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

Maude Toïgo, Manuel Nicolas, Mathieu Jonard, Luc Croisé, Louis-Michel Nageleisen, Hervé Jactel

HAL Id: hal-03179773

https://hal.inrae.fr/hal-03179773

Submitted on 25 Aug 2022

1   # Title: Temporal trends in tree defoliation and response to
2   multiple biotic and abiotic stresses

3

4   Toigo Maude[a,b], Nicolas Manuel[c], Jonard Mathieu[d], Luc Croisé[c], Nageleisen Louis-Michel[e] ,Jactel
5   Hervé[a]

6

7   [a] INRAE, University of Bordeaux, BIOGECO, F-33610 Cestas, France
8
9   b CEFE UMR 5175, CNRS – Université de Montpellier – Université Paul-Valéry Montpellier – EPHE, 1919 Route
10   de Mende, F-34293 Montpellier, France
11   [c] Office National Des Forêts, Département Recherche et Développement, Boulevard de Constance, F-77300
12   Fontainebleau
13   [d] Université catholique de Louvain, Earth and Life Institute, Croix du Sud 2, L7.05.09, 1348 Louvain-la-Neuve,
14   Belgium
15   [e] Département de la santé des forêts UMR 1434 SILVA (Université de Lorraine, AgroParisTech, Inra) Centre Inra
16   Grand Est 45280 Champenoux

17

18   Corresponding author

19   Toigo Maude, CEFE UMR 5175, CNRS – Université de Montpellier – Université Paul-Valéry Montpellier – EPHE,
20   1919 Route de Mende, F-34293 Montpellier, France

21   Telephone: 067998283

22   Email: maude.toigo@cefe.cnrs.fr

23

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

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).

71   Tree growth and defoliation are important indicators of tree vitality (Dobbertin, 2005) since

72   long interruption of tree growth or intense defoliation represent relevant indices of severe decline or

73   imminent death of trees. Numerous studies have documented long-term changes in forest growth as

74   well as biotic and abiotic determinants of tree growth through dendrochronological approaches

75   (Charney et al., 2016; Graumlich, 1991; Piovesan, Biondi, Filippo, Alessandrini, & Maugeri, 2008), but

76   similar studies on tree defoliation are less common as they require long-term monitoring of

77   permanent plots. In Europe, no clear pattern emerged from observation of long-term trend in tree

78   defoliation, the overall mean defoliation remains around 20% and changes in defoliation over time

79   are not significant or show idiosyncratic responses of tree species (Michel, Seidling, Prescher, &

80   editors, 2018) suggesting that local scale might be more relevant to detect anomalies (de la Cruz et

81   al., 2014; Johannes Eichhorn et al., 2005; Ferretti et al., 2014; Popa et al., 2017; Sousa-Silva et al.,

82   2018). Moreover tree defoliation has long been considered a relevant marker of environmental

83   changes due to its sensitivity to abiotic factors such as temperature, precipitation, wind, ozone

84   concentration, soil pH and fertility (Bussotti & Ferretti, 2009; Bussotti, Prancrazi, Matteucci, &

85   Gerosa, 2005; Drobyshev, Anderson, & Sonesson, 2007; Ferretti et al., 2014). Biotic factors such as

86   forest pests (e.g. defoliators), pathogens (e.g. leaf rusts), wild game but also tree competition (e.g.

87   stand density and composition) are also known to cause tree defoliation (Ferretti et al., 2014;

88   Pollastrini et al., 2016). Tree defoliation can thus be used as an integrative marker of multiple

89   interactive stresses (Wim De Vries et al., 2000). It is thus surprising that only few studies investigated

90   the combined and interactive effects of biotic and abiotic stresses on tree defoliation.

91   Many studies have already reported tree mortalities caused by severe droughts around the

92   world (Allen et al., 2015; N. McDowell et al., 2018; Meir et al., 2018) and this is worsening as climate

93   becomes hotter and drier (van Mantgem et al., 2009). Water stressed trees are also known to be

94   more prone to many pest insects and disease damages (Bréda, Huc, Granier, & Dreyer, 2006; Jactel et

95   al., 2012). Not only drought but also higher temperatures can enhance insect population dynamics

96   (Jactel, Koricheva, & Castagneyrol, 2019), as shown by the largest bark beetle (*Dendroctonus*

97   *ponderosa*) outbreak ever observed in North America (Carroll, Taylor, Régnière, & Safranyik, 2003)

98   after a series of mild winters. Several hundred million m^3 of trees were killed, which transformed the

99   forest ecosystem into a net source of atmospheric carbon (Kurz et al., 2008). Those examples

100 illustrate the fact that multiple biotic and abiotic stresses can cascade or synergize to alter forest

101 vitality.

102   Tree health is also closely linked to soil fertility, disequilibrium in soil nutrients and

103 atmospheric depositions. Deficit or excess in a particular element may affect tree growth or crown

104 condition. For example, high crown transparency of *Picea abies* has been related to deficiency in

105 foliar potassium (K), nitrogen (N), phosphorus (P) and iron (Fe) nutrients (Ewald, 2005). Fertilization

106 trials showed that adding potassium could increase foliar K concentration and decrease defoliation in

107 young balsam fir (Ouimet & Moore, 2015). Moderate nitrogen atmospheric deposition can exert a

108 fertilising effect, enhancing tree growth and decreasing crown defoliation (Thimonier et al., 2010).

109 Conversely, high nitrogen deposition may cause nitrate leaching (Thimonier et al., 2010) and soil

110 acidification (Flückiger & Braun, 1999) affecting tree health. High level of foliar nitrogen

111 concentration has been associated with increased tree sensitivity to frost, drought, pest and diseases

112 (W De Vries et al., 2014; Flückiger & Braun, 1999). Moreover, the fertilising effect of nitrogen supply

113 can be sustained only if other critical nutrients are not limiting. For example, nitrogen addition along

114 with deficit in phosphorus results in unbalanced N:P ratio (Flückiger & Braun, 1999), which can

115 reduce tree growth (Braun, Thomas, Quiring, & Flückiger, 2010) and increase crown defoliation

116 (Veresoglou et al., 2014). In European forests, high nitrogen deposition are currently associated with

117 unbalanced foliar N:P ratio (W De Vries et al., 2014), which is widely used as marker of nutrition

118 limitation in trees (Güsewell, 2004; Tessier & Raynal, 2003). Deficit or excess in foliar nutrients might

119 thus predispose or amplify climate change effects and biotic damages affecting tree vitality.

120   Interactions between those multiple driving stress-factors of tree health were rarely tested

121 (but see Seidl et al., 2017), yet studies are accumulating that show tree declines under more stressful

122 conditions. To make a step forward in the understanding of these interactions, we conducted a

123   thorough analysis of tree defoliation data collected during a time series of 18 years in a network of

124   forest monitoring plots (belonging to ICP Forests Level II) in France. Focusing on three major forest

125   species in Europe, European beech (*Fagus sylvatica*), pedunculate oak (*Quercus robur*) and sessile

126   oak (*Quercus petraea*), our main objectives were:

127   1.   to characterize the long-term change in tree defoliation;

128   2.   to investigate the interactive effects of local climate, foliar N:P ratio and insect damage on tree

129   crown defoliation.

130   # 2. MATERIAL AND METHODS

131   ## 2.1 Study sites

132   Tree health data and forest stand characteristics were retrieved from the database of the

133   RENECOFOR network, which is dedicated to the long-term monitoring of forest vitality in France

134   (Ulrich, 1995). The network was set up in 1992 to cover major European tree species growing in

135   temperate forests of France. In this study, we focused on three broadleaved species: sessile oak

136   (*Quercus petraea*), pedunculate oak (*Quercus robur*) and European beech (*Fagus sylvatica*), because

137   they exhibited more defoliation than coniferous species and they were present in a sufficient number

138   of plots to allow reliable statistical analyses (plots characteristics are summarized in Table 1). The

139   monitoring plots were initially established in healthy and preferably even-aged stands dominated by

140   one main tree species (Ulrich, Vannière, Duplat, Demolis, & Guyon, 1994). In order to have full time

141   series and plots in comparable ecological conditions, we removed from our dataset the plots

142   damaged by the 1999 storms and the beech plots in the few highland sites.

