



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

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## ABSTRACT

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

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## 1. Introduction

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

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

The existence of compensation has been verified in different ecosystems through experimentation (Isbell et al., 2009; Hector et al., 2010) but few results have been obtained in natural conditions without manipulation (Bai et al., 2004). In addition, the existing results mainly concern fast growing species since they are easier to study under experimental conditions (Cottingham et al., 2001). For forest ecosystems, the experimental approach is more difficult to implement, especially because of the time required to achieve results. Consequently, the results available in forestry mainly concern seedlings or young stands (Li et al., 2010). Recently Houlahan et al. (2007) showed that fluctuations in abiotic factors such as temperature and precipitation generally lead to a

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synchronous response of species, thus questioning the importance of the compensation mechanism in natural communities. The existence of compensation between tree species under natural conditions still largely remains to be demonstrated (DeClerck et al., 2006).

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

In short, the aim of our study was to determine whether there actually was growth compensation between the two species during the disturbance caused by pine sawfly. We quantified the growth variations in oak and pine during and outside of the disturbance period by analyzing ring width and we determined the relationship between the growth variations of the two species.

## 2. Methods

### 2.1. Site description and data collection

We collected the growth data in mixed oak–pine stands from the Orléans state forest. This forest is located in the plains of north-central France (47°51'N, 2°25'E) and covers 35,000 ha. The region has a semi-continental climate with a mean annual temperature of 11 °C and a mean annual precipitation of about 700 mm. Soils are characterized by a layer of sand on an impermeable layer of clay leading to periods of waterlogging in winter and periods of drought in summer. Between 2006 and 2007, we established 9 plots (ranging in size from 0.5 to 1 ha) in the southern part of the forest to study the growth in mixed oak–pine stands (Table 1). The plots were chosen to be well-balanced between oak and pine basal area, to be in the same range of diameters for each species, and to have soils as homogeneous as possible. Soil homogeneity was assessed using soil cores and flora descriptions. To avoid confounding effects with climatic variables, we also verified with his-

torical archives that plots were not strongly affected by storms or fires. The distance between plots, ranging from 1.2 km to 21.4 km, was sufficient to consider them as independent. In these plots, tree spatial pattern was analyzed in a previous study using point process statistics (Ngo Bieng et al., 2006). The spatial pattern of oaks and pines are relatively similar, not differing significantly from randomness or only slightly clustered except in three plots where the specific patterns are more clustered (Table 1). Oaks and pines are independently distributed in the plots or there is only a slight interspecific repulsion. The nine plots included other broadleaved species (mainly *Carpinus betulus* L., *Betula pendula* R. and *Sorbus torminalis* L.) but combined, they represent only 4% of the total basal area on average.

In each plot, we selected 30 oaks and 30 pines based on a stratified sampling method. The stratification variables were tree size and local environment (see Perot et al. (2010) for details). Sampled trees were cored to the pith in two perpendicular directions at a height of 1.3 m. The cores were scanned and analyzed using the WinDENDRO software, version 2005a (Regent, 2005), and ring width was measured to the nearest 0.01 mm. The COFECHA software (Grissino-Mayer, 2002) was used to cross-date the individual ring-width series. The ring width analyses were performed on a final total of 223 oaks and 271 pines. The mean oak age at breast height per plot ranged from 52 to 78 years, and that of pines from 50 to 112 years (Table 1). In any given plot, all the trees of the same species were approximately the same age, thus indicating a single cohort for pines and a single cohort for oaks. In addition, for seven plots, both the pines and oaks had approximately the same age. Pines were restricted to the canopy of the stands while oaks occupied both the canopy and the understory, except in plot P78 where oaks were almost exclusively in the understory.

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

**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 <sub>oak</sub> (m <sup>2</sup> ha <sup>-1</sup> )	BA <sub>pine</sub> (m <sup>2</sup> ha <sup>-1</sup> )	BA <sub>other</sub> (m <sup>2</sup> ha <sup>-1</sup> )	BA <sub>total</sub> (m <sup>2</sup> ha <sup>-1</sup> )	$D_{oak}$ (cm)	$D_{pine}$ (cm)	$D_{other}$ (cm)	Age <sub>oak</sub>	Age <sub>pine</sub>	$SP_{oak}$	$SP_{pine}$
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

A total of 12 climatic variables ( $\{P, T_{min}, T_{max}\} * \{GY, GS\} * \{\text{year } n, \text{year } n-1\}$ ) were tested to develop the ring width model.

