Temporal trends in tree defoliation and response to multiple biotic and abiotic stresses

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ABSTRACT

The vitality of forests depends on multiple biotic and abiotic stresses that can act in an interactive way. Tree defoliation levels are therefore subject to long-term changes and shorter-term hazards that need to be monitored in the context of ongoing climate change. In this study, we analysed the combined effects of drought, insect attack and tree nutritional status on the level of defoliation in three major hardwood species in Europe: European beech (*Fagus sylvatica*), sessile oak (*Quercus petraea*) and pedunculate oak (*Quercus robur*). The forest condition data set was collected in the long-term intensive monitoring network in France (RENECOFOR). The average level of defoliation observed was 20% but varied considerably between plots and trees. From 1997 to 2015, beech defoliation worsened by 10% while oak defoliation stabilized over time. For the three tree species, crown defoliation was generally higher in the event of insect attack (increased by 2.6% to 7.5% depending on the tree species) and under drought (increased by 5.9%), while the effect of the tree nutritional statue was less consistent (from – 5.6% to +10%) these factors acting synergistically. This study highlights the fact that the different stresses a tree species undergoes act in a complex and interactive way, with species-specific responses. In a context of increasing abiotic and biotic stresses, their combined analysis appears to be a necessity at a time when forest owners need to adapt their management to cope with climate change, particularly through the choice of tree species to be favoured in the future.

KEYWORDS

drought; pest insect; foliar nutrients; die-off; interactions; temperate forest; crown defoliation; ICP Forests; *Fagus sylvatica*; *Quercus robur*; *Quercus petraea*

1.INTRODUCTION

Coping with climate change is a major challenge for forest managers because the longevity of trees limits the capacity for rapid renewal of the species or varieties best adapted to the new abiotic constraints. To adapt existing forests or plan future plantations, they need an integrative vision of the effects of the multiple risks to which forest stands are exposed. Climate change has multiple important and interacting impacts on forests globally (McDowell et al., 2020). Forests are the terrestrial ecosystem that contributes the most to carbon sequestration worldwide (Bonan, 2008; Janssens, 2003; Pacala, 2001; Piao et al., 2009) but global warming could alter drastically functioning, reducing primary productivity and thus carbon sequestration (Lindner et al., 2010). Forest growth is favoured by an increase in CO^2 concentration (Norby et al., 2005; Walker et al., 2019), moderate increase in temperature, and in nitrogen deposition (Myneni, Keeling, Tucker, Asrar, & Nemani, 1997) as far as the other needs in water and nutrients are satisfied. Conversely, above a critical value, an increase in temperature and atmospheric compounds such as ozone, nitrogen and sulfur is expected to be detrimental to forest primary productivity through altered photosynthesis, reduced leaf area and leaf longevity (Ainsworth, Yendrek, Sitch, Collins, & Emberson, 2012; Juknys et al., 2014; Magill et al., 2004; Wittig, Ainsworth, Naidu, Karnosky, & Long, 2009).

However, these long-term trends can be affected by catastrophic events occurring at shorter time scale. Climate change is indeed characterized by an intensification of abiotic (fire, windstorms, drought) and biotic (insects and pathogens) hazards, leading to severe alteration of tree vitality (Seidl et al., 2017). In particular, drought episodes have intensified in severity and frequency (Diffenbaugh et al., 2017) and are predicted to increase further in the future (Lehner et al., 2017; Ruosteenoja, Markkanen, Venäläinen, Räisänen, & Peltola, 2018). This highlights the need to analyse past long-term changes in forest conditions along with short-term variations due to biotic and abiotic perturbations in order to better predict the complex effects of climate change on forest ecosystem productivity and vitality (Matyssek et al., 2012).

Tree growth and defoliation are important indicators of tree vitality (Dobbertin, 2005) since long interruption of tree growth or intense defoliation represent relevant indices of severe decline or imminent death of trees. Numerous studies have documented long-term changes in forest growth as well as biotic and abiotic determinants of tree growth through dendrochronological approaches (Charney et al., 2016; Graumlich, 1991; Piovesan, Biondi, Filippo, Alessandrini, & Maugeri, 2008), but similar studies on tree defoliation are less common as they require long-term monitoring of permanent plots. In Europe, no clear pattern emerged from observation of long-term trend in tree defoliation, the overall mean defoliation remains around 20% and changes in defoliation over time are not significant or show idiosyncratic responses of tree species (Michel, Seidling, Prescher, & editors, 2018) suggesting that local scale might be more relevant to detect anomalies (de la Cruz et al., 2014; Johannes Eichhorn et al., 2005; Ferretti et al., 2014; Popa et al., 2017; Sousa-Silva et al., 2018). Moreover tree defoliation has long been considered a relevant marker of environmental changes due to its sensitivity to abiotic factors such as temperature, precipitation, wind, ozone concentration, soil pH and fertility (Bussotti & Ferretti, 2009; Bussotti, Prancrazi, Matteucci, & Gerosa, 2005; Drobyshev, Anderson, & Sonesson, 2007; Ferretti et al., 2014). Biotic factors such as forest pests (e.g. defoliators), pathogens (e.g. leaf rusts), wild game but also tree competition (e.g. stand density and composition) are also known to cause tree defoliation (Ferretti et al., 2014; Pollastrini et al., 2016). Tree defoliation can thus be used as an integrative marker of multiple interactive stresses (Wim De Vries et al., 2000). It is thus surprising that only few studies investigated the combined and interactive effects of biotic and abiotic stresses on tree defoliation.