143   ## 2.2 Defoliation

144   The defoliation assessments started in 1994 on 52 dominants trees of the main tree species in each

145   plot. Then, every summer (from July 1st to August 31st), trained observers recorded defoliation using

146 classes of 5%, in comparison to a healthy referent tree nearby in the same plot, following ICP Forests

147 manual (Eichhorn et al., 2010). In particular, observers focused on defoliation in the upper and lateral

148 parts of the crown, which were not shaded. Preliminary data analysis revealed for some plots a sharp

149 increase in defoliation from 1994 to 1997. This was attributed to a methodological bias due to a

150 progressive improvement of observers' skills in the early years of the monitoring (Ferretti et al.,

151 2014). We thus decided to analyze tree defoliation from 1997 to 2015. Records from 2003 were

152 missing due to budget shortage.

153 In addition to defoliation, observers recorded the plausible causes and amount of leaf damage,

154 according to the French Forest Health Department's reference database, in the spring and summer of

155 the same year. Damage assessment protocols have changed over time. For example, the number of

156 possible causes and levels of damages increased with time. To ensure data comparability across time,

157 we decided to base our analyses on the presence/absence of insect damage instead on damage

158 intensity and to focus on the three main causes of damages (see Table A1 for more details on the

159 types of insects causing damage by tree species studied and by year).

160 To avoid any uncertainty about damage identification (e.g. confusion between insect and fungal

161 pathogen damage on leaves) we defined two categories of trees: those with the "presence of insect

162 damage" when at least one insect damage was reported in the absence of any other type of damage

163 and those with "absence of pest damage" when tree did not present any type of damage or

164 presented only traces of damage (Table 1).

2.3 Foliar nutrient analyses

166 We characterized the nutritional status of trees by considering two major limiting nutrients for tree

167 growth in French forests: nitrogen (N) and phosphorus (P) and their ratio N:P (Table 1). Reference

168 thresholds for tree foliar nutrients in Europe (Mellert & Göttlein, 2012) were used to define the

169 balanced or unbalanced foliar nutrient status of a tree (Table 1). The lower threshold for foliar N:P

170 ratio was calculated using the lowest threshold of foliar N content and the highest threshold of foliar

171   P content, the upper threshold for foliar N:P ratio was derived from the highest threshold of foliar N

172   content and the lowest threshold of foliar P content. The nutritional status of trees was assessed

173   every second year in all plots. Mature leaves in full sun were sampled in summer on a minimum of 5

174   dominant or sub-dominant trees in the immediate vicinity of the plot (Rautio, Fürst, Stefan, Raitio, &

175   Bartels, 2010). Leaves were then dried at 70°C for 24h and ground for chemical analyses. We used a

176   linear interpolation to approximate nitrogen and phosphorus values in the alternate years (when

177   leaves were not sampled).

178

179   Table 1

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

182

		Pedunculate oak	Sessile oak	European beech
Nb. of plots		9	18	12
Plot basal area (m²/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.

208   Species identity, dominance status and circumference at 1.30 m were recorded for each tree. We

209   then used the basal area (m^2/ha) of all dominant trees as an index of stand density (Table 1). Missing

210   values (during the 4 years period in between two inventories) were interpolated assuming a linear

211   increase in basal area with time.

212   ## 2.6 Statistical analyses

213   Statistical analyses were performed with R 3.4.3. We used the log-transformed median of the 5%

214   class of defoliation to normalize the model residuals. The biotic and abiotic determinants of crown

215   defoliation were investigated with a Linear Mixed-Effects Models (function lme package nlme). We

216   considered the nested sampling design and the repeated measurements of trees over time by using a

217   random effect of trees nested in plots. Residual variance was modelled with a power function of

218   fitted values and an autoregressive moving average process estimating the residual temporal

219   autocorrelation (Pinheiro & Bates, 2006). We investigated the long-term temporal trend in tree

220   defoliation by introducing a quadratic effect of the calendar year. Moreover, we tested the

221   interactions between stress drivers by including into the models two-way interactions between

222   drought index, foliar N:P ratio and presence/absence of insect damage. We measured model quality

223   by calculating the root mean square error (RMSE), which is based on the difference between

224   predicted and observed values (Janssen & Heuberger, 1995). We thus fitted the following model for

225   each tree species:

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

227    $\beta_7 \times INSECT \times DROUGHT + \beta_8 \times INSECT \times N{:}P + \beta_9 \times DROUGHT \times N{:}P + \varepsilon_{i,j}$

228

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

230

231   Where DEF is the median level of defoliation classes (in %) of tree i in plot j; $\beta_{0:9}$ are model

232   parameters for the effects of time (YEAR), stand density (G in m^2/ha), presence/absence of insect

233   damage (INSECT), drought intensity (DROUGHT) and foliar N:P ratio and their interactions two by

234   two; $b_{0,i}$ is the plot random effect and $b_{0,i,j}$ is the tree random effect.

235   We eventually applied a correction factor when we back-transformed the values fitted by the model

236   in the logarithmic scale to avoid the systematic underestimation of crown defoliation inherent to the

237   log transformation (Chave et al., 2014; Finney, 1941; Shen & Zhu, 2008):

238 $$\widehat{DEF} = \exp(\log\widehat{(DEF)} + CF)$$

239   Where $\widehat{DEF}$ is the average crown defoliation that is predicted by the model; $\log\widehat{(DEF)}$ is the average

240   log-transformed value of crown defoliation that is predicted by the model and CF is the correction

241   factor:

242 $$CF = \frac{RSE^2}{2}$$

243   Where RSE is the residual square error.

3 RESULTS

245   The mean level of defoliation observed was 20%, but the standard deviations associated with

246   random effects in the models indicated important inter-plot and inter-individual variability (Table 2).

3.1 Effect of stand density on tree defoliation

248   Crown defoliation of European beech and pedunculate oak increased significantly (Table 2) with plot

249   basal area (tree density) respectively by 0.4% and 0.3% per m^2/ha, whereas it decreased significantly

250   by 0.4% per m^2/ha in sessile oak.

3.2 Long term changes in tree defoliation

252   The three tree species exhibited contrasting temporal trends of tree defoliation over the period

253   1997-2015 (Table 2, Fig. 1). European beech defoliation increased significantly all along the period

254 (Fig. 1) at a rate of 0.5 % per year. Long-term changes in sessile oak defoliation exhibited a humped

255 shape with an increase from 1997 to 2008 followed by a slight decrease in defoliation from 2008 to

256 2015. Defoliation of the pedunculate oak showed an opposite trend with a gradual decrease until

257 2011.

3.3 Tree defoliation in presence/absence of insect damage

258

259 Trees damaged by pest insects were significantly more defoliated than trees not damaged by insects

260 in the three species (Table 2), at an average value of drought index and foliar N:P nutrient content.

261 The increase of crown defoliation due to insect damage was of 7.5 % in European beech, 4.7% in

262 sessile oak and 2.6% in pedunculate oak, as estimated by models.

3.4 Interaction between insect damage and drought

263

264 For European beech, crown defoliation was significantly aggravated by drought, but only in trees

265 damaged by pest insects (Table 2, Fig. 2), i.e. significant drought x insect interaction (estimate=-0.08

266 ± 0.03; P=0.01). Tree defoliation increased by 5.9% from very wet (drought index =-1.5) to very dry

267 (drought index = 1.5) conditions in trees damaged by insects, as estimated by the model.

268 Regarding sessile and pedunculate oak, the aggravation of crown defoliation was similar in the

269 presence and in the absence of insect damage (P > 0.05, Table 2, Fig.2) and was in average of 2.9%

270 for sessile oak and 3.4% for pedunculate oak between very wet (drought index =-1.5) and very dry

271 (drought index = 1.5) conditions.

