

Growth compensation in an oak-pine mixed forest following an outbreak of pine sawfly (*Diprion pini*)

T. Pérot, P. Vallet, F. Archaux

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6
7 **Title:**

8 Growth compensation in an oak-pine mixed forest following an outbreak of pine sawfly
9 (*Diprion pini*)

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11 **List of authors:**

12 **Perot, T.**^{1*} (thomas.perot@irstea.fr), **Vallet, P.**¹ (patrick.vallet@irstea.fr) & **Archaux, F.**¹
13 (frederic.archaux@irstea.fr)

14 1 Irstea, Forest Ecosystems Research Unit, Domaine des Barres, 45290 Nogent-sur-
15 Vernisson, France.

16
17 * Corresponding author: Thomas Perot, Irstea, Forest Ecosystems Research Unit, Domaine
18 des Barres, 45 290 Nogent-sur-Vernisson, France; Tel.: +33 2 38 95 09 65; Fax: +33 2 38 95
19 03 46. E-mail address : thomas.perot@irstea.fr.

1 **Abstract:**

2 Growth compensations following a disturbance have been found in different species
3 communities through experimentation, but there are few results obtained in natural
4 conditions, in particular for forest ecosystems. The objective of this study was to determine
5 whether there was growth compensation in a mixed oak-pine forest following a biotic
6 disturbance: an outbreak of pine sawfly (*Diprion pini*) that caused massive defoliation of
7 pines in Europe in the early 1980s. The data were collected in mixed oak-pine stands located
8 in the plains of north-central France. We measured the ring widths of 223 oaks and 271 pines
9 in nine mixed stands over a period ranging from 1972 to 2005. We established a model which
10 incorporated climatic effects in order to predict the ring width under undisturbed conditions
11 and to quantify the response of each species to the disturbance. We found that the growth of
12 both species varied synchronously with a positive covariation outside of the disturbance.
13 During the disturbance, the growth of both species covaried negatively especially in the plots
14 where pine had been the most severely affected. For the year following the peak of the
15 defoliations, the reduction in growth for pine was strong and ranged from -27% to -92%
16 depending on the plot. In addition, the more significant the reduction in growth for pine, the
17 more significant the increase in growth for oak. We found that a 100% reduction in pine
18 growth was accompanied by a 61% increase in oak growth for the three years following the
19 most severe defoliation. These results demonstrate that compensation between the two tree
20 species following the insect outbreak did occur. We suggest that growth compensations would
21 especially occur in the case of severe biotic disturbances but probably not in the case of
22 climatic fluctuations.

23

24 **Keywords:** Growth compensation; Mixed forest; Biotic disturbance; *Quercus petraea*; *Pinus*
25 *sylvestris*; *Diprion pini*.

26 **1. Introduction**

27 Mixed species forests are widespread. In Europe, mixed forests represent more than 70%
28 of the total forested area (MCPFE et al., 2007). Interactions among tree species have long
29 been studied (Assmann, 1970), but the effect of is poorly understood. Recent studies have led
30 to contrasting conclusions: even though mixed stands have often proved to be more
31 productive than pure stands (Pretzsch and Schutze, 2009; Vallet and Perot, 2011; Perot and
32 Picard, 2012), some studies have shown a null or negative effect of on productivity (Chen
33 and Klinka, 2003). A number of underlying mechanisms have been proposed to explain these
34 empirical findings. For example, Pretzsch et al. (2010) studied the productivity of pure and
35 mixed stands of Norway spruce and European beech, and suggested among other hypotheses,
36 that beech litter stimulates bio-element turnover on poor sites thus improving spruce nutrition.
37 However, such hypotheses remain tentative.

38 Growth compensation could also explain the increased productivity in mixed stands.
39 There is growth compensation among species if the decrease in the productivity of a species is
40 associated with an increase in productivity of another species (Loreau et al., 2002).
41 Compensation can occur after a change in environmental conditions or following a
42 disturbance. This mechanism may influence the level and stability of ecosystem productivity
43 (Tilman, 1999; Yachi and Loreau, 1999) and is the basis of the "insurance hypothesis" which
44 is being widely studied and debated in ecology (McNaughton, 1977; Hector et al., 2010;
45 Eklöf et al., 2012).

46 The existence of compensation has been verified in different ecosystems through
47 experimentation (Isbell et al., 2009; Hector et al., 2010) but few results have been obtained in
48 natural conditions without manipulation (Bai et al., 2004). In addition, the existing results
49 mainly concern fast growing species since they are easier to study under experimental
50 conditions (Cottingham et al., 2001). For forest ecosystems, the experimental approach is

51 more difficult to implement, especially because of the time required to achieve results.
52 Consequently, the results available in forestry mainly concern seedlings or young stands (Li et
53 al., 2010). Recently Houlahan et al. (2007) showed that fluctuations in abiotic factors such as
54 temperature and precipitation generally lead to a synchronous response of species, thus
55 questioning the importance of the compensation mechanism in natural communities. The
56 existence of compensation between tree species under natural conditions still largely remains
57 to be demonstrated (DeClerck et al., 2006).

58 In this work, we focus on the case of a biotic disturbance affecting a mixed forest of
59 sessile oak (*Quercus petraea* L.) and Scots pine (*Pinus Sylvestris* L.) in central France. The
60 disturbance was an outbreak of pine sawfly (*Diprion pini* L., Hymenoptera: Diprionidae), an
61 insect whose larvae feed only on pine needles (Barre et al., 2002) sometimes resulting in
62 complete defoliation and causing extensive damage in central and northern Europe (Geri,
63 1988). In the Orléans state forest, where our study was carried out, massive attacks were
64 observed in the early 1980s in all stands where pines were present (Geri and Goussard, 1984).
65 Because the pine sawfly is a host-specific insect, the competition from pines for light and
66 underground resources was probably greatly reduced throughout the infestation. In addition,
67 during such an outbreak, of insect feces and tissue is deposited on the soil, thus providing an
68 important source of nutrients for plants (de Groot and Turgeon, 1998). We therefore
69 hypothesize that the growth of oak in mixed oak-pine stands is particularly favored during
70 outbreaks of pine sawfly, and that this results in growth compensation between the two tree
71 species.

72 In short, the aim of our study was to determine whether there actually was growth
73 compensation between the two species during the disturbance caused by pine sawfly. We
74 quantified the growth variations in oak and pine during and outside of the disturbance period

75 by analyzing ring width and we determined the relationship between the growth variations of
76 the two species.