Many studies have already reported tree mortalities caused by severe droughts around the world (Allen et al., 2015; N. McDowell et al., 2018; Meir et al., 2018) and this is worsening as climate becomes hotter and drier (van Mantgem et al., 2009). Water stressed trees are also known to be more prone to many pest insects and disease damages (Bréda, Huc, Granier, & Dreyer, 2006; Jactel et al., 2012). Not only drought but also higher temperatures can enhance insect population dynamics (Jactel, Koricheva, & Castagneyrol, 2019), as shown by the largest bark beetle (*Dendroctonus* *ponderosa*) outbreak ever observed in North America (Carroll, Taylor, Régnière, & Safranyik, 2003) after a series of mild winters. Several hundred million m^3 of trees were killed, which transformed the forest ecosystem into a net source of atmospheric carbon (Kurz et al., 2008). Those examples illustrate the fact that multiple biotic and abiotic stresses can cascade or synergize to alter forest vitality.

Tree health is also closely linked to soil fertility, disequilibrium in soil nutrients and atmospheric depositions. Deficit or excess in a particular element may affect tree growth or crown condition. For example, high crown transparency of *Picea abies* has been related to deficiency in foliar potassium (K), nitrogen (N), phosphorus (P) and iron (Fe) nutrients (Ewald, 2005). Fertilization trials showed that adding potassium could increase foliar K concentration and decrease defoliation in young balsam fir (Ouimet & Moore, 2015). Moderate nitrogen atmospheric deposition can exert a fertilising effect, enhancing tree growth and decreasing crown defoliation (Thimonier et al., 2010). Conversely, high nitrogen deposition may cause nitrate leaching (Thimonier et al., 2010) and soil acidification (Flückiger & Braun, 1999) affecting tree health. High level of foliar nitrogen concentration has been associated with increased tree sensitivity to frost, drought, pest and diseases (W De Vries et al., 2014; Flückiger & Braun, 1999). Moreover, the fertilising effect of nitrogen supply can be sustained only if other critical nutrients are not limiting. For example, nitrogen addition along with deficit in phosphorus results in unbalanced N:P ratio (Flückiger & Braun, 1999), which can reduce tree growth (Braun, Thomas, Quiring, & Flückiger, 2010) and increase crown defoliation (Veresoglou et al., 2014). In European forests, high nitrogen deposition are currently associated with unbalanced foliar N:P ratio (W De Vries et al., 2014), which is widely used as marker of nutrition limitation in trees (Güsewell, 2004; Tessier & Raynal, 2003). Deficit or excess in foliar nutrients might thus predispose or amplify climate change effects and biotic damages affecting tree vitality.

Interactions between those multiple driving stress-factors of tree health were rarely tested (but see Seidl et al., 2017), yet studies are accumulating that show tree declines under more stressful conditions. To make a step forward in the understanding of these interactions, we conducted a thorough analysis of tree defoliation data collected during a time series of 18 years in a network of forest monitoring plots (belonging to ICP Forests Level II) in France. Focusing on three major forest species in Europe, European beech (*Fagus sylvatica*), pedunculate oak (*Quercus robur*) and sessile oak (*Quercus petraea*), our main objectives were:

1. to characterize the long-term change in tree defoliation;
2. to investigate the interactive effects of local climate, foliar N:P ratio and insect damage on tree crown defoliation.

2. MATERIAL AND METHODS

2.1 Study sites

Tree health data and forest stand characteristics were retrieved from the database of the RENECOFOR network, which is dedicated to the long-term monitoring of forest vitality in France (Ulrich, 1995). The network was set up in 1992 to cover major European tree species growing in temperate forests of France. In this study, we focused on three broadleaved species: sessile oak (*Quercus petraea*), pedunculate oak (*Quercus robur*) and European beech (*Fagus sylvatica*), because they exhibited more defoliation than coniferous species and they were present in a sufficient number of plots to allow reliable statistical analyses (plots characteristics are summarized in Table 1). The monitoring plots were initially established in healthy and preferably even-aged stands dominated by one main tree species (Ulrich, Vannière, Duplat, Demolis, & Guyon, 1994). In order to have full time series and plots in comparable ecological conditions, we removed from our dataset the plots damaged by the 1999 storms and the beech plots in the few highland sites.

2.2 Defoliation

The defoliation assessments started in 1994 on 52 dominants trees of the main tree species in each plot. Then, every summer (from July 1st to August 31st), trained observers recorded defoliation using classes of 5%, in comparison to a healthy referent tree nearby in the same plot, following ICP Forests manual (Eichhorn et al., 2010). In particular, observers focused on defoliation in the upper and lateral parts of the crown, which were not shaded. Preliminary data analysis revealed for some plots a sharp increase in defoliation from 1994 to 1997. This was attributed to a methodological bias due to a progressive improvement of observers' skills in the early years of the monitoring (Ferretti et al., 2014). We thus decided to analyze tree defoliation from 1997 to 2015. Records from 2003 were missing due to budget shortage.

In addition to defoliation, observers recorded the plausible causes and amount of leaf damage, according to the French Forest Health Department's reference database, in the spring and summer of the same year. Damage assessment protocols have changed over time. For example, the number of possible causes and levels of damages increased with time. To ensure data comparability across time, we decided to base our analyses on the presence/absence of insect damage instead on damage intensity and to focus on the three main causes of damages (see Table A1 for more details on the types of insects causing damage by tree species studied and by year).

To avoid any uncertainty about damage identification (e.g. confusion between insect and fungal pathogen damage on leaves) we defined two categories of trees: those with the "presence of insect damage" when at least one insect damage was reported in the absence of any other type of damage and those with "absence of pest damage" when tree did not present any type of damage or presented only traces of damage (Table 1).