3.5 Interaction between insect damage and foliar N: P ratio

272

273 Crown defoliation of European beech increased with higher foliar N:P ratio in trees that were not

274 damaged by insects (Table 2). The variation in tree defoliation estimated by the model was of +10%

275 between low (16) to high (33) level of foliar N:P ratio (Fig. 3). Conversely, the slope of the

276 relationship between defoliation and foliar N:P ratio was not significantly different from zero for

277   European beech trees damaged by insects, i.e. significant interaction N:P x insect (estimate=-

278   0.045±0.006; P<0.001).

279   In sessile oak, the effect of foliar N:P ratio was not significant in trees that were not damaged by

280   insects but was negative in trees with an insect damage (-3.5% between low (16) and high (33) level

281   of foliar N:P ratio Table 2), i.e. significant N:P x insect interaction (estimate=-0.007±0.004; P=0.04).

282   The trends were more pronounced in pedunculate oak: crown defoliation decreased significantly

283   with higher values of foliar N:P ratio with a steeper slope in trees damaged by insects than in trees

284   not damage by insects (-5.6 % for tree damage by insect and -2.6% between low (16) and high (33)

285   level of foliar N:P ratio), i.e. significant N:P x Insect interaction (estimate=-0.008±0.004; P=0.03).

286   ## 3.6 Interaction between drought and foliar N: P ratio

287   In pedunculate oak, there was a significant interaction between drought and foliar N:P ratio

288   (estimate=-0.008±0.002; P<0.001, Table 2). Trees were more defoliated under dryer conditions and

289   at lower levels of foliar N:P ratio (Fig. 4). The interaction between drought and foliar N:P ratio was

290   not significant in European beech and sessile oak (P>0.05).

291   Table 2

292   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
293   transformed) at the tree level in European beech (*Fagus sylvatica*), sessile oak (*Quercus petraea*) and pedunculate oak (*Quercus robur*). Model estimates
294   (*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
295   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
296   error of the linear mixed models.

297

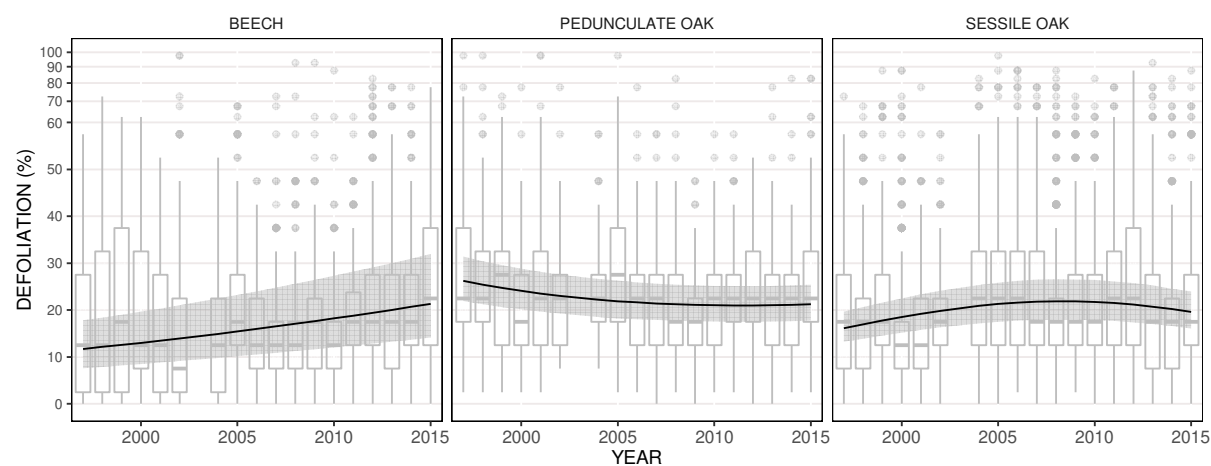| Species					Fixed effects							Random effects (*sd*)		
					Drought and Insect damage		Drought x Insect damage	Foliar N: P ratio and Insect damage		Foliar N: P ratio x Insect damage	Drought X Foliar N:P ratio			
	Year	Year^2	Basal area	Insect damage	Absence	Presence	Δ Abs .- Pre.	Absence	Presence	Δ Abs. - Pre.		Plot	Tree	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**			

298

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%
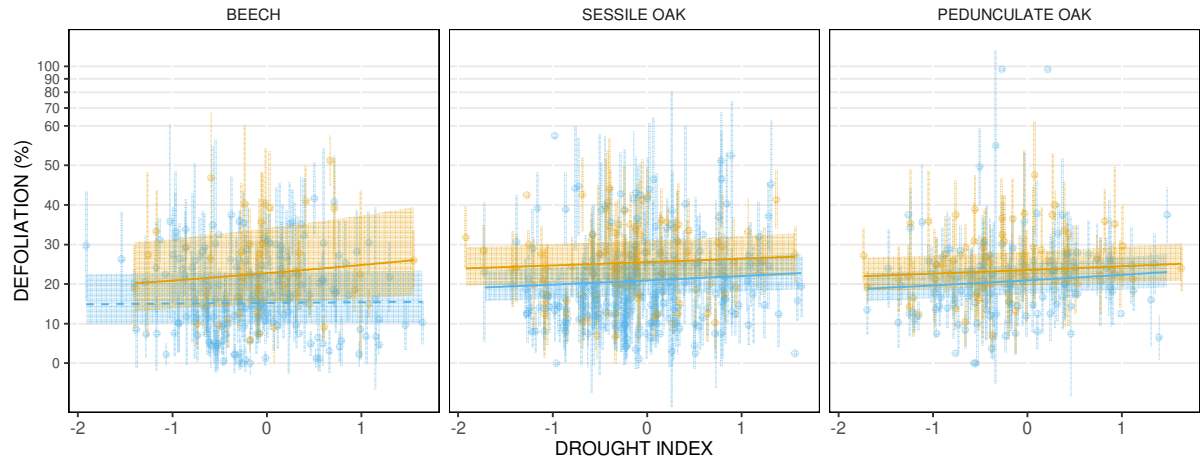
Fig. 2. Effect of drought index on crown defoliation in European beech, sessile oak and pedunculated oak in absence (blue) and presence (yellow) of insect damage. The raw data are represented by an average value of crown defoliation by plot (dots) and its standard deviation (vertical lines). Solid lines 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%
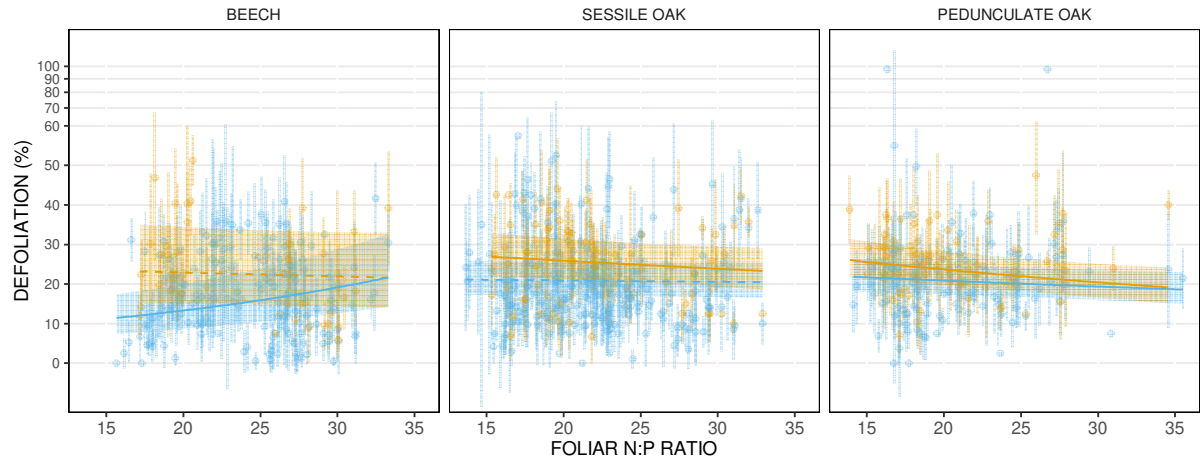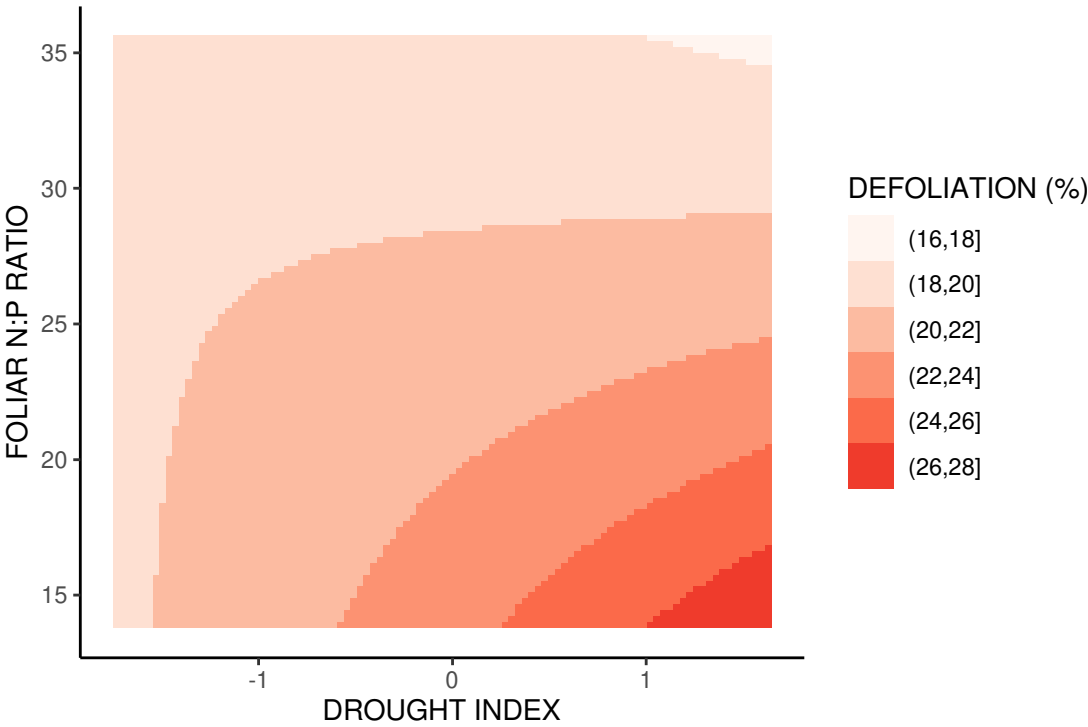
Fig. 3. Effect of foliar N: P ratio on crown defoliation in European beech, sessile oak and pedunculated oak in absence (blue) and presence (yellow) of insect damage. The raw data are represented by an average value of crown defoliation by plot (dots) and its standard deviation (vertical lines). Solid 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%