77 **2. Methods**

78 ***2.1 Site description and data collection***

79 We collected the growth data in mixed oak-pine stands from the Orléans state forest. This
80 forest is located in the plains of north-central France (47°51'N, 2°25'E) and covers 35 000 ha.
81 The region has a semi-continental climate with a mean annual temperature of 11°C and a
82 mean annual precipitation of about 700 mm. Soils are characterized by a layer of sand on an
83 impermeable layer of clay leading to periods of waterlogging in winter and periods of drought
84 in summer. Between 2006 and 2007, we established 9 plots (ranging in size from 0.5 to 1 ha)
85 in the southern part of the forest to study the growth in mixed oak-pine stands (Table 1). . The
86 distance between plots, ranging from 1.2 km to 21.4 km, was sufficient to consider them as
87 independent. In these plots, tree was analyzed in a previous study using point process
88 statistics (Ngo Bieng et al., 2006). The of oaks and pines are relatively similar, not differing
89 significantly from randomness or only slightly clustered where the specific are more
90 clustered (Table 1). . The nine plots included other broadleaved species (mainly *Carpinus*
91 *betulus* L., *Betula pendula* R. and *Sorbus torminalis* L.) but combined, they represent only 4%
92 of the total basal area on average.

93 In each plot, we selected 30 oaks and 30 pines based on a stratified sampling method. The
94 stratification variables were tree size and local environment (see Perot et al., 2010 for details).
95 Sampled trees were cored to the pith in two perpendicular directions at a height of 1.3 m. The
96 cores were scanned and analyzed using the WinDENDRO software, version 2005a (Regent,
97 2005), and ring width was measured to the nearest 0.01 mm. The COFECHA software
98 (Grissino-Mayer, 2002) was used to cross-date the individual ring-width series. The ring

99 width analyses were performed on a final total of 223 oaks and 271 pines. The mean oak age
100 at breast height per plot ranged from 52 to 78 years, and that of pines from 50 to 112 years
101 (Table 1). In any given plot, all the trees of the same species were approximately the same
102 age, thus indicating a single cohort for pines and a single cohort for oaks. In addition, for
103 seven plots, both the pines and oaks had approximately the same age. Pines were restricted to
104 the canopy of the stands while oaks occupied both the canopy and the understory, except in
105 plot P78 where oaks were almost exclusively in the understory.

106 To take into account the effect of climate on annual tree growth, we used data from the
107 meteorological station in Nogent-sur-Vernison (47°50'N, 02°45'E) located at an average
108 distance of 23 km from our plots. We used three climatic variables: monthly precipitation (P),
109 monthly minimum temperature (T_{min}) and monthly maximum temperature (T_{max}) from 1972 to
110 2005. For the study area, the growing season lasts from April to October (Lebourgeois et al.,
111 2010). We therefore calculated the climatic variables during the growing season (GS).
112 Because climatic conditions in the late fall and winter may contribute to the growth in the
113 following spring, we also calculated the climatic variables over the growing year (GY) that is,
114 for a given year n , the period from November of year $n-1$ to October of year n . In addition, for
115 a ring corresponding to a given year n , we tested the effect of the climatic variables of the
116 year $n-1$. Indeed, it has been demonstrated that the growing conditions of one year may
117 influence the growth of the following year (Barbaroux and Breda, 2002). Finally, to avoid the
118 influence of any particular month in a given year, we only used variables calculated for the
119 entire growing season or growing year. A total of twelve climatic variables ($\{P, T_{min},$
120 $T_{max}\} * \{GY, GS\} * \{year n, year n-1\}$) were tested to develop the ring width model.

121 **2.2 Ring width modeling under undisturbed conditions**

122 The outbreak of the early 1980s in central France was a typical outbreak for the pine
123 sawfly in the Atlantic plains of Europe (Geri and Goussard, 1984). . Total defoliation was

124 observed in autumn 1981 in the southern part of the Orléans forest but by autumn 1982, the
125 sawfly population had declined to very low levels. However, the insect has a complex life
126 cycle involving diapause phenomena (Hamel et al., 1998). During an outbreak, after the main
127 peak in population, secondary peaks can occur for several years because of adults emerging
128 after prolonged diapause.

129 Tree ring series generally exhibit a temporal trend related to tree age or to long-term
130 changes (Bontemps et al., 2010). To properly study the effect of a disturbance, it is necessary
131 to take this temporal trend into account (Cook and Kairiukstis, 1990). To model the temporal
132 trend, we chose a polynomial form because the studied period was relatively short (1972-
133 2005) and because model predictions outside of the studied period were not of interest in this
134 study. For each tree species, we developed a ring width model which takes into account a
135 temporal trend, a precipitation effect and a temperature effect. To correctly estimate the
136 climatic effects, we fitted the models with data from outside the disturbance period. The
137 temporal trend observed in the tree ring series generally varied from one tree to another in the
138 same stand, particularly because all of the trees had not experienced the same history. Some
139 of them had always been dominant whereas others had always been suppressed. Similarly, the
140 response of individual trees to climate may depend on their canopy position (Merian and
141 Lebourgeois, 2011). Following our sampling design, we included a plot random effect and a
142 tree random effect nested within plots. To account for tree level variability, we also
143 introduced a tree random component in the parameters related to the temporal trend and the
144 climatic effects. Our analyses showed a tree random effect on precipitation but not on
145 temperature. The general model fitted for a given species was a linear mixed-effect model
146 written as follows:

$$147 \quad RW_{k,i,t} = (\mu_0 + \mu_k + \mu_i) + (\alpha_0 + \alpha_i)t + (\beta_0 + \beta_i)t^2 + (\gamma_0 + \gamma_i)P + \lambda_0 T + \varepsilon_{k,i,t} \quad (1)$$

148 Where k is a plot, i is a tree, t the time variable in years ($t = 1$ corresponds to the year
 149 1972), $RW_{k,i,t}$ is the ring width for tree i in plot k at time t , P and T are respectively the
 150 precipitation variables and the temperature variables tested in this study (see section 2.1), $\{\mu_0,$
 151 $\alpha_0, \beta_0, \gamma_0, \lambda_0\}$ are the model parameters estimated for the fixed effects (time and climatic
 152 variables), μ_k is the random part of the model related to the plot level variability, $\{\mu_i, \alpha_i, \beta_i,$
 153 $\gamma_i\}$ correspond to the random part of the model related to tree level variability, and $\varepsilon_{k,i,t}$ is the
 154 residual part of the model.