2.3 Foliar nutrient analyses

We characterized the nutritional status of trees by considering two major limiting nutrients for tree growth in French forests: nitrogen (N) and phosphorus (P) and their ratio N:P (Table 1). Reference thresholds for tree foliar nutrients in Europe (Mellert & Göttlein, 2012) were used to define the balanced or unbalanced foliar nutrient status of a tree (Table 1). The lower threshold for foliar N:P ratio was calculated using the lowest threshold of foliar N content and the highest threshold of foliar

P content, the upper threshold for foliar N:P ratio was derived from the highest threshold of foliar N content and the lowest threshold of foliar P content. The nutritional status of trees was assessed every second year in all plots. Mature leaves in full sun were sampled in summer on a minimum of 5 dominant or sub-dominant trees in the immediate vicinity of the plot (Rautio, Fürst, Stefan, Raitio, & Bartels, 2010). Leaves were then dried at 70°C for 24h and ground for chemical analyses. We used a linear interpolation to approximate nitrogen and phosphorus values in the alternate years (when leaves were not sampled).

Table 1

Overview of stand and tree characteristics and range of ecological conditions in the selected plots for pedunculate oak (*Quercus robur*), sessile oak (*Quercus petraea*) and European beech (*Fagus sylvatica*) from 1997 to 2015: average, minimum and maximum values (in brackets) are specified.

		Pedunculate oak	Sessile oak	European beech
Nb. of plots		9	18	12
Plot basal area (m^2/ha)		18 (7.4-26)	21 (5.8-29)	21 (8.4-36)
Stand age in 2015		93 (55-154)	114 (75-159)	92 (61-128)
Species Phenology	budburst	21 april (24 feb.-27 may)	20 april (29 mar.-14 juil.)	29 april (8 apr.-25 may)
	leaf yellowing	23 oct. (23 sep.-11 dec.)	25 oct. (21 sep.-2 dec.)	20 oct. (15 aug.-2 dec.)
Nb. of observed trees		506	1019	671
Tree defoliation (%)		26 (0-100)	23 (0-100)	21 (0-95)
Occurrence of presence/absence of insect damage	absence	2849	7831	5259
	presence	1242	1998	1067
Foliar N: P ratio		21 (14-36)	22 (14-33)	24 (16-33)
Nutritional status (% of obs.)	intermediate	49	34	20
	high	51	66	80
Altitude (m)		188 (20-370)	208 (80-330)	286 (50-700)
Annual temperature (°C)		11.4 (9.4-14.0)	11.2 (9.3-13.4)	10.8 (8.8-13.9)
Annual precipitation (mm)		876 (497-1641)	802 (435-1315)	960 (502-1765)
Standardized Precipitation-Evapotranspiration Index		0.76 (-4-5.5)	0.71 (-4.9-5.9)	0.77 (-3.9-5.4)

2.4 Drought index

We estimated drought intensity by using the Standardized Precipitation-Evaporation Index (SPEI) (Vicente-Serrano, Beguería, & López-Moreno, 2010). It is extensively used because it can be compared across locations and aggregated at different time scales. Time series of SPEI were calculated on a monthly basis using the difference between the sum of precipitations and the potential evapotranspiration. Precipitations and potential evapotranspiration were obtained from the SAFRAN model of METEO FRANCE at a daily time step for every sampled plot from 1997 to 2015. Potential evapotranspiration was estimated using the Penman-Monteith method according to FAO recommendations (Smith, 1995).

We estimated drought intensity for two distinct periods corresponding to the previous year and the year of defoliation assessment, respectively. We calculated SPEI of the previous year on a timescale of 6 months from May to October, to match with the period of broadleaved tree growth. The length of tree growth period was estimated using leaf phenology of the 36 dominants trees, every year on every plot. We used the date at which budburst occurred in at least 90% of dominants trees as the start of the growth period and the date at which 90% of dominants trees were yellowing as the end of the growth period (Table 1). We calculated SPEI of the year of defoliation assessment on a timescale of 3 months (May to July). July is the month at the end of which most of the plots have been visited for defoliation assessment. Finally, to account for the drought experienced by trees during both the previous year and the year of defoliation assessment, we averaged the two values of SPEI. To facilitate the interpretation of analyses outcomes, we used minus SPEI ('– SPEI') instead of 'SPEI' as drought index, so that a high and positive value of SPEI indicates an intense drought (Table 1).

2.5 Plot Basal Area

A complete dendrometric inventory of all trees with a diameter at breast height (DBH) above 5 cm within the inner part of the plots (0.5 ha) was made every 5 years as well as before and after logging.

Species identity, dominance status and circumference at 1.30 m were recorded for each tree. We then used the basal area (m^2/ha) of all dominant trees as an index of stand density (Table 1). Missing values (during the 4 years period in between two inventories) were interpolated assuming a linear increase in basal area with time.

