 2008, 2007). Ultimately, this can affect

529   carbon storage and lead to dieback (Bréda et al., 2006). GPP depends on 1/ the duration

530   and intensity of the water deficit cumulated over the growing season, and 2/ the growing

531   season length, i.e. the period of carbon uptake by the stand (Granier et al., 2008).

532   The negative effect of the previous year's water deficit can be explained by a dysfunction in

533   carbon storage. Skomarkova et al. (2006) showed that 20% of the ring-width in corresponds

534   to carbon stored during the previous year. The previous year's level of growth may therefore

535   explain part of the ongoing year's growth. However, in addition to a delayed effect of the non-

536   structural carbohydrate amount on radial growth, beech trees may sacrifice growth to sustain

537   allocation to carbon storage. In young beech trees that had been submitted to an extremely

538   long and intense drought period, Chuste et al. (2019) observed that carbon was allocated in

539   storage at the expense of primary and secondary growth, that were severely reduced.

540

541   The sensitivity of both LL and rwi to soil water deficit and mean April-to-August temperature

542   could be a result of carbon partitioning among secondary and primary growth and

543   reproduction (Drobyshev et al., 2010; Innes, 1994; Mund et al., 2010; Seidling, 2007).

544   Leaf and flower production depend on carbon concentrations during the previous year

545   (Cochard et al., 2005; Hoch et al., 2013; Miyazaki, 2013). Several authors show that after a

546   hot dry summer, beeches can sometimes produce a large number of flowers (Etzold et al.,

547   2016; Hacket-Pain et al., 2017; Nussbaumer et al., 2018; Piovesan and Adams, 2002;

548   Vacchiano et al., 2018). This may lead to a trade-off between leaf production and

549   reproduction. In addition, heavy fruit production can also decrease the number of leaves per

550   ground area because primordial leaf buds are replaced by flower buds (Müller-Haubold et al.,

551   2015). Microphylly can also lead to an abnormally high assessment of leaf loss. The

552   observer may confuse leaf loss and a more transparent crown with smaller leaves.

553   Fruit development depends on newly assimilated carbon and this can lead to a competition

554   for carbon between growth and reproduction (Hacket-Pain et al., 2017; Hoch, 2005; Hoch et

555   al., 2013; Miyazaki, 2013). In our study, however, when we added the presence or absence

556   of fructification, we found no relationship between reproduction and radial growth. However,

557   fructification, the product of flowering, did significantly increase leaf loss (i.e. primary growth

558   and leaf mass) in two ecological regions (Northern and Eastern lowlands). However, the fact

559   that fructification observations were not mandatory or systematic for the ICP Network data

560   we used may have caused an underestimation of the effect of fructification on growth and/or

561   leaf loss in our study.

562   Both rwi and LL responded to current- and previous-year bud burst date (estimated through

563   modelling). While an earlier bud burst date induces cambium activation and lengthens the

564   growing season (Davi et al., 2006), it also exposes the tree to a higher risk of late frost

565   damage in April. In our study, an early leaf unfolding in the previous year appeared to be an

566   advantage for both secondary and primary growth. Granier et al. (2008) observed that

567   canopy photosynthesis (GPP) depended on growing season length, i.e. the period of carbon

568   uptake. A high assimilation rate increases C storage, allows wider tree rings in twigs, and

569   enables buds to preformat a large number of leaf primordia. Indeed, the width of the

570   outermost ring is positively correlated to xylem conductance to the buds (Cochard et al.,

571 2005). For beech, radial growth initiation is synchronous with leaf unfolding (Barbaroux and

572 Bréda, 2002) and is closely dependent on leaf photosynthesis (Granier et al., 2008, Michelot

573 et al., 2012). If previous-year leaf unfolding occurs early and there is no late frost damage,

574 the growing season is longer and there is therefore more assimilated carbon available for the

575 preformation of next year's leaves and tree growth. For the current year, an early bud burst

576 reduces radial growth without any deleterious effects to crown condition. However, we

577 observed an effect of late frost on crown condition in mountainous regions. This agrees with

578 other studies of frost damage on current growth and leaf loss (Dittmar et al., 2006; Menzel et

579 al., 2015; Nolè et al., 2018; Príncipe et al., 2017); the intensity and frequency of late frosts

580 increase with altitude (Cailleret and Davi, 2011). The newly formed leaves are damaged and

581 the tree needs to mobilize more stored carbohydrates to create new foliation. The second

582 foliation is nitrogen-depleted and therefore less efficient; furthermore, there is less carbon

583 available to preform next year's leaves (Augspurger, 2009; Awaya et al., 2009; Bascietto et

584 al., 2018).