155 Preliminary results showed that the variance of the residuals increased with the adjusted
 156 values and that there was a temporal autocorrelation between the observations. To correct the
 157 heteroscedasticity, we modeled the variance of the residuals with the fitted values and a power
 158 function (Eq. 2) as suggested by Pinheiro and Bates (2000).

$$159 \text{Var}(\varepsilon_{i,t}) = \sigma^2 |(\text{fitted value}_{i,t})|^{2\delta} \quad (2)$$

160 To model the temporal autocorrelation, we used classical autoregressive – moving
 161 average models (Pinheiro and Bates, 2000).

162 ***2.3 Measuring the disturbance effect on growth and determining the relationship*** 163 ***between growth variations of each species***

164 To measure the effect of the disturbance on the growth of a species, we calculated for
 165 each tree and each year the relative difference between the observed ring width and the ring
 166 width predicted by the model under undisturbed conditions (RD):

$$167 RD_i = \frac{(y_i - \hat{y}_i)}{\hat{y}_i}$$

168 where y_i and \hat{y}_i are respectively the observed and the predicted ring width for a tree i .
 169 RD is similar to relative tree-ring indices used in dendrochronology (Cook and Kairiukstis,
 170 1990). We then calculated the mean relative differences (MRD) for each year, each plot and
 171 each species:

172
$$MRD_{species,plot,year} = \frac{1}{n} \sum_{i=1}^n RD_{i,species,plot,year}$$

173 where n is the number of trees in a plot for one species. In undisturbed conditions,
 174 changes in MRD correspond to the effects of factors not included in the model such as
 175 unmeasured climatic factors, or to special events such as silvicultural actions. For the
 176 disturbance period, MRD represents the relative difference between the observed growth and
 177 the growth expected if there had been no disturbance. MRD is a relative index valid for a
 178 given species in a given stand. We used this index to study the changes in the growth of oak
 179 compared to those of pine. For the disturbance period, we obtained 54 values for each species
 180 (6 years * 9 plots). Growth compensation between the two species should lead to a negative
 181 correlation between the oak $MRDs$ and those of pine. In other words, during the disturbance
 182 and for a given year, a strong reduction in pine growth should be associated to a strong
 183 increase in oak growth. To test this hypothesis, we performed a covariance analysis on the
 184 disturbance period (1981-1986) between the oak $MRDs$ and the pine $MRDs$ with year as a
 185 factor. In this analysis, plot was treated as a random effect, to allow the intercept to vary with
 186 location (preliminary results showed no plot random effect on the slope for this analysis). To
 187 verify that the disturbance did indeed lead to a shift in the correlation between growth
 188 variations of the species, we also performed a covariance analysis on the 1972-2005 period
 189 between the oak $MRDs$ and the pine $MRDs$ with a disturbance factor and a plot random
 190 component.

191 All the models were fitted using the R software version 2.14.0 (R Development Core
 192 Team, 2011) with the lme function of the nlme package (Pinheiro et al., 2011). Modeling the
 193 variance and the temporal autocorrelation of eq. 1 were also performed with the lme function.
 194 To compare different models, we used the For the final adjustments, the model parameters
 195 were estimated using the restricted maximum likelihood method (REML).

196 **3. Results**

197 **3.1 Results from ring width models**

198 The climatic variables included in the oak model were total precipitation over the current
199 growing year and average maximum temperature over the growing season of the previous
200 year (Table 2). For pine, the climatic variables of the ring width model were total
201 precipitation over the current growing year and average minimum temperature over the
202 current growing season. For both species, total precipitation over the growing year is the
203 climatic variable that best explained ring width variability. The parameters of the time
204 variable indicate that the shape of the growth curve over the studied period is not the same for
205 oak and pine. On average, the growth of pine trees before the disturbance decreases while that
206 of the oak trees increases. These results confirm the need to model the temporal trend and the
207 climatic effects for each species in order to correctly estimate the disturbance effect on ring
208 width.

209 **3.2 Changes in oak and pine growth after the pine sawfly attack**

210 As we expected, pine growth decreased during the disturbance period (Figure 1) and
211 varied from one plot to another. The greatest decrease occurred in 1982 with an average *MRD*
212 of -63% ($-92\% < MRD < -27\%$). The *MRD* then increased until 1985 with an average of -17%
213 ($-39\% < MRD < 3\%$). In 1986, the *MRD* decreased again with an average of -43% ($-60\% <$
214 *MRD* $< -26\%$).

215 For oak, the results show that there is an overall increase in growth during the
216 disturbance. As for pine, the oak reaction varied from one plot to another. The growth
217 increase was the greatest in 1982 with an average *MRD* of 45% ($7\% < MRD < 80\%$), then
218 *MRD* gradually decreased until 1986 with an average of 7% ($-18\% < MRD < 33\%$).

219 **3.3 Relationship between the growth variations of the two species during and outside**
220 ***the disturbance period***

221 The results show a positive correlation between the *MRD* of the two species over the
222 undisturbed period and a negative correlation over the disturbance period (Figure 2).

223 The covariance analysis on the 1972-2005 period revealed that the slope of the regression
224 between the oak *MRD* and the pine *MRD* over the undisturbed period was 0.38. During the
225 disturbance period this slope was -0.69 (Table 3).

226 The covariance analysis performed on the disturbance period shows that the effect of the
227 pine *MRD* on the oak *MRD* was significant (Table 4). For each year of the disturbance, a
228 reduction in pine growth was associated to an increase in oak growth. The covariance analysis
229 also shows that the intensity of the oak response depended on the growth year. For the years
230 1981 and 1986, a reduction in pine growth of 100% resulted in an increase in oak growth of
231 30% while for the years 1982 to 1985, a reduction in pine growth of 100% resulted in an
232 increase in oak growth of 61%.