## 2.2. Ring width modeling under undisturbed conditions

The outbreak of the early 1980s in central France was a typical outbreak for the pine sawfly in the Atlantic plains of Europe (Geri and Goussard, 1984). It was a brief outbreak with especially one year with a high level of insect population. Total defoliation was observed in autumn 1981 in the southern part of the Orléans forest but by autumn 1982, the sawfly population had declined to very low levels. However, the insect has a complex life cycle involving diapause phenomena (Hamel et al., 1998). During an outbreak, after the main peak in population, secondary peaks can occur for several years because of adults emerging after prolonged diapause. According to available data, the first defoliations in the forest stands that we studied were observed during the autumn of 1980 (Laurent-Hervouet, 1986) and attacks occurred until 1985 (Rousselet, 1999). We defined the disturbance period of the outbreak as the growing years following the first defoliation (year 1981) to the growing year following the last defoliation (year 1986).

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

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

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

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

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

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

## 2.3. Measuring the disturbance effect on growth and determining the relationship between growth variations of each species

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

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

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

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

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

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

## 3. Results

### 3.1. Results from ring width models

The climatic variables included in the oak model were total precipitation over the current growing year and average maximum temperature over the growing season of the previous year (Table 2). For pine, the climatic variables of the ring width model were total precipitation over the current growing year and average minimum

**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. *T<sub>minGS</sub>*: average minimum temperature during the growing season. *T<sub>maxGS</sub><sub>n-1</sub>*: average maximum temperature during the growing season of the previous year.  $\sigma_{\text{plot}}$  and  $\sigma_{\text{tree}}$  are the random parameters of the model.  $\delta$  is the parameter of the variance model (see Eq. (2)).  $\theta_1$  and  $\theta_2$  are the parameters of the moving average autocorrelation model.

	Parameters estimates							
	Intercept $\mu_0$ (mm)	$t \alpha_0$ (mm year <sup>-1</sup> )	$t^2 \beta_0$ (mm year <sup>-1</sup> )	$P \gamma_0$ (mm mm <sup>-1</sup> )	$T_{minGS} \lambda_0$ (mm °C <sup>-1</sup> )	$\delta$	$\theta_1$	$\theta_2$
<i>Pine</i>								
Estimates	2.36	-0.0423	$8.91 \times 10^{-4}$	$1.34 \times 10^{-3}$	-0.159	0.794	0.446	0.124
Std. error	0.07	0.0037	$0.966 \times 10^{-4}$	$0.04 \times 10^{-3}$	0.006			
P-value	<0.001	<0.001	<0.001	<0.001	<0.001	RSE	df	AIC
$\sigma_{\text{tree}}$	0.461	0.0492	$12.2 \times 10^{-4}$	$0.49 \times 10^{-3}$		0.305	7313	6600
$\sigma_{\text{plot}}$	0.065							
<i>Oak</i>								
	Intercept	$t$	$t^2$	$P$	$T_{maxGS_{n-1}}$	$\delta$	$\theta_1$	$\theta_2$
Estimates	1.10	0.0283	$-6.91 \times 10^{-4}$	$0.954 \times 10^{-3}$	-0.0313	0.890	0.532	0.240
Std. error	0.072	0.0032	$0.93 \times 10^{-4}$	$0.041 \times 10^{-3}$	0.0026			
P-value	<0.001	<0.001	<0.001	<0.001	<0.001	RSE	df	AIC
$\sigma_{\text{tree}}$	0.343	0.0330	$9.82 \times 10^{-4}$	$0.527 \times 10^{-3}$		0.323	6017	4848
$\sigma_{\text{plot}}$	0.133							

temperature over the current growing season. For both species, total precipitation over the growing year is the climatic variable that best explained ring width variability. The parameters of the time variable indicate that the shape of the growth curve over the studied period is not the same for oak and pine. On average, the growth of pine trees before the disturbance decreases while that of the oak trees increases. These results confirm the need to model the temporal trend and the climatic effects for each species in order to correctly estimate the disturbance effect on ring width.