319

320

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).

347 The temporal pattern was quite different in oak species. Sessile oak exhibited a deterioration trend

348 approximatively until 2007, which was followed by a period of slight recovery, while pedunculate oak

349 showed a general trend for a slow crown condition improvement. Oak species are more drought

350 tolerant than European beech (Rubio-Cuadrado et al., 2018). It is thus possible that in the recent

351 years, from 2007 onward, precipitations were below the tolerance threshold of European beech but

352 above the tolerance thresholds of oaks. Higher CO_2 concentration causes an increase in

353 carbohydrates and a reduction in N, thus increasing C:N ratio which is unfavorable to leaf feeders. It

354 can also enhance C-based tree defenses against defoliating herbivores (Robinson, Ryan, & Newman,

355 2012) and particularly against gypsy moth, a common oak defoliator (Foss, Mattson, & Trier, 2013).

356 The lack of degradation, or even the slight improvement, in oak crown conditions might thus be due

357 to positive effects of CO_2 enrichment on tree growth and defense against leaf feeders

358 counterbalancing negative effects of droughts on tree health.

359 4.2 Effects of Intraspecific competition, insect damage, drought and foliar N:P

360 High tree density emerged as a cause of defoliation in all three species, probably due to increased

361 competition for canopy space (Getzin et al., 2008; Hajek et al., 2015). Competing trees may also be

362 more prone to pest attacks, due to trade-offs between growth and defenses (Huang et al., 2019).

363 This calls for new studies targeting the effect of forest thinning on resistance to multiple stresses

364 (Jactel et al., 2009).

365 Tree defoliation usually increases with summer drought of the current year (Seidling, 2007) because

366 leaf abscission allows avoiding disruption of sap flow flux and xylem cavitation (Bréda et al., 2006).

367 Defoliation can also arise from lagged effect of previous summer drought (Seidling, 2007), which can

368 affect carbohydrates reserves and bud viability (Bréda et al., 2006).

369 The negative effect of foliar N:P ratio on tree defoliation did not exhibit a consistent pattern among

370 the studied tree species contrary to what was observed at the European scale. Veresoglou et al.

371 (2014) found a segmented response of tree defoliation to foliar N:P, with a positive relationship

372   between nutrient content and defoliation beyond the breaking point of 14.8 in broadleaved species

373   (corresponding to the minimum level of the foliar N:P ratio observed in our study). We found such a

374   positive correlation (higher defoliation at higher level of N:P ratio, *i.e.* high level of N and low level of

375   P) only for European beech not damaged by insect. European beech covered a larger range of N:P

376   ratio than oak species for which approximatively 80% of the observations belong to the intermediate

377   group. The increase in defoliation observed in European beech may thus arise from the fact that

378   European beech occurs in sites with a stronger nutritional imbalance of N and P than oaks.

379   In all three species, insect damaged trees exhibited significantly higher defoliation than non-attacked

380   trees, which confirms the significant impact of insect feeding on crown condition (Kozlov, Lanta,

381   Zverev, & Zvereva, 2015). We found a higher sensitivity of sessile oak than pedunculate oak to insect

382   attack, which is consistent with recent findings on the sensitivity of sessile oak to the oak

383   processionary moth (Damestoy et al., 2020). From a management point of view, the sessile oak

384   appears be more resistant to drought events than the pedunculate oak, suggesting that sessile oak

385   should be favored to adapt oak forests to climate change. However, this choice could be made at the

386   cost of making oak stands more vulnerable to attack by defoliators. This trade-off calls for caution

387   when choosing to favor one tree species over another in a substitution logic and suggests that mixing

388   tree species would be a more effective long-term strategy for dealing with multiple risks (Jactel et al.,

389   2017; Sousa-Silva et al., 2018). Both beech and oak species can be infested by many insect

390   defoliators, with for example 41 species of Lepidoptera associated with European beech and 189

391   with pedunculate oak and sessile oak in Britain (Kennedy & Southwood, 1984). In addition, it has

392   been demonstrated that insect damage can accelerate leaf abscission, thus explaining higher

393   defoliation recorded in early summer on insect damaged trees (Zvereva & Kozlov, 2014).