233 **4. Discussion**

234 **4.1 Growth compensation in mixed forests**

235 In this study, we hoped to determine whether there was growth compensation between
236 two tree species following a biotic disturbance affecting one tree species only in mixed stands
237 of sessile oak and Scots pine. Our results show, as expected, that the pines suffered a decrease
238 in growth after the pine sawfly attack. The greatest decrease in growth for pine was observed
239 in 1982, which is logical since peak defoliation in the forest occurred in autumn 1981 (Geri
240 and Goussard, 1984). In 1982, we estimated that pine growth had decreased by between 27%
241 and 92% compared to a situation without disturbance. This variability indicates that the
242 intensity of defoliation was not uniform throughout the forest. According to the meta-analysis

243 conducted by Jactel and Brockerhoff (2007), damage caused by oligophagous insects like the
244 pine sawfly is less severe in mixed forests than in pure forests. Three main mechanisms have
245 been proposed to explain this effect: a decrease in host concentration, making host trees more
246 difficult to locate (Vehvilainen et al., 2006), chemical barriers provided by the alternative
247 species (Jactel et al., 2011) and an increase in natural enemies benefitting from the presence
248 of several tree species for their life cycle (Kaitaniemi et al., 2007). The initial variability in
249 stand composition may thus explain part of the variability that we observed in the response of
250 pine.

251 Concurrent to the decrease in growth for pines, our results show that the growth of oak in
252 mixed stands increased during the disturbance period. . As we suggested in the introduction of
253 this article, this compensation can be explained by reduced competition from the defoliated
254 pine for light and underground resources. It can also be explained by the fertilizing effect
255 associated with insect feces and dead tissue (de Groot and Turgeon, 1998). Both mechanisms,
256 the reduction in interspecific competition and the fertilizing effect, are likely to come into
257 play simultaneously and the available data do not make it possible . However, the covariance
258 analysis performed on the disturbance period shows that the growth variation of oak for the
259 three years following peak defoliation is not simply related to the growth variation of pine
260 over the same period (Table 4). This result could be explained by the fact that just after peak
261 defoliation, the oaks may have benefited from both the reduction in interspecific competition
262 and the fertilizing effect. The fertilizing effect after peak defoliation would have a short term
263 impact while the reduction in interspecific competition would have a longer-term impact
264 because it would take the affected pine trees several years to recover full foliage.

265 . Some of them on herbivory insects, such as the gypsy moth (*Lymantria dispar* L.) and
266 the western spruce budworm (*Choristoneura fumiferana* Clem.), are comparable to our study.
267 Some authors have shown an increase in growth for tree species classified as non-host species

268 (Muzika and Liebhold, 1999; Jedlicka et al., 2004), while others did not observe any effect
269 (Naidoo and Lechowicz, 2001). However, the compensation phenomenon between species
270 *per se* has rarely been studied. In addition, tree species found in mixed stands are sometimes
271 secondary hosts for the insect responsible for the disturbance and this makes the analysis
272 more difficult, . In addition, the impact of climatic factors is sometimes not taken into account
273 because climatic data are not always available for long-term series. To our knowledge, our
274 study is the first that clearly shows growth compensation between two tree species following
275 a disturbance caused by a biotic agent in a natural forest ecosystem.

276 The relationship between the response of oak and that of pine shows some variability
277 (Figure 2). The response of oak is probably dependent on the intensity of the interspecific
278 competition prior to the disturbance, which in turn depends on and on the developmental
279 stage of both species when the attack occurred. Future investigations are necessary to evaluate
280 the stand features that influence tree species growth responses following pine sawfly
281 defoliations in mixed forests.

282 ***4.2 Interspecific growth compensation: a mechanism that would especially occur in the*** 283 ***case of biotic disturbances***

284 In undisturbed conditions, our results show that the *MRD* of oak and pine are positively
285 correlated (Figure 2). This suggests that, in undisturbed conditions, changes in environmental
286 conditions have the same overall effect on both species. Houlahan et al. (2007) and Valone
287 and Barber (2008) who found that, in natural communities, species abundance co-varies
288 positively rather than negatively, which is the opposite of what would be expected if the
289 compensation phenomena were important. Houlahan et al. (2007) and Valone and Barber
290 (2008) also suggest that abiotic factors such as rainfall and temperature are the most important
291 explanatory factors for interannual fluctuations in species abundance within communities and
292 that coexisting species respond in similar ways to these climatic factors. This is the case in

293 our study where annual precipitation is an abiotic factor synchronizing the two species.
294 Valone and Barber (2008) conclude that compensatory effect was not a strong mechanism in
295 stabilizing fluctuations in natural terrestrial communities. This statement is consistent with
296 what we observed in undisturbed conditions. However, it no longer holds true for the
297 disturbance period where we have shown growth compensation between the two species. The
298 result of the growth compensation that we observed is a shift in the correlation between the
299 growth of the two species (Figure 2). This shift corresponds to a temporary phase opposition
300 between the growth of oak and the growth of pine, well-illustrated by the results obtained in
301 Plot P534 (Figure 3).

302 Before the attack by the pine sawfly, the growths of the two species were well
303 synchronized with a positive covariation. After the attack, the growths of two species were
304 still synchronized but showed a negative covariation. After a period of about seven years, the
305 of both species once again a positive covariation. Even total, defoliation by the pine sawfly
306 does not systematically kill the tree; a large percentage of the population typically survives
307 (Augustaitis, 2007), but affected pine trees take several years to recover normal growth. The
308 benefit observed on oak growth after pine defoliation ends when interspecific competition for
309 resources is restored and when the fertilizing effect disappears. Fluctuations in tree growth are
310 then once again mainly driven by climatic factors as they were before the disturbance and the
311 growth of the two species co-vary positively. This result shows that in a mixed stand subject
312 to biotic disturbances, the production function can be stabilized through differences in species
313 response to the disturbance. Oak leaves, unlike those of pine, were not consumed by the pine
314 sawfly. This difference is responsible for the growth compensation that we observed. There
315 probably would have been no compensation if the stands had been mixed with two pine
316 species both vulnerable to defoliation (eg *Pinus sylvestris* and *Pinus nigra*). Our results
317 reinforce the idea that the diversity in species response to the disturbance is more important

318 than simple species diversity (DeClerck et al., 2006; Jactel and Brockerhoff, 2007) and we
319 suggest that growth compensations play an important role in stabilizing the production
320 function for an ecosystem affected by periodic biotic disturbances. From a practical point of
321 view, the results of this study show the importance of managing for mixed forests in an
322 environment affected by biotic disturbances to minimize potential production losses. .