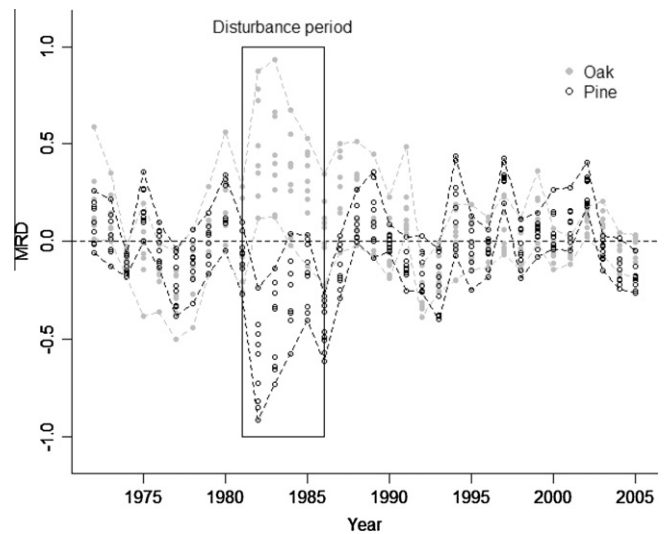
3.2. Changes in oak and pine growth after the pine sawfly attack

As we expected, pine growth decreased during the disturbance period (Fig. 1) and varied from one plot to another. The greatest decrease occurred in 1982 with an average MRD of -63% (-92% < MRD < -27%). The MRD then increased until 1985 with an average of -17% (-39% < MRD < 3%). In 1986, the MRD decreased again with an average of -43% (-60% < MRD < -26%). For oak, the results show that there is an overall increase in growth during the disturbance. As for pine, the oak reaction varied

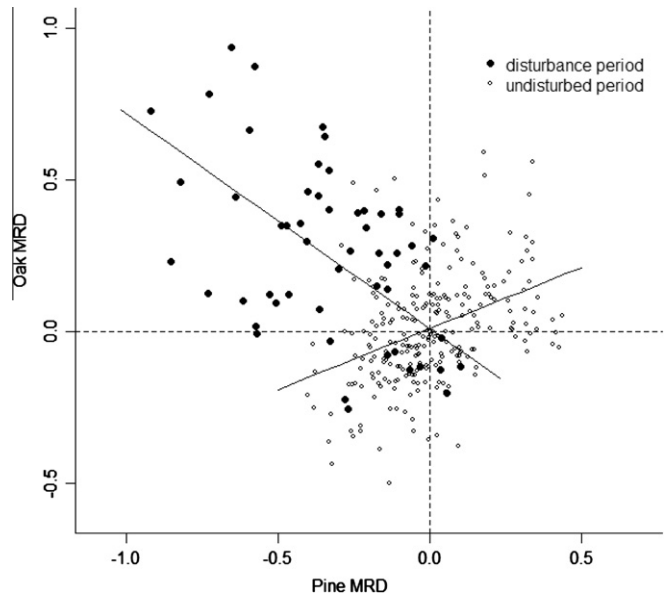
from one plot to another. The growth increase was the greatest in 1982 with an average MRD of 45% (7% < MRD < 80%), then MRD gradually decreased until 1986 with an average of 7% (-18% < MRD < 33%).

3.3. Relationship between the growth variations of the two species during and outside the disturbance period

The results show a positive correlation between the MRD of the two species over the undisturbed period and a negative correlation over the disturbance period (Fig. 2). The covariance analysis on the 1972–2005 period revealed that the slope of the regression between the oak MRD and the pine MRD over the undisturbed period was 0.38. During the disturbance period this slope was -0.69 (Table 3). The covariance analysis performed on the disturbance period shows that the effect of the pine MRD on the oak MRD was significant (Table 4). For each year of the disturbance, a reduction in pine