2.6 Statistical analyses

Statistical analyses were performed with R 3.4.3. We used the log-transformed median of the 5% class of defoliation to normalize the model residuals. The biotic and abiotic determinants of crown defoliation were investigated with a Linear Mixed-Effects Models (function lme package nlme). We considered the nested sampling design and the repeated measurements of trees over time by using a random effect of trees nested in plots. Residual variance was modelled with a power function of fitted values and an autoregressive moving average process estimating the residual temporal autocorrelation (Pinheiro & Bates, 2006). We investigated the long-term temporal trend in tree defoliation by introducing a quadratic effect of the calendar year. Moreover, we tested the interactions between stress drivers by including into the models two-way interactions between drought index, foliar N:P ratio and presence/absence of insect damage. We measured model quality by calculating the root mean square error (RMSE), which is based on the difference between predicted and observed values (Janssen & Heuberger, 1995). We thus fitted the following model for each tree species:

$$\ln(DEF_{i,j}) = \beta_0 + b_{0,i} + b_{0,i,j} + \beta_1 \times YEAR + \beta_2 \times YEAR^2 + \beta_3 \times G + \beta_4 \times INSECT + \beta_5 \times DROUGHT + \beta_6 \times N{:}P + \beta_7 \times INSECT \times DROUGHT + \beta_8 \times INSECT \times N{:}P + \beta_9 \times DROUGHT \times N{:}P + \varepsilon_{i,j}$$

$$b_{0,i} \sim \mathcal{N}(0,\sigma_1^2)\ ;\ b_{0,i,j} \sim \mathcal{N}(0,\sigma_2^2)\ ;\ \varepsilon_{i,j} \sim \mathcal{N}(0,\sigma^2)$$

Where DEF is the median level of defoliation classes (in %) of tree i in plot j; $\beta_{0:9}$ are model parameters for the effects of time (YEAR), stand density (G in m^2/ha), presence/absence of insect damage (INSECT), drought intensity (DROUGHT) and foliar N:P ratio and their interactions two by two; $b_{0,i}$ is the plot random effect and $b_{0,i,j}$ is the tree random effect.

We eventually applied a correction factor when we back-transformed the values fitted by the model in the logarithmic scale to avoid the systematic underestimation of crown defoliation inherent to the log transformation (Chave et al., 2014; Finney, 1941; Shen & Zhu, 2008):

$$\widehat{DEF} = \exp(\widehat{\log(DEF)} + CF)$$

Where $\widehat{DEF}$ is the average crown defoliation that is predicted by the model; $\widehat{\log(DEF)}$ is the average log-transformed value of crown defoliation that is predicted by the model and CF is the correction factor:

$$CF = \frac{RSE^2}{2}$$

Where RSE is the residual square error.

3 RESULTS

The mean level of defoliation observed was 20%, but the standard deviations associated with random effects in the models indicated important inter-plot and inter-individual variability (Table 2).

3.1 Effect of stand density on tree defoliation

Crown defoliation of European beech and pedunculate oak increased significantly (Table 2) with plot basal area (tree density) respectively by 0.4% and 0.3% per m^2/ha, whereas it decreased significantly by 0.4% per m^2/ha in sessile oak.

3.2 Long term changes in tree defoliation

The three tree species exhibited contrasting temporal trends of tree defoliation over the period 1997-2015 (Table 2, Fig. 1). European beech defoliation increased significantly all along the period

(Fig. 1) at a rate of 0.5 % per year. Long-term changes in sessile oak defoliation exhibited a humped shape with an increase from 1997 to 2008 followed by a slight decrease in defoliation from 2008 to 2015. Defoliation of the pedunculate oak showed an opposite trend with a gradual decrease until 2011.

3.3 Tree defoliation in presence/absence of insect damage

Trees damaged by pest insects were significantly more defoliated than trees not damaged by insects in the three species (Table 2), at an average value of drought index and foliar N:P nutrient content. The increase of crown defoliation due to insect damage was of 7.5 % in European beech, 4.7% in sessile oak and 2.6% in pedunculate oak, as estimated by models.

3.4 Interaction between insect damage and drought

For European beech, crown defoliation was significantly aggravated by drought, but only in trees damaged by pest insects (Table 2, Fig. 2), i.e. significant drought x insect interaction (estimate=-0.08 ± 0.03; P=0.01). Tree defoliation increased by 5.9% from very wet (drought index =-1.5) to very dry (drought index = 1.5) conditions in trees damaged by insects, as estimated by the model.

Regarding sessile and pedunculate oak, the aggravation of crown defoliation was similar in the presence and in the absence of insect damage ($P > 0.05$, Table 2, Fig.2) and was in average of 2.9% for sessile oak and 3.4% for pedunculate oak between very wet (drought index =-1.5) and very dry (drought index = 1.5) conditions.

3.5 Interaction between insect damage and foliar N: P ratio

Crown defoliation of European beech increased with higher foliar N:P ratio in trees that were not damaged by insects (Table 2). The variation in tree defoliation estimated by the model was of +10% between low (16) to high (33) level of foliar N:P ratio (Fig. 3). Conversely, the slope of the relationship between defoliation and foliar N:P ratio was not significantly different from zero for

European beech trees damaged by insects, i.e. significant interaction N:P x insect (estimate=-0.045±0.006; P<0.001).

In sessile oak, the effect of foliar N:P ratio was not significant in trees that were not damaged by insects but was negative in trees with an insect damage (-3.5% between low (16) and high (33) level of foliar N:P ratio Table 2), i.e. significant N:P x insect interaction (estimate=-0.007±0.004; P=0.04).

The trends were more pronounced in pedunculate oak: crown defoliation decreased significantly with higher values of foliar N:P ratio with a steeper slope in trees damaged by insects than in trees not damage by insects (-5.6 % for tree damage by insect and -2.6% between low (16) and high (33) level of foliar N:P ratio), i.e. significant N:P x Insect interaction (estimate=-0.008±0.004; P=0.03).

3.6 Interaction between drought and foliar N: P ratio

In pedunculate oak, there was a significant interaction between drought and foliar N:P ratio (estimate=-0.008±0.002; P<0.001, Table 2). Trees were more defoliated under dryer conditions and at lower levels of foliar N:P ratio (Fig. 4). The interaction between drought and foliar N:P ratio was not significant in European beech and sessile oak (P>0.05).