394   ## 4.3 Interactions between pest damages, drought and foliar N: P ratio

395   In all tree species, we could observe significantly higher damage (defoliation) in trees that were both

396   attacked by insects and under drought conditions. Interestingly, in our study, we found that the

397 combined effects of drought and insect attack were additive for oaks but synergistic for European

398 beech (Fig. 2). This suggests that, in oak trees, insect damages and drought cumulated their effect on

399 tree defoliation whereas, in beech trees, insect damages increased with water stress intensity. This is

400 consistent with the general pattern of higher forest insect damage following droughts (Ferretti et al.,

401 2014; Logan, Regniere, & Powell, 2003; Rouault et al., 2006; Toïgo, Barraquand, Barnagaud, Piou, &

402 Jactel, 2017) and more particularly the higher susceptibility of water stressed trees to defoliating

403 insects (Jactel et al., 2012). The direct effect of drought on forest insect herbivores, e.g. on survival

404 and fecundity, lacks experimental evidence (Jactel et al., 2019). By contrast, it is well known that

405 drought can indirectly benefit forest defoliators through improved host plant quality (e.g. higher

406 nitrogen content (Jactel et al., 2012)) or reduced plant resistance (Castagneyrol, Jactel, et al., 2018;

407 Holopainen et al., 2018). It would now be necessary to better identify the species of defoliating

408 insects attacking oaks on the one hand and beeches on the other hand to understand why the

409 synergy between drought and insect attacks was only observed in the case of European beech.

410 We also showed cumulative, negative effects of pest damage and low N:P ratio on all tree

411 species. This confirms that nutrient imbalance has to be considered when searching the causes of

412 tree crown decline. One possible explanation for the combined effect of pest feeding and low N:P is

413 that insect herbivory is higher on leaf with low N content as more leaf tissue have to be consumed to

414 meet the nutritional requirement of insect herbivores (i.e. compensatory feeding, (Castagneyrol,

415 Moreira, et al., 2018)). In one species, beech, we detected a synergistic effect of insect damage and

416 low N:P leaf ratio, with no effect of nutrient imbalance in undamaged trees and large defoliation

417 increase with increasing N:P in damage trees. This might be due to specific nutrient requirements of

418 *Orchestes fagi*, the main insect defoliator of European beech in our sample.

4.4 PERSPECTIVES AND LIMITATIONS

420 Our study has several limitations. Tree crown conditions, and in particular level of defoliation, are

421 difficult to estimate accurately. However, observers involved in ICP forests network were trained

422 each year with inter-calibration workshops. In addition, a selection of plots (16 out of 102) between

423 2001-2005 and 2008-2009 was controlled to assess the quality of the observations of crown

424 defoliation (Ferretti et al., 2014). The observation bias (the difference in score between the field

425 team and the control team) was between ± 5% for 76% of the defoliation scores and ± 10% for 92%

426 of them. This confirms the reliability of crown defoliation score attributed on the field. In addition,

427 we focused on the three tree species with largest sample size and only retained trees for which all

428 necessary data were available. We therefore believe that our results on long-term trend and

429 explanatory factors are conservative. More problematic is the lack of precise information on the

430 insect species that made the observed leaf damage. This would have required collecting branches

431 and assessing a sample of leaves, which is technically and economically difficult. Nevertheless, a

432 more focused long-term study on a few well-known and easily monitored insect defoliators would

433 provide more insights into physiological processed involved in drought, nutrient imbalance and pest

434 damage. Likewise, other potential interactive drivers of crown conditions like storm, air pollution or

435 presence of mycorrhizae would be worth considering.

5 CONCLUSIONS

437 Our findings confirm the gradual worsening of crown condition in European beech and the

438 stabilization in oaks, which has been observed at the European scale, suggesting species-specific

439 response to ongoing climate changes. They also demonstrate that events of crown defoliation result

440 from the complex interplay between biotic and abiotic stresses, which are more or less relevant to

441 particular tree species. In particular, insect attacks deteriorated crown condition, especially after dry

442 periods for the three broadleaved species while the effect of imbalanced nutritional status was less

443 consistent among tree species. More importantly, we showed that these stress factors generally act

444 synergistically. It therefore seems important for the adaptive management of forests to address

445 issues related to forest conditions in an integrative way, especially in a context where biotic and

446 abiotic hazards are likely to intensify. Long-term monitoring of forest condition remains more useful

447   than ever, but it should be accompanied by a more accurate analysis of the causes of decline, in

448   order to better predict future trends and better adapt forests to future threats.

ACKNOWLEDGMENTS
449

453

REFERENCES

Ainsworth, E. A., Yendrek, C. R., Sitch, S., Collins, W. J., & Emberson, L. D. (2012). The Effects of
Tropospheric Ozone on Net Primary Productivity and Implications for Climate Change. *Annual Review of Plant Biology*, *63*(1), 637–661. https://doi.org/10.1146/annurev-arplant-042110-103829

Allen, C. D., Breshears, D. D., & McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, *6*(8), art129. https://doi.org/10.1890/ES15-00203.1

Bonan, G. B. (2008). Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests. *Science*, *320*(5882), 1444–1449. https://doi.org/10.1126/science.1155121

Braun, S., Thomas, V. F. D., Quiring, R., & Flückiger, W. (2010). Does nitrogen deposition increase forest production? The role of phosphorus. *Environmental Pollution*, *158*(6), 2043–2052. https://doi.org/10.1016/j.envpol.2009.11.030

Bréda, N., Huc, R., Granier, A., & Dreyer, E. (2006). Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, *63*(6), 625–644. https://doi.org/10.1051/forest:2006042

Bussotti, F., & Ferretti, M. (2009). Visible injury, crown condition, and growth responses of selected Italian forests in relation to ozone exposure. *Environmental Pollution*, *157*(5), 1427–1437. https://doi.org/10.1016/j.envpol.2008.09.034

Bussotti, F., Prancrazi, M., Matteucci, G., & Gerosa, G. (2005). Leaf morphology and chemistry in Fagus sylvatica (beech) trees as affected by site factors and ozone: results from CONECOFOR permanent monitoring plots in Italy. *Tree Physiology*, *25*(2), 211–219.

Carroll, A. L., Taylor, S. W., Régnière, J., & Safranyik, L. (2003). *Effect of climate change on range expansion by the mountain pine beetle in British Columbia*. Pages 223-232 in TL Shore et

479   al.(eds) Mountain Pine Beetle Symposium: Challenges and Solutions, Oct. 30-31, 2003.

480   Kelowna BC. Natural Resources Canada, Infromation Report BC-X-399, Victoria.

481   Castagneyrol, B., Jactel, H., & Moreira, X. (2018). Anti-herbivore defences and insect herbivory:

482   Interactive effects of drought and tree neighbours. *Journal of Ecology*.

483   https://doi.org/10.1111/1365-2745.12956

484   Castagneyrol, B., Moreira, X., & Jactel, H. (2018). Drought and plant neighbourhood interactively

485   determine herbivore consumption and performance. *Scientific Reports*, *8*(1).

486   https://doi.org/10.1038/s41598-018-24299-x

487   Charney, N. D., Babst, F., Poulter, B., Record, S., Trouet, V. M., Frank, D., Enquist, B. J., & Evans, M. E.

488   K. (2016). Observed forest sensitivity to climate implies large changes in 21st century North

489   American forest growth. *Ecology Letters*, *19*(9), 1119–1128.

490   https://doi.org/10.1111/ele.12650

491   Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B. C., Duque, A.,

492   Eid, T., Fearnside, P. M., Goodman, R. C., Henry, M., Martínez-Yrízar, A., Mugasha, W. A.,

493   Muller-Landau, H. C., Mencuccini, M., Nelson, B. W., Ngomanda, A., Nogueira, E. M., Ortiz-

494   Malavassi, E., … Vieilledent, G. (2014). Improved allometric models to estimate the

495   aboveground biomass of tropical trees. *Global Change Biology*, *20*(10), 3177–3190.

496   https://doi.org/10.1111/gcb.12629

497   Damestoy, T., Jactel, H., Belouard, T., Schmuck, H., Plomion, C., & Castagneyrol, B. (2020). Tree

498   species identity and forest composition affect the number of oak processionary moth

499   captured in pheromone traps and the intensity of larval defoliation. *Agricultural and Forest*

500   *Entomology*. https://doi.org/10.1111/afe.12371

501   de la Cruz, A. C., Gil, P. M., Fernández-Cancio, Á., Minaya, M., Navarro-Cerrillo, R. M., Sánchez-

502   Salguero, R., & Grau, J. M. (2014). Defoliation triggered by climate induced effects in Spanish

503   ICP Forests monitoring plots. *Forest Ecology and Management*, *331*, 245–255.

504   https://doi.org/10.1016/j.foreco.2014.08.010

505 De Vries, W, Dobbertin, M., Solberg, S., Van Dobben, H., & Schaub, M. (2014). Impacts of acid

506   deposition, ozone exposure and weather conditions on forest ecosystems in Europe: an

507   overview. *Plant and Soil*, *380*(1–2), 1–45.