**Fig. 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.



**Fig. 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 1 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.



**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.  $\sigma$  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 $d_j$ is the random part of the slope related to the plot level variability.							
Coefficients	Estimate	Std. error	P-value	$\sigma$	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.  $\sigma$  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 1982–1985), $m_j$ is the random part of the intercept related to the plot level variability.							
Coefficients	Estimate	Std. error	P-value	$\sigma$	RSE	df	AIC
$m$	–0.0930	0.0603	0.192	0.147	0.123	43	–33.3
$m_1$ (year 1982–1985)	0.311	0.037	<0.001				
$d$	–0.388	0.080	<0.001				

growth was associated to an increase in oak growth. The covariance analysis also shows that the intensity of the oak response depended on the growth year. For the years 1981 and 1986, a reduction in pine growth of 100% resulted in an increase in oak growth of 30% while for the years 1982–1985, a reduction in pine growth of 100% resulted in an increase in oak growth of 61%.

## 4. Discussion

### 4.1. Growth compensation in mixed forests

In this study, we hoped to determine whether there was growth compensation between two tree species following a biotic disturbance affecting one tree species only in mixed stands of sessile oak and Scots pine. Our results show, as expected, that the pines suffered a decrease in growth after the pine sawfly attack. The greatest decrease in growth for pine was observed in 1982, which is logical since peak defoliation in the forest occurred in autumn 1981 (Geri and Goussard, 1984). In 1982, we estimated that pine growth had decreased by between 27% and 92% compared to a situation without disturbance. This variability indicates that the intensity of defoliation was not uniform throughout the forest. According to the meta-analysis conducted by Jactel and Brockerhoff (2007), damage caused by oligophagous insects like the pine sawfly is less severe in mixed forests than in pure forests. Three main mechanisms have been proposed to explain this effect: a decrease in host concentration, making host trees more difficult to locate (Vehviläinen et al., 2006), chemical barriers provided by the alternative species (Jactel et al., 2011) and an increase in natural enemies benefitting from the presence of several tree species for their life cycle (Kaitaniemi et al., 2007). The initial variability in stand composition may thus explain part of the variability that we observed in the response of pine.

Concurrent to the decrease in growth for pines, our results show that the growth of oak in mixed stands increased during the disturbance period. Moreover, our results show that the oak response is correlated to the pine response. For a given year during the disturbance period, the more the growth of pine decreased, the more the growth of oak increased. These results support the hypothesis of a growth compensation between the two species following the pine sawfly outbreak. As we suggested in the introduction of this article, this compensation can be explained by reduced competition from

the defoliated pine for light and underground resources. It can also be explained by the fertilizing effect associated with insect feces and dead tissue (de Groot and Turgeon, 1998). Both mechanisms, the reduction in interspecific competition and the fertilizing effect, are likely to come into play simultaneously and the available data do not make it possible to distinguish their influence. However, the covariance analysis performed on the disturbance period shows that the growth variation of oak for the three years following peak defoliation is not simply related to the growth variation of pine over the same period (Table 4). This result could be explained by the fact that just after peak defoliation, the oaks may have benefited from both the reduction in interspecific competition and the fertilizing effect. The fertilizing effect after peak defoliation would have a short term impact while the reduction in interspecific competition would have a longer-term impact because it would take the affected pine trees several years to recover full foliage.

Other studies have studied tree species response to biotic disturbances in mixed forests. Some of them on herbivory insects, such as the gypsy moth (*Lymantria dispar* L.) and the western spruce budworm (*Choristoneura fumiferana* Clem.), are comparable to our study. Some authors have shown an increase in growth for tree species classified as non-host species (Muzika and Liebhold, 1999; Jedlicka et al., 2004), while others did not observe any effect (Naidoo and Lechowicz, 2001). However, the compensation phenomenon between species *per se* has rarely been studied. In addition, tree species found in mixed stands are sometimes secondary hosts for the insect responsible for the disturbance and this makes the analysis more difficult, which is not the case in our study. In addition, the impact of climatic factors is sometimes not taken into account because climatic data are not always available for long-term series. To our knowledge, our study is the first that clearly shows growth compensation between two tree species following a disturbance caused by a biotic agent in a natural forest ecosystem.