Table 2

Summary of the effects of year, stand density (Basal area), presence/absence of insect damage, drought index and foliar N:P ratio on crown defoliation (log transformed) at the tree level in European beech (*Fagus sylvatica*), sessile oak (*Quercus petraea*) and pedunculate oak (*Quercus robur*). Model estimates (*est.*) are given with associated standard deviation (*sd*) and p-values (*pval*). Significant effects (*pval*<0.05) are in bold. Random effects (*sd*) correspond to the standard deviation of the random effect at the plot level and the random effect of trees nested within plots, RMSE corresponds to the root mean square error of the linear mixed models.

Species	Fixed effects											Random effects (*sd*)		
	Year	Year^2	Basal area	Insect damage	Drought and Insect damage		Drought x Insect damage	Foliar N: P ratio and Insect damage		Foliar N: P ratio x Insect damage	Drought X Foliar N:P ratio	Plot	Tree	
					Absence	Presence	Δ Abs .- Pre.	Absence	Presence	Δ Abs. - Pre.				RMSE
European beech												0.68	0.000090	0.8
est.	**0.042**	-0.00024	**0.025**	**0.43**	0.012	**0.093**	**0.080**	**0.041**	-0.0046	**-0.045**	0.0045			
sd	**0.009**	0.00040	**0.005**	**0.03**	0.013	**0.029**	**0.032**	**0.0039**	0.0064	**0.006**	0.0028			
pval	**<0.001**	0.56	**<0.001**	**<0.001**	0.35	**0.002**	**0.012**	**<0.001**	0.47	**<0.001**	0.11			
Sessile oak												0.42	0.28	0.63
est.	**0.069**	**-0.0028**	**-0.019**	**0.22**	**0.059**	**0.037**	-0.023	-0.0019	**-0.009**	**-0.0070**	-0.0020			
sd	**0.0057**	**0.0003**	**0.003**	**0.016**	**0.0083**	**0.014**	0.016	0.0034	**0.005**	**0.0035**	0.0019			
pval	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.007**	0.16	0.56	**0.048**	**0.044**	0.29			
Pedunculate oak												0.28	0.27	0.51
est.	**-0.038**	**0.0012**	**0.014**	**0.14**	**0.077**	**0.045**	-0.032	**-0.0092**	**-0.018**	**-0.0083**	**-0.0076**			
sd	**0.006**	**0.0003**	**0.005**	**0.02**	**0.011**	**0.018**	0.021	**0.0035**	**0.005**	**0.0039**	**0.0022**			
pval	**<0.001**	**<0.001**	**0.0012**	**<0.001**	**<0.001**	**0.011**	0.13	**0.0087**	**<0.001**	**0.032**	**<0.001**			

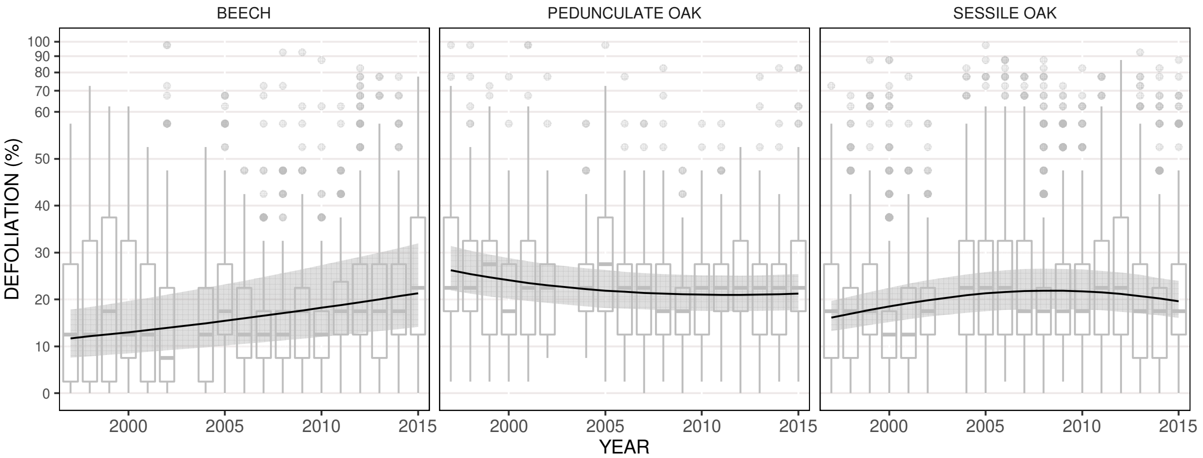

Fig. 1. Temporal change in percentage of defoliation from 1997 to 2015 in European beech, sessile oak and pedunculate oak. Boxplots represent the distribution of raw data. Solid lines represent the crown defoliation of a tree predicted by models after a back-transformation of the logarithmic values at an average level of stand density, N:P ratio and drought index. Shaded areas represent the confidence intervals at 95%