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335 **6. References**

- 336 Assmann, E., 1970. The principles of forest yield study. Pergamon press, Oxford - New York
337 - Toronto - Sydney - Braunschweig.
- 338 Augustaitis, A., 2007. Pine sawfly (*Diprion pini* L.) - Related changes in Scots pine crown
339 defoliation and possibilities of recovery. *Pol J Environ Stud* 16, 363-369.
- 340 Bai, Y.F., Han, X.G., Wu, J.G., Chen, Z.Z., Li, L.H., 2004. Ecosystem stability and
341 compensatory effects in the Inner Mongolia grassland. *Nature* 431, 181-184.

342 Barbaroux, C., Breda, N., 2002. Contrasting distribution and seasonal dynamics of
343 carbohydrate reserves in stem wood of adult ring-porous sessile oak and diffuse-
344 porous beech trees. *Tree Physiol* 22, 1201-1210.

345 Barre, F., Milsant, F., Palasse, C., Prigent, V., Goussard, F., Geri, C., 2002. Preference and
346 performance of the sawfly *Diprion pini* on host and non-host plants of the genus
347 *Pinus*. *Entomol Exp Appl* 102, 229-237.

348 Bontemps, J.D., Hervé, J.C., Dhôte, J.F., 2010. Dominant radial and height growth reveal
349 comparable historical variations for common beech in north-eastern France. *For Ecol*
350 *Manag* 259, 1455-1463.

351 Chen, H.Y.H., Klinka, K., 2003. Aboveground productivity of western hemlock and western
352 redcedar mixed-species stands in southern coastal British Columbia. *For Ecol Manag*
353 184, 55-64.

354 Cook, E.R., Kairiukstis, L.A., 1990. *Methods of Dendrochronology. Applications in the*
355 *environmental sciences*. Kluwer Academic Publishers, Dordrecht, Boston, London.

356 Cottingham, K.L., Brown, B.L., Lennon, J.T., 2001. Biodiversity may regulate the temporal
357 variability of ecological systems. *Ecol Lett* 4, 72-85.

358 de Groot, P., Turgeon, J.J., 1998. Insect-pine interactions. In: Richardson, D.M. (Ed.),
359 *Ecology and biogeography of Pinus*. Cambridge university Press, Cambridge, UK,
360 pp. 354-380.

361 DeClerck, F.A.J., Barbour, M.G., Sawyer, J.O., 2006. Species richness and stand stability in
362 conifer forests of the Sierra Nevada. *Ecology* 87, 2787-2799.

363 Eklöf, J.S., Alsterberg, C., Havenhand, J.N., Sundbäck, K., Wood, H.L., Gamfeldt, L., 2012.
364 Experimental climate change weakens the insurance effect of biodiversity. *Ecol Lett*
365 15, 864-872.

366 Geri, C., 1988. The pine sawfly in central France. In: Berryman, A.A. (Ed.), Dynamics of
367 Forest Insect Populations. Patterns, Causes, Implications. Plenum Press, New-York,
368 pp. 377–405.

369 Geri, C., Goussard, F., 1984. Evolution d'une nouvelle gradation de lophyre du pin (*Diprion*
370 *pini* L.) dans le sud du Bassin Parisien. I. - Développement de la gradation jusqu'en
371 1982 et relation avec les facteurs du milieu. *Annales Des Sciences Forestieres* 41,
372 376-403.

373 Grissino-Mayer, H.D., 2002. Research report evaluating crossdating accuracy: a manual and
374 tutorial for the computer program COFECHA. *Tree-Ring Research* 57, 205-221.

375 Hamel, M., Geri, C., Auger-Rozenberg, A., 1998. The effects of 20-hydroxyecdysone on
376 breaking diapause of *Diprion pini* L. (Hym., Diprionidae). *Physiol Entomol* 23, 337-
377 346.

378 Hector, A., Hautier, Y., Saner, P., Wacker, L., Bagchi, R., Joshi, J., Scherer-Lorenzen, M.,
379 Spehn, E.M., Bazeley-White, E., Weilenmann, M., Caldeira, M.C., Dimitrakopoulos,
380 P.G., Finn, J.A., Huss-Danell, K., Jumpponen, A., Mulder, C.P.H., Palmborg, C.,
381 Pereira, J.S., Siamantziouras, A.S.D., Terry, A.C., Troumbis, A.Y., Schmid, B.,
382 Loreau, M., 2010. General stabilizing effects of plant diversity on grassland
383 productivity through population asynchrony and overyielding. *Ecology* 91, 2213-
384 2220.

385 Houlahan, J.E., Currie, D.J., Cottenie, K., Cumming, G.S., Ernest, S.K.M., Findlay, C.S.,
386 Fuhlendorf, S.D., Gaedke, U., Legendre, P., Magnuson, J.J., McArdle, B.H.,
387 Muldavin, E.H., Noble, D., Russell, R., Stevens, R.D., Willis, T.J., Woiwod, I.P.,
388 Wondzell, S.M., 2007. Compensatory dynamics are rare in natural ecological
389 communities. *Proc Natl Acad Sci U S A* 104, 3273-3277.

390 Isbell, F.I., Polley, H.W., Wilsey, B.J., 2009. Biodiversity, productivity and the temporal
391 stability of productivity: patterns and processes. *Ecol Lett* 12, 443-451.

392 Jactel, H., Birgersson, G., Andersson, S., Schlyter, F., 2011. Non-host volatiles mediate
393 associational resistance to the pine processionary moth. *Oecologia* 166, 703-711.

394 Jactel, H., Brockerhoff, E.G., 2007. Tree diversity reduces herbivory by forest insects. *Ecol*
395 *Lett* 10, 835-848.

396 Jedlicka, J., Vandermeer, J., Aviles-Vazquez, K., Barros, O., Perfecto, I., 2004. Gypsy moth
397 defoliation of oak trees and a positive response of red maple and black cherry: An
398 example of indirect interaction. *Am Midl Nat* 152, 231-236.

399 Kaitaniemi, P., Riihimaki, J., Koricheva, J., Vehvilainen, H., 2007. Experimental evidence for
400 associational resistance against the European pine sawfly in mixed tree stands. *Silva*
401 *Fenn* 41, 259-268.

402 Laurent-Hervouet, N., 1986. Radial growth losses in some species of *Pinus* due to 2 forest
403 defoliators .2. Case of the pine sawfly in the Bassin Parisien. *Ann For Sci* 43, 419-
404 440.