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

#### 4.2. Interspecific growth compensation: a mechanism that would especially occur in the case of biotic disturbances

In undisturbed conditions, our results show that the MRD of oak and pine are positively correlated (Fig. 2). This suggests that, in undisturbed conditions, changes in environmental conditions have the same overall effect on both species. This result observed on species growth is consistent with those found on species abundance by Houlahan et al. (2007) and Valone and Barber (2008) who found that, in natural communities, species abundance covaries positively rather than negatively, which is the opposite of what would be expected if the compensation phenomena were important. Houlahan et al. (2007) and Valone and Barber (2008) also suggest that abiotic factors such as rainfall and temperature are the most important explanatory factors for interannual fluctuations in species abundance within communities and that coexisting species respond in similar ways to these climatic factors. This is the case in our study where annual precipitation is an abiotic factor synchronizing the two species. Valone and Barber (2008) conclude that compensatory effect was not a strong mechanism in stabilizing abundance fluctuations in natural terrestrial communities. This statement is consistent with what we observed on species growth in undisturbed conditions. However, it no longer holds true for the disturbance period where we have shown growth compensation between the two species. The result of the growth compensation that we observed is a quick and strong shift in the correlation between the growth of the two species (Fig. 2). This shift corresponds to a temporary phase opposition between the growth of oak and the growth of pine, well-illustrated by the results obtained in Plot P534 (Fig. 3).

Before the attack by the pine sawfly, the growths of the two species were well synchronized with a positive covariation. After the attack, the growths of two species were still synchronized but showed a negative covariation. After a period of about seven years, the ring widths of both species once again show a positive covariation. Even total, defoliation by the pine sawfly does not systematically kill the tree; a large percentage of the population typically survives (Augustaitis, 2007), but affected pine trees take several years to recover normal growth. The benefit observed on oak growth after pine defoliation ends when interspecific competition for resources is restored and when the fertilizing effect disappears. Fluctuations in tree growth are then once again mainly

driven by climatic factors as they were before the disturbance and the growth of the two species co-vary positively. This result shows that in a mixed stand subject to biotic disturbances, the production function can be stabilized through differences in species response to the disturbance. Oak leaves, unlike those of pine, were not consumed by the pine sawfly. This difference is responsible for the growth compensation that we observed. There probably would have been no compensation if the stands had been mixed with two pine species both vulnerable to defoliation (eg. *P. sylvestris* and *Pinus nigra*). Our results reinforce the idea that the diversity in species response to the disturbance is more important than simple species diversity (DeClerck et al., 2006; Jactel and Brockerhoff, 2007) and we suggest that growth compensations play an important role in stabilizing the production function for an ecosystem affected by periodic biotic disturbances. From a practical point of view, the results of this study show the importance of managing for mixed forests in an environment affected by biotic disturbances to minimize potential production losses. It is also important to promote mixtures with species that potentially have different responses to disturbances.

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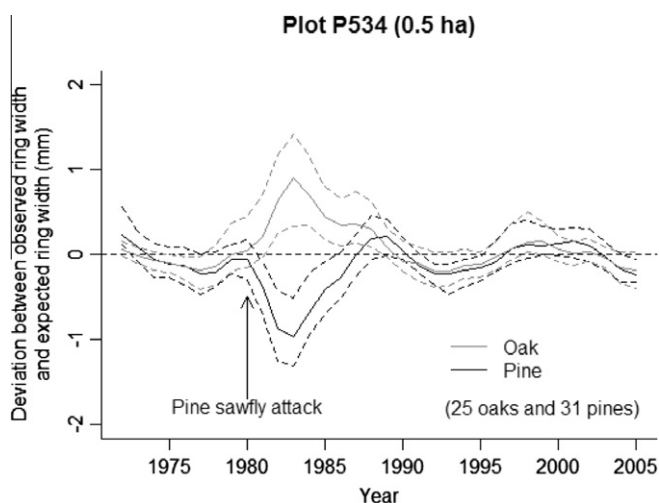


Fig. 3. Difference between the observed ring width and the ring width expected under undisturbed conditions according to the growth year for the sample trees on plot P534. The solid line represents the median values obtained for the sample trees. The dashed curves represent the first and third quartiles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

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