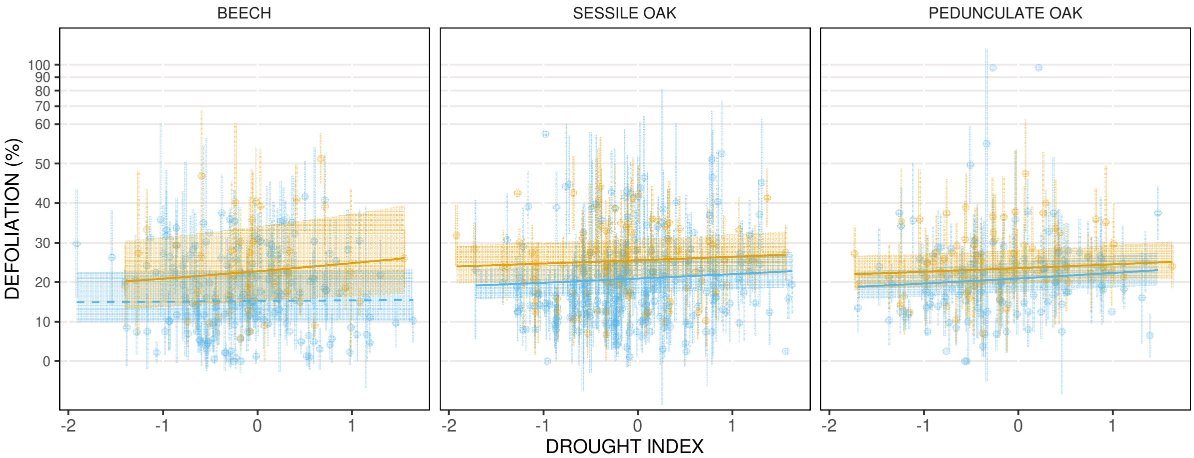

Fig. 2. Effect of drought index on crown defoliation in European beech, sessile oak and pedunculated oak in absence (blue) and presence (yellow) of insect damage. The raw data are represented by an average value of crown defoliation by plot (dots) and its standard deviation (vertical lines). Solid lines represent the crown defoliation of a tree predicted by the models after a back-transformation of the logarithmic values at an average value of stand density, N: P ratio and for a median year (2006). The line patterns indicate whether the slope of the relationship was significant (solid line) or not (dashed line). Shaded areas represent the confidence intervals to the regression lines at 95%

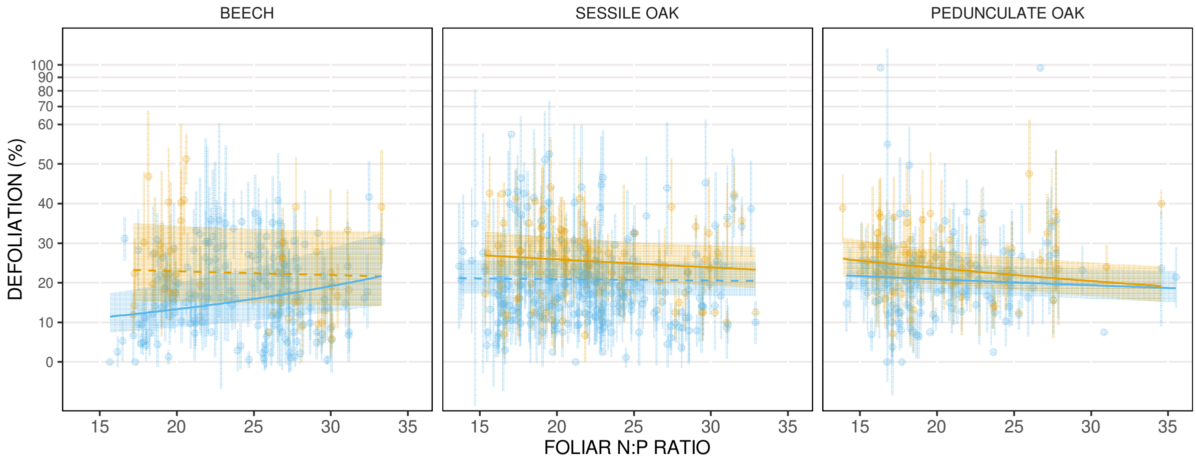

Fig. 3. Effect of foliar N: P ratio on crown defoliation in European beech, sessile oak and pedunculated oak in absence (blue) and presence (yellow) of insect damage. The raw data are represented by an average value of crown defoliation by plot (dots) and its standard deviation (vertical lines). Solid lines represent the crown defoliation of a tree predicted by the models after a back-transformation of the logarithmic values at an average value of stand density, drought index and for a median year (2006). The line patterns indicate whether the slope of the relationship was significant (solid line) or not (dashed line); Shaded areas represent the confidence intervals to the regression lines at 95%