405 Lebourgeois, F., Pierrat, J.C., Perez, V., Piedallu, C., Cecchini, S., Ulrich, E., 2010.
406 Simulating phenological shifts in French temperate forests under two climatic change
407 scenarios and four driving global circulation models. *Int J Biometeorol* 54, 563-581.

408 Li, Q.A., Liang, Y., Tong, B., Du, X.J., Ma, K.P., 2010. Compensatory effects between *Pinus*
409 *massoniana* and broadleaved tree species. *Journal of Plant Ecology-Uk* 3, 183-189.

410 Loreau, M., Downing, A., Emmerson, M., Gonzalez, A., Hughes, J., Inchausti, P., Joshi, J.,
411 Norberg, J., Sala, O., 2002. A new look at the relationship between diversity and
412 stability. In, *Biodiversity and ecosystem functioning : synthesis and perspectives*.
413 Oxford University Press, Oxford, UK, pp. 79-91.

414 McNaughton, S.J., 1977. Diversity and stability of ecological communities - comment on role
415 of empiricism in ecology. *Am Nat* 111, 515-525.

416 MCPFE, UNECE, FAO, 2007. State of Europe's forests 2007. MCPFE, Warsaw.

417 Merian, P., Lebourgeois, F., 2011. Size-mediated climate-growth relationships in temperate
418 forests: a multi-species analysis. *For Ecol Manag* 261, 1382-1391.

419 Muzika, R.M., Liebhold, A.M., 1999. Changes in radial increment of host and nonhost tree
420 species with gypsy moth defoliation. *Can J For Res* 29, 1365-1373.

421 Naidoo, R., Lechowicz, M.J., 2001. Effects of gypsy moth on radial growth of deciduous
422 trees. *For Sci* 47, 338-348.

423 Ngo Bieng, M.A., Ginisty, C., Goreaud, F., Perot, T., 2006. A first typology of Oak and Scots
424 pine mixed stands in the Orleans forest (France), based on the canopy spatial
425 structure. *N Z J For Sci* 36, 325-346.

426 Perot, T., Goreaud, F., Ginisty, C., Dhôte, J.F., 2010. A model bridging distance-dependent
427 and distance-independent tree models to simulate the growth of mixed forests. *Ann*
428 *For Sci* 67, 502p501-502p511.

429 Perot, T., Picard, N., 2012. Mixture enhances productivity in a two-species forest: evidence
430 from a modelling approach. *Ecol Res* 27, 83-94.

431 Pinheiro, J.C., Bates, D.M., 2000. *Mixed-effects models in S and S-PLUS*. Springer, New
432 York.

433 Pinheiro, J.C., Bates, D.M., DebRoy, S., Sarkar, D., the R Development Core Team, 2011.
434 *nlme: linear and nonlinear mixed effects models*. R package version 3.1-101.

435 Pretzsch, H., Block, J., Dieler, J., Hoang Dong, P., Kohnle, U., Nagel, J., Spellmann, H.,
436 Zingg, A., 2010. Comparison between the productivity of pure and mixed stands of
437 Norway spruce and European beech along an ecological gradient. *Ann For Sci* 67,
438 712.

439 Pretzsch, H., Schütze, G., 2009. Transgressive overyielding in mixed compared with pure
440 stands of Norway spruce and European beech in Central Europe: evidence on stand
441 level and explanation on individual tree level. *Eur. J. For. Res.* 128, 183-204.

442 R Development Core Team, 2011. R: A language and environment for statistical computing.
443 R Foundation for Statistical Computing, Vienna, Austria.

444 Regent, I., 2005. *Windendro 2005a: manual for tree-ring analysis*. Université du Québec à
445 Chicoutimi.

446 Rousselet, J., 1999. Sex determination, diapause and karyotype evolution in conifer sawflies.
447 Investigations on *Diprion pini* (L.), an outbreak forest pest species. In, *Science de la*
448 *vie*. University of Tours, Tours, France, p. 128.

449 Tilman, D., 1999. The ecological consequences of changes in biodiversity: A search for
450 general principles. *Ecology* 80, 1455-1474.

451 Vallet, P., Perot, T., 2011. Silver fir stand productivity is enhanced when mixed with Norway
452 spruce: evidence based on large-scale inventory data and a generic modelling
453 approach. *J Veg Sci* 22, 932-942.

454 Valone, T.J., Barber, N.A., 2008. An empirical evaluation of the insurance hypothesis in
455 diversity-stability models. *Ecology* 89, 522-531.

456 Vehviläinen, H., Koricheva, J., Ruohomäki, K., Johansson, T., Valkonen, S., 2006. Effects of
457 tree stand species composition on insect herbivory of silver birch in boreal forests.
458 *Basic Appl. Ecol.* 7, 1-11.

459 Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating
460 environment: The insurance hypothesis. *Proc Natl Acad Sci U S A* 96, 1463-1468.

461

7. Tables

Table 1: Dendrometric characteristics of the plots in the Orléans Forest, France. BA = basal area; Other = other broadleaf tree species.

D = mean diameter at a height of 130 cm; Age = mean age of the cored trees at a height of 130 cm. For diameters and ages, values represent the mean with the standard deviation in parentheses; SP_{oak} and SP_{pine} are respectively spatial pattern of oaks and pines for the canopy layer, R = random pattern and Cl = clustered pattern.