585 As opposed to previous findings, we observed that the accumulation of negative daily

586 maximum temperatures during winter impaired radial growth. As mentioned earlier, a

587 reduction in growth is usually interpreted as the result of damage to buds or young leaves

588 after a late frost. Oddly, the negative influence we observed on beech occurred for cold

589 temperatures accumulated during the dormancy period. Indeed, the reduction in growth with

590 winter temperatures cannot be attributed to bud damage. Winter buds have a high tolerance

591 to cold temperatures, though this tolerance decreases as budburst approaches (Gömöry and

592 Paule, 2011; Menzel et al., 2015). Lenz et al. (2016) demonstrated high frost resistance in

593 the upper parts of the tree, with temperatures of -40°C damaging only 50% of the buds.

594 However, as in previous, more local dendrochronological studies (Di Filippo et al., 2007;

595 Dittmar et al., 2003; Weigel et al., 2018), we observed a relationship between winter

596 temperatures and growth at national and regional scales. Power (1994) reported a significant

597 impact of winter temperatures from December to February on apical growth, i.e. primary

598 growth, on twigs of declining beech trees. This negative impact could lead to increased leaf

599 loss the following summer.

600 A deficiency in the frost hardening process is one possible explanation for beech growth

601 sensitivity to negative temperatures during winter. Converting starch to soluble sugars is

602 essential for hardening; this is observed through a decrease in starch and an increase in

603 soluble sugar content during winter (Barbaroux and Bréda, 2002; Charra-Vaskou et al.,

604 2012). If a harsh winter is preceded by a summer drought or any event that could impair

605 carbon storage, reserves may not be fully restored by the time hardening begins, thus

606 leading to less efficient protection against freezing temperatures. These observations

607 encourage us to deepen our understanding of the processes responsible for this result at

608 different compartmental levels (crown, trunk, roots).

609 Thanks to data provided by the French Forest Health Department (DSF) on the causes of

610 observed leaf symptoms, we were able to explain most of the significant symptoms we found

611 on beech leaves in our study. In the Northern region, leaf loss increased with leaf coloration

612 (yellow, red), and a high proportion of abnormal leaf coloration occurred in the years

613 following the exceptionally early drought in 2011. Constantly increasing leaf consumption by

614 phyllophagous insects in the Alps has been observed since 2005 (data not shown here), thus

615 explaining the increase in leaf loss. Unfortunately, the insects causing the consumption have

616 not been clearly identified. Beech weevils have been recorded since 2011; however, their

617 impact remains unknown. Finally, the leaf necrosis we observed was the result of a frost in

618 2012.

619   4.3. Assessment of the relationship between rwi and LL

620   4.3.1. Leaf loss is a poor predictor of radial growth inter-annual variability

621 At the national scale and in the different ecological regions, there was a slight though

622 continuous decrease in radial growth with leaf loss. The typical vertical canopy profile and

623 differentiated leaves of the beech tree can explain our result. Leaf area is mostly distributed

624   in the upper and middle part of the crown (Holdaway et al., 2008) with small, thick sun-

625   exposed leaves at the top, and thinner larger leaves in the middle and at the bottom of the

626   canopy (Hagemeier and Leuschner, 2019). The sun-exposed leaves have higher

627   photosynthetic rates (higher maximum CO_2 assimilation rates, maximum stomatal

628   conductance) than do the shaded leaves (Scartazza et al., 2016; Urban et al., 2007). Only

629   the upper third of the crown is assessed (Eichhorn et al., 2016) where the photosynthesis

630   rate is maximum. Therefore, annual recorded leaf loss corresponds to a potential decrease in

631   carbon assimilation rate. However, leaf loss in the sun-exposed upper crown also induces a

632   reduction in transpiration. Thanks to a trade-off between transpiration and assimilation, leaf

633   loss should therefore have a limited impact on radial growth thanks to a more limited soil

634   water shortage.