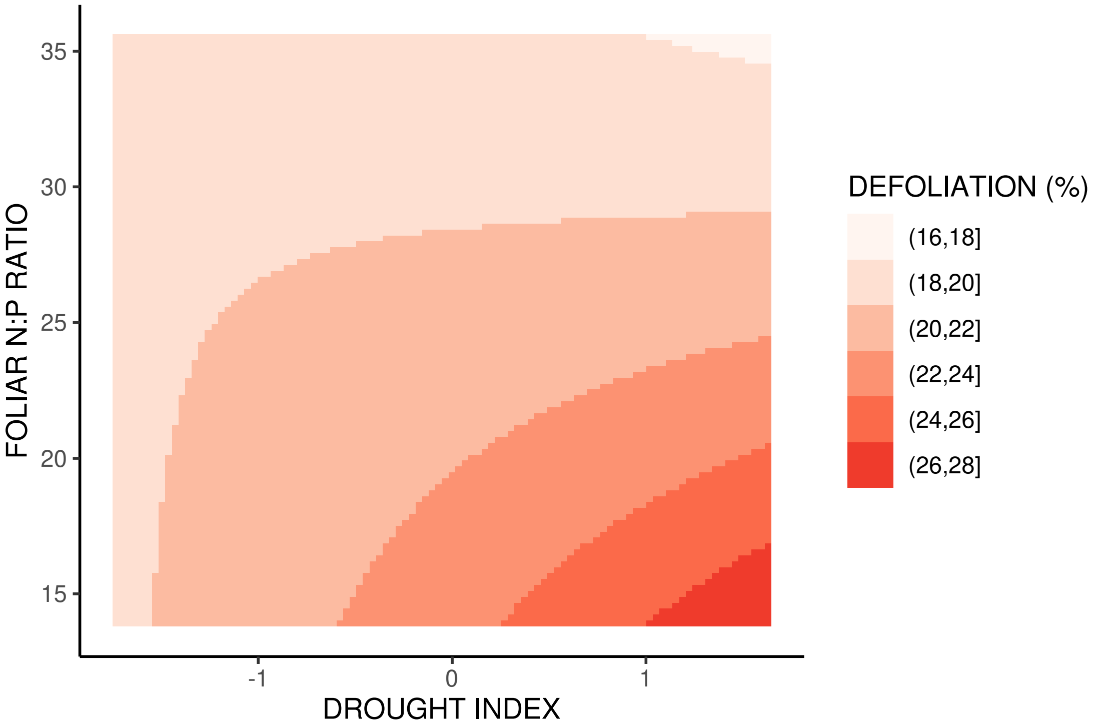

Fig. 4. Interacting effect of foliar N:P ratio and drought intensity on defoliation in pedunculate oak (values back transformed). Defoliation levels have been divided into 2% interval categories including the lowest value of the interval but not the highest value.

4 DISCUSSION

Long-term changes in defoliation that have been observed at the European scale are low or non-existent for European beech and temperate hardwood oaks (Michel et al., 2018). However, in France, until the end of the 2000s, oaks and beeches seemed to show an increase in defoliation (Ferretti et al., 2014). Despite a high variability between plots and between trees, our study updated the trends at the French level and confirmed the increase in beech defoliation. We also showed a stabilization of defoliation for both oaks more in line with what was observed at the European level. Furthermore, we found that tree defoliation was in general exacerbated by the presence of insect damage and drought events. The effect of the tree nutritional status was more species specific. Interestingly, we also detected interactive effects between these factors, which lead to additive or synergistic effects of stresses for most tree species.

4.1 Long term change in tree defoliation

We found a long-term trend of declining crown condition in European beech forests, as tree defoliation was consistently increasing with time. This is consistent with a previous study conducted in the same forest monitoring network in France (Ferretti et al., 2014), which reported a similar increase during the period 1997-2009. Recently, Sousa-Silva et al. (2018) observed a similar pattern in Belgian forests from 1997 to 2015 and suggested that the decline in European beech condition was related to a progressive increase in drought intensity over time. European beech is a species well known for its high susceptibility to dry conditions (Rubio-Cuadrado et al., 2018) with strong negative correlations between drought intensity and growth loss (Farahat & Linderholm, 2018; Lebourgeois, Bréda, Ulrich, & Granier, 2005; Seynave, Gégout, Hervé, & Dhôte, 2008) and most species distribution models have predicted European beech decline in the future under dryer conditions (e.g. Saltré, Duputié, Gaucherel, & Chuine, 2015).

The temporal pattern was quite different in oak species. Sessile oak exhibited a deterioration trend approximatively until 2007, which was followed by a period of slight recovery, while pedunculate oak showed a general trend for a slow crown condition improvement. Oak species are more drought tolerant than European beech (Rubio-Cuadrado et al., 2018). It is thus possible that in the recent years, from 2007 onward, precipitations were below the tolerance threshold of European beech but above the tolerance thresholds of oaks. Higher CO2 concentration causes an increase in carbohydrates and a reduction in N, thus increasing C:N ratio which is unfavorable to leaf feeders. It can also enhance C-based tree defenses against defoliating herbivores (Robinson, Ryan, & Newman, 2012) and particularly against gypsy moth, a common oak defoliator (Foss, Mattson, & Trier, 2013). The lack of degradation, or even the slight improvement, in oak crown conditions might thus be due to positive effects of CO2 enrichment on tree growth and defense against leaf feeders counterbalancing negative effects of droughts on tree health.

4.2 Effects of Intraspecific competition, insect damage, drought and foliar N:P

High tree density emerged as a cause of defoliation in all three species, probably due to increased competition for canopy space (Getzin et al., 2008; Hajek et al., 2015). Competing trees may also be more prone to pest attacks, due to trade-offs between growth and defenses (Huang et al., 2019). This calls for new studies targeting the effect of forest thinning on resistance to multiple stresses (Jactel et al., 2009).

Tree defoliation usually increases with summer drought of the current year (Seidling, 2007) because leaf abscission allows avoiding disruption of sap flow flux and xylem cavitation (Bréda et al., 2006). Defoliation can also arise from lagged effect of previous summer drought (Seidling, 2007), which can affect carbohydrates reserves and bud viability (Bréda et al., 2006).

The negative effect of foliar N:P ratio on tree defoliation did not exhibit a consistent pattern among the studied tree species contrary to what was observed at the European scale. Veresoglou et al. (2014) found a segmented response of tree defoliation to foliar N:P, with a positive relationship between nutrient content and defoliation beyond the breaking point of 14.8 in broadleaved species (corresponding to the minimum level of the foliar N:P ratio observed in our study). We found such a positive correlation (higher defoliation at higher level of N:P ratio, *i.e.* high level of N and low level of P) only for European beech not damaged by insect. European beech covered a larger range of N:P ratio than oak species for which approximatively 80% of the observations belong to the intermediate group. The increase in defoliation observed in European beech may thus arise from the fact that European beech occurs in sites with a stronger nutritional imbalance of N and P than oaks.