508 De Vries, Wim, Klap, J. M., & Erisman, J. W. (2000). Effects of environmental stress on forest crown

509   condition in Europe. Part I: Hypotheses and approach to the study. *Water, Air, and Soil*

510   *Pollution*, *119*(1), 317–333. https://doi.org/10.1023/A:1005157509454

511 Diffenbaugh, N. S., Singh, D., Mankin, J. S., Horton, D. E., Swain, D. L., Touma, D., Charland, A., Liu, Y.,

512   Haugen, M., Tsiang, M., & Rajaratnam, B. (2017). Quantifying the influence of global warming

513   on unprecedented extreme climate events. *Proceedings of the National Academy of Sciences*,

514   *114*(19), 4881–4886. https://doi.org/10.1073/pnas.1618082114

515 Dobbertin, M. (2005). Tree growth as indicator of tree vitality and of tree reaction to environmental

516   stress: a review. *European Journal of Forest Research*, *124*(4), 319–333.

517   https://doi.org/10.1007/s10342-005-0085-3

518 Drobyshev, I., Anderson, S., & Sonesson, K. (2007). Crown condition dynamics of oak in southern

519   Sweden 1988'999. *Environmental Monitoring and Assessment*, *134*(1–3), 199–210.

520   https://doi.org/10.1007/s10661-007-9610-9

521 Eichhorn, J, Roskams, P., Ferretti, M., Mues, V., Szepesi, A., & Durrant, D. (2010). Visual assessment

522   of crown condition and damaging agents. Manual Part IV. *Manual on Methods and Criteria*

523   *for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution*

524   *on Forests*, 49.

525 Eichhorn, Johannes, Icke, R., Isenberg, A., Paar, U., & Schönfelder, E. (2005). Temporal development

526   of crown condition of beech and oak as a response variable for integrated evaluations.

527   *European Journal of Forest Research*, *124*(4), 335–347. https://doi.org/10.1007/s10342-005-

528   0097-z

529   Ewald, J. (2005). Ecological background of crown condition, growth and nutritional status of Picea

530   abies (L.) Karst. in the Bavarian Alps. *European Journal of Forest Research*, *124*(1), 9–18.

531   https://doi.org/10.1007/s10342-004-0051-5

532   Farahat, E., & Linderholm, H. W. (2018). Growth–climate relationship of European beech at its

533   northern distribution limit. *European Journal of Forest Research*, *137*(5), 619–629.

534   https://doi.org/10.1007/s10342-018-1129-9

535   Ferretti, M., Nicolas, M., Bacaro, G., Brunialti, G., Calderisi, M., Croisé, L., Frati, L., Lanier, M.,

536   Maccherini, S., Santi, E., & Ulrich, E. (2014). Plot-scale modelling to detect size, extent, and

537   correlates of changes in tree defoliation in French high forests. *Forest Ecology and*

538   *Management*, *311*, 56–69. https://doi.org/10.1016/j.foreco.2013.05.009

539   Finney, D. (1941). On the distribution of a variate whose logarithm is normally distributed.

540   *Supplement to the Journal of the Royal Statistical Society*, *7*(2), 155–161.

541   Flückiger, W., & Braun, S. (1999). Nitrogen and Its Effect on Growth, Nutrient Status and Parasite

542   Attacks in Beech and Norway Spruce. *Water, Air, and Soil Pollution*, *116*(1), 99–110.

543   https://doi.org/10.1023/A:1005298609109

544   Foss, A. R., Mattson, W. J., & Trier, T. M. (2013). Effects of Elevated Co_2 Leaf Diets on Gypsy Moth

545   (Lepidoptera: Lymantriidae) Respiration Rates. *Environmental Entomology*, *42*(3), 503–514.

546   https://doi.org/10.1603/EN12074

547   Getzin, S., Wiegand, K., Schumacher, J., & Gougeon, F. A. (2008). Scale-dependent competition at the

548   stand level assessed from crown areas. *Forest Ecology and Management*, *255*(7), 2478–2485.

549   Graumlich, L. J. (1991). Subalpine Tree Growth, Climate, and Increasing CO_2: An Assessment of

550   Recent Growth Trends. *Ecology*, *72*(1), 1–11. https://doi.org/10.2307/1938895

551   Güsewell, S. (2004). N: P ratios in terrestrial plants: variation and functional significance. *New*

552   *Phytologist*, *164*(2), 243–266.

553 Hajek, P., Seidel, D., & Leuschner, C. (2015). Mechanical abrasion, and not competition for light, is the

554 dominant canopy interaction in a temperate mixed forest. *Forest Ecology and Management*,

555 *348*, 108–116.

556 Holopainen, J. K., Virjamo, V., Ghimire, R. P., Blande, J. D., Julkunen-Tiitto, R., & Kivimäenpää, M.

557 (2018). Climate Change Effects on Secondary Compounds of Forest Trees in the Northern

558 Hemisphere. *Frontiers in Plant Science*, *9*, 1445. https://doi.org/10.3389/fpls.2018.01445

559 Huang, J., Hammerbacher, A., Weinhold, A., Reichelt, M., Gleixner, G., Behrendt, T., Van Dam, N. M.,

560 Sala, A., Gershenzon, J., & Trumbore, S. (2019). Eyes on the future–evidence for trade-offs

561 between growth, storage and defense in Norway spruce. *New Phytologist*, *222*(1), 144–158.

562 Jactel, H., Bauhus, J., Boberg, J., Bonal, D., Castagneyrol, B., Gardiner, B., Gonzalez-Olabarria, J. R.,

563 Koricheva, J., Meurisse, N., & Brockerhoff, E. G. (2017). Tree Diversity Drives Forest Stand

564 Resistance to Natural Disturbances. *Current Forestry Reports*, *3*(3), 223–243.

565 https://doi.org/10.1007/s40725-017-0064-1

566 Jactel, H., Koricheva, J., & Castagneyrol, B. (2019). Responses of forest insect pests to climate change:

567 not so simple. *Current Opinion in Insect Science*, *35*, 103–108.

568 https://doi.org/10.1016/j.cois.2019.07.010

569 Jactel, H., Nicoll, B. C., Branco, M., Gonzalez-Olabarria, J. R., Grodzki, W., Långström, B., Moreira, F.,

570 Netherer, S., Orazio, C., Piou, D., Santos, H., Schelhaas, M. J., Tojic, K., & Vodde, F. (2009).

571 The influences of forest stand management on biotic and abiotic risks of damage. *Annals of*

572 *Forest Science*, *66*(7), 701–701. https://doi.org/10.1051/forest/2009054

573 Jactel, H., Petit, J., Desprez-Loustau, M.-L., Delzon, S., Piou, D., Battisti, A., & Koricheva, J. (2012).

574 Drought effects on damage by forest insects and pathogens: a meta-analysis. *Global Change*

575 *Biology*, *18*(1), 267–276. https://doi.org/10.1111/j.1365-2486.2011.02512.x

576 Janssen, P. H. M., & Heuberger, P. S. C. (1995). Calibration of process-oriented models. *Ecological*

577 *Modelling*, *83*(1), 55–66.