635   However, even though we observed slowed radial growth starting from 5% leaf loss, values

636   did not fall below normal (rwi=1) until a 20% leaf loss was reached. This threshold must be

637   interpreted with precaution. While we did find a relationship between LL and rwi, LL ranked

638   low. This is because the correlation between growth and leaf loss only occurs in case of

639   extreme events, as shown by our joint analysis of leaf loss and radial growth pointer years;

640   no relationship occurs in cases of slight or moderate defoliation. Almost all of the pointer

641   years were due to climatic factors accounting for both the small radial increment and high

642   leaf loss (Table A.2). Often, severe soil water deficits were involved (lag effects form 2003's

643   extreme summer drought and heat wave, a direct impact of the early drought event in spring

644   of 2011). In fact, in the regions where LL appeared to predict radial growth, removing the

645   common pointer years for the two indicators decreased the ability of LL to explain the

646   variation in radial growth (rwi above 1). Drobyshev et al.'s (2007) and Sánchez-Salguero et

647   al.'s (2013) results are in complete accordance with our findings. In their study, more

648   significant differences in increment were observed between healthy crowns (class 1, < 25 %)

649   and heavily declining crowns (class 3, > 60 %) than between other crown classes. Therefore,

650   leaf loss is a good indicator of growth potential only in case of extreme events and when leaf

651 loss is high. As supported by Seidling et al. (2012), leaf loss and radial growth are only

652 weakly correlated.

653   4.3.2.   Crown condition, a poorer descriptor of tree vitality than radial growth

654 Leaf loss showed fewer significant relationships with the selected climate variables than did

655 radial growth. The LL series of common beech did not show as clear a common signal as did

656 rwi, as indicated by high between-tree variability in the leaf loss series and by a smaller

657 "Gleichläufigkeit" coefficient (year-to-year agreement between the series). In accordance with

658 earlier studies, we confirm that tree-ring series reflect exogenous signals more clearly for

659 common beech (Dittmar et al., 2003).

660 Describing crown condition and morphology enables forest managers to detect severe tree

661 dysfunction through discoloration, abnormal leaf loss or branch mortality (Innes, 1998; Ling

662 et al., 1993; Power, 1994). However, the multiple factors influencing inter-annual variations in

663 leaf deficiency are challenging to disentangle (Innes et al., 1993). Our surprisingly strong

664 GINI results for leaf loss, indicating a higher year-to-year variability than for growth, first led

665 us to question the reliability of the observations made by the pairs of operators. We

666 investigated this issue but found no clear relationship imputable to operator inconsistency.

667 Nevertheless, the GINI coefficient clearly increased when more than one pair of operators

668 assessed a given plot. Even though overall assessment quality has recently improved

669 (Ferretti et al., 2014; Meining et al., 2016), it is important to keep in mind that one of the main

670 weaknesses in the ICP monitoring network is operator subjectivity, which can lead to

671 inconsistency among assessments related to different sky conditions, observation years and

672 countries.

673 5. Conclusions

674 Using the machine-learning algorithm Random Forest to identify the response of inter-annual

675 leaf loss or radial growth to biotic and abiotic constraints proved to be effective. The climatic

676 drivers of radial growth we found through this approach are in accordance with previous

677 studies. Several have an effect on both radial growth and crown condition, though previous-

678 year climatic variables tend to control leaf loss while radial growth is more sensitive to

679 current-year climate. There is a common sensitivity to soil water deficit but with different time

680 lags. Primary and secondary growth are related to each other through hydraulic structure or

681 resource partitioning. With regard to its use as an indicator of tree health, leaf loss captured

682 fewer pointer years than did radial growth. Leaf loss only explained a reduction in radial

683 growth in the case of extreme leaf loss events. Furthermore, radial growth, unlike leaf loss,

684 presented a strong common signal among trees, allowing us to study tree response to abiotic

685 factors with more assurance. Radial growth also allowed us to carry out a retrospective

686 analysis of living conditions thanks to more reliable measurements. A rigorous

687 dendrochronological approach including coring to the pith can help to accurately measure the

688 effect of age and is possibly more cost-effective than estimating a poor quality indicator like

689 leaf loss every year. A study comparing our results on beech with other species, including

690 coniferous trees, is underway in order to conclusively assess the performance of annual

691 visual estimations of leaf loss.

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