Plot	Area (ha)	BA _{oak} (m ² .ha ⁻¹)	BA _{pine} (m ² .ha ⁻¹)	BA _{other} (m ² .ha ⁻¹)	BA _{total} (m ² .ha ⁻¹)	D _{oak} (cm)	D _{pine} (cm)	D _{other} (cm)	Age _{oak}	Age _{pine}	SP _{oak}	SP _{pine}
P108	0.80	9.6	19.8	1.4	30.8	17.7 (6.74)	36.2 (5.31)	12.9 (4.11)	68 (4.3)	66 (2.5)	R	R
P178	1.00	16.5	10.0	1.5	28.0	21.5 (10.49)	36.5 (7.56)	14.1 (5.28)	78 (4.6)	77 (1.8)	Cl	Cl
P184	0.75	10.9	12.0	2.1	25.1	17.5 (8.88)	36.3 (7.76)	12.7 (4.17)	71 (8.6)	68 (4.2)	R	Cl
P216_2	0.50	11.2	12.1	0.9	24.1	17.0 (6.39)	27.8 (7.6)	11.8 (4.92)	52 (2.8)	50 (2.2)	R	R
P255	1.00	12.6	10.5	1.1	24.2	17.8 (7.54)	31.7 (6.25)	15.2 (5.86)	69 (5.9)	62 (4.6)	R	R
P534	0.50	12.2	19.6	1.0	32.7	16.6 (6.54)	37.4 (6.5)	13 (4.78)	59 (2.3)	83 (3.2)	R	R
P563	0.50	13.6	11.9	0.2	25.7	25.1 (10.12)	35.6 (4.58)	11.3 (2.56)	70 (3.1)	69 (2.3)	R	R
P57	1.00	11.2	11.4	0.4	23.0	16.7 (6.36)	34.3 (6.41)	11.6 (3.65)	67 (7.1)	62 (3.1)	Cl	Cl
P78	0.70	14.7	16.5	1.0	32.2	20.1 (7.48)	42.2 (8.79)	13.9 (5.06)	62 (5.2)	112 (17.5)	R	R

Table 2: Parameter estimates and statistical results of the ring width models for oak and pine (see Eq. 1). P : precipitations during the growing season. $TminGS$: average minimum temperature during the growing season. $TmaxGS_{n-1}$: average maximum temperature during the growing season of the previous year. σ_{plot} and σ_{tree} are the random parameters of the model. δ is the parameter of the variance model (see Eq. 2). θ_1 and θ_2 are the parameters of the moving average autocorrelation model.

		Parameters estimates							
		Intercept	t	t^2	P	$TminGS$			
		μ_0 (mm)	α_0 (mm.year ⁻¹)	β_0 (mm.year ⁻¹)	γ_0 (mm.mm ⁻¹)	λ_0 (mm.°C ⁻¹)	δ	θ_1	θ_2
Pine	Estimates	2.36	-0.0423	8.91×10^{-4}	1.34×10^{-3}	-0.159	0.794	0.446	0.124
	Std. error	0.07	0.0037	0.966×10^{-4}	0.04×10^{-3}	0.006			
	P-value	<0.001	<0.001	<0.001	<0.001	<0.001	RSE	df	AIC
	σ_{tree}	0.461	0.0492	12.2×10^{-4}	0.49×10^{-3}		0.305	7313	6600
	σ_{plot}	0.065							
		Intercept	t	t^2	P	$TmaxGS_{n-1}$	δ	θ_1	θ_2
Oak	Estimates	1.10	0.0283	-6.91×10^{-4}	0.954×10^{-3}	-0.0313	0.890	0.532	0.240
	Std. error	0.072	0.0032	0.93×10^{-4}	0.041×10^{-3}	0.0026			
	P-value	<0.001	<0.001	<0.001	<0.001	<0.001	RSE	df	AIC
	σ_{tree}	0.343	0.0330	9.82×10^{-4}	0.527×10^{-3}		0.323	6017	4848
	σ_{plot}	0.133							

Table 3: Results of the covariance analysis for the 1972-2005 period between oak mean relative deviation (MRD) and pine MRD with a disturbance factor. σ is the standard deviation of the random effect.

Fitted model: $MRD_{oak,k,j,t} = m + (d_k + d_j)MRD_{pine,k,j,t} + \varepsilon_{k,j,t}$

k = level of the disturbance factor (0 = undisturbed and 1 = disturbance); j = plot; t = year

d_k is the disturbance effect on the slope and d_i is the random part of the slope related to the plot level variability.

Coefficients	Estimate	Std. error	P-value	σ	RSE	df	AIC
m (Intercept)	0.00337	0.0109	0.975	0.150	0.180	295	-153
d_0 (undisturbed period)	0.383	0.081	<0.001				
d_1 (disturbance period)	-0.689	0.083	<0.001				

Table 4: Results of the covariance analysis for the disturbance period (1981-1986) between oak mean relative deviation (MRD) and pine MRD with a year factor. The year coefficients from 1982 to 1985 were pooled because they were not significantly different. σ is the standard deviation of the random effect.

Fitted model: $MRD_{oak,j,t} = m + m_j + m_t + (d)MRD_{pine,j,t} + \varepsilon_{j,t}$

j = plot; t = year; m_t is the year effect on the intercept (two level, 0 = year 1981 and 1986 and 1 = year 1982 to 1985), m_j is the random part of the intercept related to the plot level variability.

Coefficients	Estimate	Std. error	P-value	σ	RSE	df	AIC
m	-0.0930	0.0603	0.192	0.147	0.123	43	-33.3
m_1 (year 1982 to 1985)	0.311	0.037	<0.001				
d	-0.388	0.080	<0.001				

8. Figure legends

Figure 1: Mean relative deviation (*MRD*) for oak and pine over the 1972-2005 period including the disturbance period (1981-1986). Each point is the species *MRD* for one plot. The dashed lines connect the minimum and maximum values on the nine plots for each species.

Figure 2: Mean relative deviation (*MRD*) between observed ring width and predicted ring width under undisturbed conditions of oak according to the *MRD* of pine. Each point is the species *MRD* for one plot at one year. Results are given for the undisturbed period and for the disturbance period. Solid lines are the regression lines obtained for the undisturbed period and for the disturbance period.

Figure 3: Difference between the observed ring width and the ring width expected under undisturbed conditions according to the growth year for the sample trees on plot P534. The solid line represents the median values obtained for the sample trees. The dashed curves represent the first and third quartiles of the values.