In all three species, insect damaged trees exhibited significantly higher defoliation than non-attacked trees, which confirms the significant impact of insect feeding on crown condition (Kozlov, Lanta, Zverev, & Zvereva, 2015). We found a higher sensitivity of sessile oak than pedunculate oak to insect attack, which is consistent with recent findings on the sensitivity of sessile oak to the oak processionary moth (Damestoy et al., 2020). From a management point of view, the sessile oak appears be more resistant to drought events than the pedunculate oak, suggesting that sessile oak should be favored to adapt oak forests to climate change. However, this choice could be made at the cost of making oak stands more vulnerable to attack by defoliators. This trade-off calls for caution when choosing to favor one tree species over another in a substitution logic and suggests that mixing tree species would be a more effective long-term strategy for dealing with multiple risks (Jactel et al., 2017; Sousa-Silva et al., 2018). Both beech and oak species can be infested by many insect defoliators, with for example 41 species of Lepidoptera associated with European beech and 189 with pedunculate oak and sessile oak in Britain (Kennedy & Southwood, 1984). In addition, it has been demonstrated that insect damage can accelerate leaf abscission, thus explaining higher defoliation recorded in early summer on insect damaged trees (Zvereva & Kozlov, 2014).

4.3 Interactions between pest damages, drought and foliar N: P ratio

In all tree species, we could observe significantly higher damage (defoliation) in trees that were both attacked by insects and under drought conditions. Interestingly, in our study, we found that the combined effects of drought and insect attack were additive for oaks but synergistic for European beech (Fig. 2). This suggests that, in oak trees, insect damages and drought cumulated their effect on tree defoliation whereas, in beech trees, insect damages increased with water stress intensity. This is consistent with the general pattern of higher forest insect damage following droughts (Ferretti et al., 2014; Logan, Regniere, & Powell, 2003; Rouault et al., 2006; Toïgo, Barraquand, Barnagaud, Piou, & Jactel, 2017) and more particularly the higher susceptibility of water stressed trees to defoliating insects (Jactel et al., 2012). The direct effect of drought on forest insect herbivores, e.g. on survival and fecundity, lacks experimental evidence (Jactel et al., 2019). By contrast, it is well known that drought can indirectly benefit forest defoliators through improved host plant quality (e.g. higher nitrogen content (Jactel et al., 2012)) or reduced plant resistance (Castagneyrol, Jactel, et al., 2018; Holopainen et al., 2018). It would now be necessary to better identify the species of defoliating insects attacking oaks on the one hand and beeches on the other hand to understand why the synergy between drought and insect attacks was only observed in the case of European beech.

We also showed cumulative, negative effects of pest damage and low N:P ratio on all tree species. This confirms that nutrient imbalance has to be considered when searching the causes of tree crown decline. One possible explanation for the combined effect of pest feeding and low N:P is that insect herbivory is higher on leaf with low N content as more leaf tissue have to be consumed to meet the nutritional requirement of insect herbivores (i.e. compensatory feeding, (Castagneyrol, Moreira, et al., 2018)). In one species, beech, we detected a synergistic effect of insect damage and low N:P leaf ratio, with no effect of nutrient imbalance in undamaged trees and large defoliation increase with increasing N:P in damage trees. This might be due to specific nutrient requirements of *Orchestes fagi*, the main insect defoliator of European beech in our sample.

4.4 PERSPECTIVES AND LIMITATIONS

Our study has several limitations. Tree crown conditions, and in particular level of defoliation, are difficult to estimate accurately. However, observers involved in ICP forests network were trained each year with inter-calibration workshops. In addition, a selection of plots (16 out of 102) between 2001-2005 and 2008-2009 was controlled to assess the quality of the observations of crown defoliation (Ferretti et al., 2014). The observation bias (the difference in score between the field team and the control team) was between ± 5% for 76% of the defoliation scores and ± 10% for 92% of them. This confirms the reliability of crown defoliation score attributed on the field. In addition, we focused on the three tree species with largest sample size and only retained trees for which all necessary data were available. We therefore believe that our results on long-term trend and explanatory factors are conservative. More problematic is the lack of precise information on the insect species that made the observed leaf damage. This would have required collecting branches and assessing a sample of leaves, which is technically and economically difficult. Nevertheless, a more focused long-term study on a few well-known and easily monitored insect defoliators would provide more insights into physiological processed involved in drought, nutrient imbalance and pest damage. Likewise, other potential interactive drivers of crown conditions like storm, air pollution or presence of mycorrhizae would be worth considering.

5 CONCLUSIONS

Our findings confirm the gradual worsening of crown condition in European beech and the stabilization in oaks, which has been observed at the European scale, suggesting species-specific response to ongoing climate changes. They also demonstrate that events of crown defoliation result from the complex interplay between biotic and abiotic stresses, which are more or less relevant to particular tree species. In particular, insect attacks deteriorated crown condition, especially after dry periods for the three broadleaved species while the effect of imbalanced nutritional status was less consistent among tree species. More importantly, we showed that these stress factors generally act synergistically. It therefore seems important for the adaptive management of forests to address issues related to forest conditions in an integrative way, especially in a context where biotic and abiotic hazards are likely to intensify. Long-term monitoring of forest condition remains more useful than ever, but it should be accompanied by a more accurate analysis of the causes of decline, in order to better predict future trends and better adapt forests to future threats.

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