578   Janssens, I. A. (2003). Europe's Terrestrial Biosphere Absorbs 7 to 12% of European Anthropogenic

579   CO2 Emissions. *Science*, *300*(5625), 1538–1542. https://doi.org/10.1126/science.1083592

580   Juknys, R., Augustaitis, A., Venclovienė, J., Kliučius, A., Vitas, A., Bartkevičius, E., & Jurkonis, N. (2014).

581   Dynamic response of tree growth to changing environmental pollution. *European Journal of*

582   *Forest Research*, *133*(4), 713–724. https://doi.org/10.1007/s10342-013-0712-3

583   Kennedy, C. E. J., & Southwood, T. R. E. (1984). The Number of Species of Insects Associated with

584   British Trees: A Re-Analysis. *Journal of Animal Ecology*, *53*(2), 455–478.

585   https://doi.org/10.2307/4528

586   Kozlov, M. V., Lanta, V., Zverev, V., & Zvereva, E. L. (2015). Global patterns in background losses of

587   woody plant foliage to insects: Latitudinal patterns in insect herbivory. *Global Ecology and*

588   *Biogeography*, *24*(10), 1126–1135. https://doi.org/10.1111/geb.12347

589   Kurz, W. A., Dymond, C. C., Stinson, G., Rampley, G. J., Neilson, E. T., Carroll, A. L., Ebata, T., &

590   Safranyik, L. (2008). Mountain pine beetle and forest carbon feedback to climate change.

591   *Nature*, *452*(7190), 987–990. https://doi.org/10.1038/nature06777

592   Lebourgeois, F., Bréda, N., Ulrich, E., & Granier, A. (2005). Climate-tree-growth relationships of

593   European beech (Fagus sylvatica L.) in the French Permanent Plot Network (RENECOFOR).

594   *Trees*, *19*(4), 385–401. https://doi.org/10.1007/s00468-004-0397-9

595   Lehner, F., Coats, S., Stocker, T. F., Pendergrass, A. G., Sanderson, B. M., Raible, C. C., & Smerdon, J. E.

596   (2017). Projected drought risk in 1.5°C and 2°C warmer climates: Drought in 1.5°C and 2°C

597   Warmer Climates. *Geophysical Research Letters*, *44*(14), 7419–7428.

598   https://doi.org/10.1002/2017GL074117

599   Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon,

600   S., Corona, P., Kolström, M., Lexer, M. J., & Marchetti, M. (2010). Climate change impacts,

601   adaptive capacity, and vulnerability of European forest ecosystems. *Forest Ecology and*

602   *Management*, *259*(4), 698–709. https://doi.org/10.1016/j.foreco.2009.09.023

603 Logan, J. A., Regniere, J., & Powell, J. A. (2003). Assessing the impacts of global warming on forest

604   pest dynamics. *Frontiers in Ecology and the Environment*, *1*(3), 130–137.

605 Magill, A. H., Aber, J. D., Currie, W. S., Nadelhoffer, K. J., Martin, M. E., McDowell, W. H., Melillo, J.

606   M., & Steudler, P. (2004). Ecosystem response to 15 years of chronic nitrogen additions at

607   the Harvard Forest LTER, Massachusetts, USA. *Forest Ecology and Management*, *196*(1), 7–

608   28. https://doi.org/10.1016/j.foreco.2004.03.033

609 Matyssek, R., Wieser, G., Calfapietra, C., De Vries, W., Dizengremel, P., Ernst, D., Jolivet, Y.,

610   Mikkelsen, T. N., Mohren, G., & Le Thiec, D. (2012). Forests under climate change and air

611   pollution: gaps in understanding and future directions for research. *Environmental Pollution*,

612   *160*, 57–65.

613 McDowell, N., Allen, C. D., Anderson-Teixeira, K., Brando, P., Brienen, R., Chambers, J., Christoffersen,

614   B., Davies, S., Doughty, C., Duque, A., Espirito-Santo, F., Fisher, R., Fontes, C. G., Galbraith, D.,

615   Goodsman, D., Grossiord, C., Hartmann, H., Holm, J., Johnson, D. J., … Xu, X. (2018). Drivers

616   and mechanisms of tree mortality in moist tropical forests. *New Phytologist*, *219*(3), 851–

617   869. https://doi.org/10.1111/nph.15027

618 McDowell, N. G., Allen, C. D., Anderson-Teixeira, K., Aukema, B. H., Bond-Lamberty, B., Chini, L.,

619   Clark, J. S., Dietze, M., Grossiord, C., & Hanbury-Brown, A. (2020). Pervasive shifts in forest

620   dynamics in a changing world. *Science*, *368*(6494).

621 Meir, P., Mencuccini, M., Binks, O., da Costa, A. L., Ferreira, L., & Rowland, L. (2018). Short-term

622   effects of drought on tropical forest do not fully predict impacts of repeated or long-term

623   drought: gas exchange versus growth. *Philosophical Transactions of the Royal Society B:

624   Biological Sciences*, *373*(1760), 20170311. https://doi.org/10.1098/rstb.2017.0311

625 Mellert, K. H., & Göttlein, A. (2012). Comparison of new foliar nutrient thresholds derived from van

626   den Burg's literature compilation with established central European references. *European

627   Journal of Forest Research*, *131*(5), 1461–1472. https://doi.org/10.1007/s10342-012-0615-8

628   Michel, A., Seidling, W., Prescher, A.-K., & editors. (2018). *Forest Condition in Europe: 2018 Technical*

629   *Report of ICP Forest: Report under the UNECE Convention on Long-Range Transboundary Air*

630   *Pollution (Air Convention).* (p. 92). BFM Austrian Research Centre for Forests.

631   Myneni, R. B., Keeling, C. D., Tucker, C. J., Asrar, G., & Nemani, R. R. (1997). Increased plant growth in

632   the northern high latitudes from 1981 to 1991. *Nature*, *386*(6626), 698–702.

633   https://doi.org/10.1038/386698a0

634   Norby, R. J., DeLucia, E. H., Gielen, B., Calfapietra, C., Giardina, C. P., King, J. S., Ledford, J., McCarthy,

635   H. R., Moore, D. J. P., Ceulemans, R., De Angelis, P., Finzi, A. C., Karnosky, D. F., Kubiske, M.

636   E., Lukac, M., Pregitzer, K. S., Scarascia-Mugnozza, G. E., Schlesinger, W. H., & Oren, R.

637   (2005). Forest response to elevated CO2 is conserved across a broad range of productivity.

638   *Proceedings of the National Academy of Sciences*, *102*(50), 18052–18056.

639   https://doi.org/10.1073/pnas.0509478102

640   Ouimet, R., & Moore, J.-D. (2015). Effects of fertilization and liming on tree growth, vitality and

641   nutrient status in boreal balsam fir stands. *Forest Ecology and Management*, *345*, 39–49.

642   https://doi.org/10.1016/j.foreco.2015.02.032

643   Pacala, S. W. (2001). Consistent Land- and Atmosphere-Based U.S. Carbon Sink Estimates. *Science*,

644   *292*(5525), 2316–2320. https://doi.org/10.1126/science.1057320

645   Piao, S., Fang, J., Ciais, P., Peylin, P., Huang, Y., Sitch, S., & Wang, T. (2009). The carbon balance of

646   terrestrial ecosystems in China. *Nature*, *458*(7241), 1009–1013.

647   https://doi.org/10.1038/nature07944

648   Pinheiro, J., & Bates, D. (2006). *Mixed-effects models in S and S-PLUS*. Springer Science & Business

649   Media.

650   Piovesan, G., Biondi, F., Filippo, A. D., Alessandrini, A., & Maugeri, M. (2008). Drought-driven growth

651   reduction in old beech (Fagus sylvatica L.) forests of the central Apennines, Italy. *Global*

652   *Change Biology*, *14*(6), 1265–1281. https://doi.org/10.1111/j.1365-2486.2008.01570.x

653   Pollastrini, M., Feducci, M., Bonal, D., Fotelli, M., Gessler, A., Grossiord, C., Guyot, V., Jactel, H.,

654   Nguyen, D., Radoglou, K., & Bussotti, F. (2016). Physiological significance of forest tree

655   defoliation: Results from a survey in a mixed forest in Tuscany (central Italy). *Forest Ecology*

656   *and Management*, *361*, 170–178. https://doi.org/10.1016/j.foreco.2015.11.018

657   Popa, I., Badea, O., & Silaghi, D. (2017). Influence of climate on tree health evaluated by defoliation in

658   the ICP level I network (Romania). *IForest - Biogeosciences and Forestry*, *10*(3), 554–560.