9. Figures

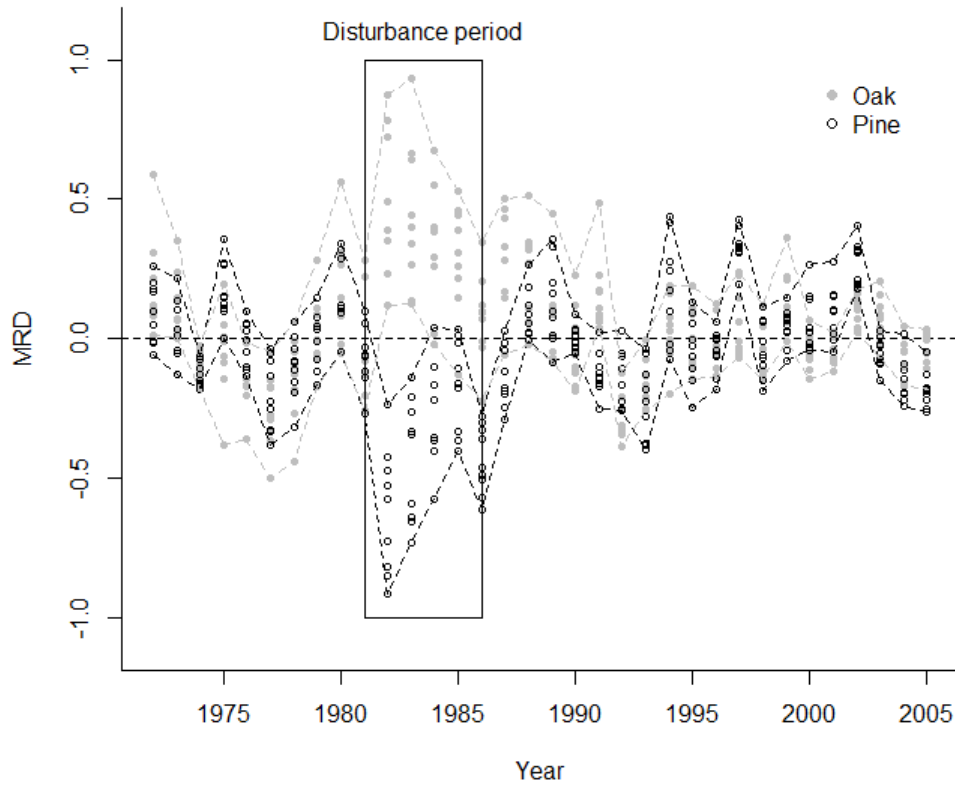


Figure 1

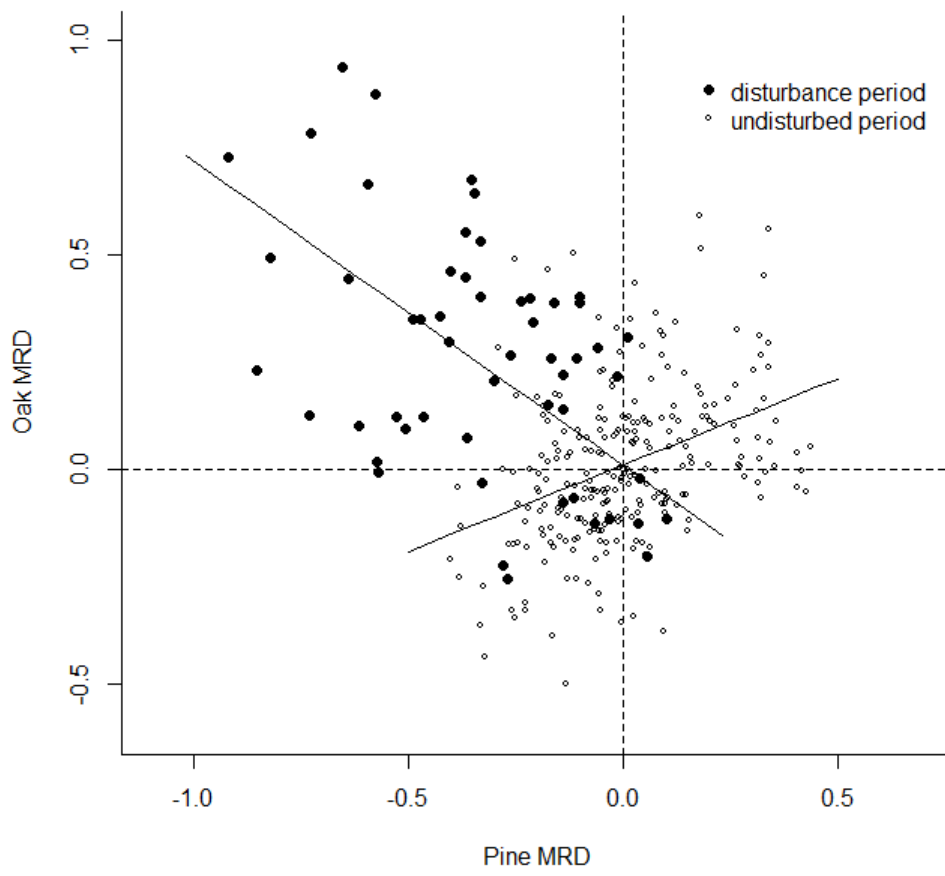


Figure 2

Plot P534 (0.5 ha)

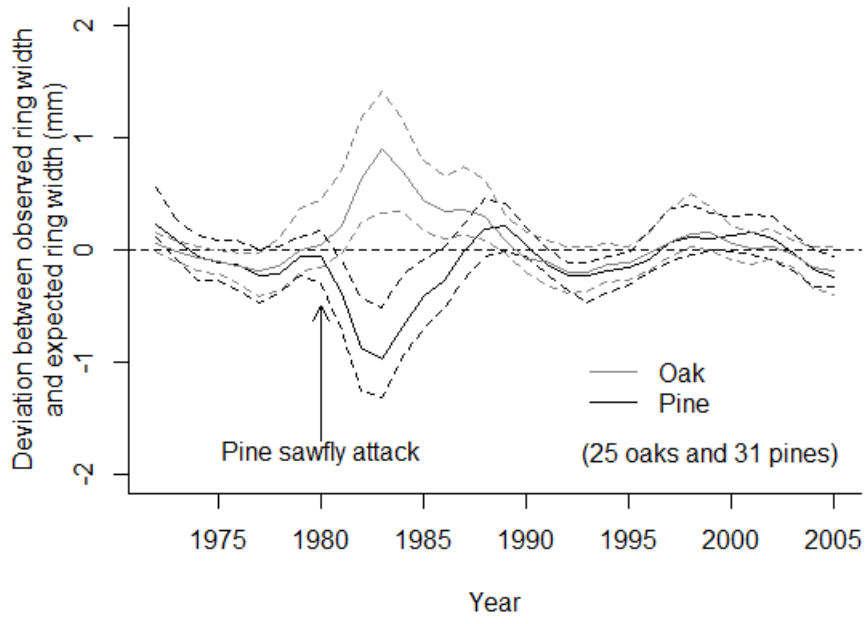


Figure 3