659   https://doi.org/10.3832/ifor2202-009

660   Rautio, P., Fürst, A., Stefan, K., Raitio, H., & Bartels, U. (2010). Part XII: Sampling and Analysis of

661   Needles and Leaves. In *Manual on methods and criteria for harmonized sampling,*

662   *assessment, monitoring and analysis of the effects of air pollution on forests* (p. 19). UNECE

663   ICP Forests Programme Coordinating Centre.

664   Robinson, E. A., Ryan, G. D., & Newman, J. A. (2012). A meta-analytical review of the effects of

665   elevated CO2 on plant-arthropod interactions highlights the importance of interacting

666   environmental and biological variables: Tansley review. *New Phytologist*, *194*(2), 321–336.

667   https://doi.org/10.1111/j.1469-8137.2012.04074.x

668   Rouault, G., Candau, J.-N., Lieutier, F., Nageleisen, L.-M., Martin, J.-C., & Warzée, N. (2006). Effects of

669   drought and heat on forest insect populations in relation to the 2003 drought in Western

670   Europe. *Annals of Forest Science*, *63*(6), 613–624.

671   Rubio-Cuadrado, Á., Camarero, J. J., del Río, M., Sánchez-González, M., Ruiz-Peinado, R., Bravo-

672   Oviedo, A., Gil, L., & Montes, F. (2018). Long-term impacts of drought on growth and forest

673   dynamics in a temperate beech-oak-birch forest. *Agricultural and Forest Meteorology*, *259*,

674   48–59. https://doi.org/10.1016/j.agrformet.2018.04.015

675   Ruosteenoja, K., Markkanen, T., Venäläinen, A., Räisänen, P., & Peltola, H. (2018). Seasonal soil

676   moisture and drought occurrence in Europe in CMIP5 projections for the 21st century.

677   *Climate Dynamics*, *50*(3–4), 1177–1192. https://doi.org/10.1007/s00382-017-3671-4

678 Saltré, F., Duputié, A., Gaucherel, C., & Chuine, I. (2015). How climate, migration ability and habitat

679   fragmentation affect the projected future distribution of European beech. *Global Change*

680   *Biology*, *21*(2), 897–910. https://doi.org/10.1111/gcb.12771

681 Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D.,

682   Petr, M., & Honkaniemi, J. (2017). Forest disturbances under climate change. *Nature Climate*

683   *Change*, *7*(6), 395.

684 Seidling, W. (2007). Signals of summer drought in crown condition data from the German Level I

685   network. *European Journal of Forest Research*, *126*(4), 529–544.

686   https://doi.org/10.1007/s10342-007-0174-6

687 Seynave, I., Gégout, J.-C., Hervé, J.-C., & Dhôte, J.-F. (2008). Is the spatial distribution of European

688   beech (*Fagus sylvatica* L.) limited by its potential height growth? *Journal of Biogeography*,

689   *35*(10), 1851–1862. https://doi.org/10.1111/j.1365-2699.2008.01930.x

690 Shen, H., & Zhu, Z. (2008). Efficient mean estimation in log-normal linear models. *Journal of*

691   *Statistical Planning and Inference*, *138*(3), 552–567.

692   https://doi.org/10.1016/j.jspi.2006.10.016

693 Smith, M. (1995). Revision of FAO methodologies for crop water requirements. *Nuclear Techniques in*

694   *Soil-Plant Studies for Sustainable Agriculture and Environmental Preservation*, *987*, 385–397.

695 Sousa-Silva, R., Verheyen, K., Ponette, Q., Bay, E., Sioen, G., Titeux, H., Van de Peer, T., Van

696   Meerbeek, K., & Muys, B. (2018). Tree diversity mitigates defoliation after a drought-induced

697   tipping point. *Global Change Biology*. https://doi.org/10.1111/gcb.14326

698 Tessier, J. T., & Raynal, D. J. (2003). Use of nitrogen to phosphorus ratios in plant tissue as an

699   indicator of nutrient limitation and nitrogen saturation. *Journal of Applied Ecology*, *40*(3),

700   523–534.

701 Thimonier, A., Graf Pannatier, E., Schmitt, M., Waldner, P., Walthert, L., Schleppi, P., Dobbertin, M., &

702   Kräuchi, N. (2010). Does exceeding the critical loads for nitrogen alter nitrate leaching, the

703   nutrient status of trees and their crown condition at Swiss Long-term Forest Ecosystem

704   Research (LWF) sites? *European Journal of Forest Research*, *129*(3), 443–461.

705   https://doi.org/10.1007/s10342-009-0328-9

706 Toïgo, M., Barraquand, F., Barnagaud, J.-Y., Piou, D., & Jactel, H. (2017). Geographical variation in

707   climatic drivers of the pine processionary moth population dynamics. *Forest Ecology and*

708   *Management*, *404*, 141–155. https://doi.org/141-155

709 Ulrich, E. (1995). Le réseau renecofor : objectifs et réalisation. *Revue Forestière Française*, *2*, 107.

710   https://doi.org/10.4267/2042/26634

711 Ulrich, E., Vannière, B., Duplat, P., Demolis, C., & Guyon, J.-P. (1994). *RENECOFOR – Manuel de*

712   *référence n1 pour la sélection et l'implantation des placettes permanentes* (Office National

713   des Forêts, Département des Recherches Techniques).

714 van Mantgem, P. J., Stephenson, N. L., Byrne, J. C., Daniels, L. D., Franklin, J. F., Fule, P. Z., Harmon,

715   M. E., Larson, A. J., Smith, J. M., Taylor, A. H., & Veblen, T. T. (2009). Widespread Increase of

716   Tree Mortality Rates in the Western United States. *Science*, *323*(5913), 521–524.

717   https://doi.org/10.1126/science.1165000

718 Veresoglou, S. D., Peñuelas, J., Fischer, R., Rautio, P., Sardans, J., Merilä, P., Tabakovic-Tosic, M., &

719   Rillig, M. C. (2014). Exploring continental-scale stand health–N: P ratio relationships for

720   European forests. *New Phytologist*, *202*(2), 422–430.

721 Vicente-Serrano, S. M., Beguería, S., & López-Moreno, J. I. (2010). A Multiscalar Drought Index

722   Sensitive to Global Warming: The Standardized Precipitation Evapotranspiration Index.

723   *Journal of Climate*, *23*(7), 1696–1718. https://doi.org/10.1175/2009JCLI2909.1

724 Walker, A. P., De Kauwe, M. G., Medlyn, B. E., Zaehle, S., Iversen, C. M., Asao, S., Guenet, B., Harper,

725   A., Hickler, T., Hungate, B. A., Jain, A. K., Luo, Y., Lu, X., Lu, M., Luus, K., Megonigal, J. P., Oren,

726   R., Ryan, E., Shu, S., … Norby, R. J. (2019). Decadal biomass increment in early secondary

727   succession woody ecosystems is increased by CO2 enrichment. *Nature Communications*,

728   *10*(1), 454. https://doi.org/10.1038/s41467-019-08348-1

729   Wittig, V. E., Ainsworth, E. A., Naidu, S. L., Karnosky, D. F., & Long, S. P. (2009). Quantifying the

730   impact of current and future tropospheric ozone on tree biomass, growth, physiology and

731   biochemistry: a quantitative meta-analysis. *Global Change Biology*, *15*(2), 396–424.

732   Zvereva, E. L., & Kozlov, M. V. (2014). Effects of herbivory on leaf life span in woody plants: a meta-

733   analysis. *Journal of Ecology*, *102*(4), 873–881. https://doi.org/10.1111/1365-2745.12252

734