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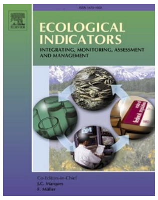

Tree canopy defoliation can reveal growth decline in mid-latitude temperate forests

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ABSTRACT

Climate and weather fluctuations and changes are the most important environmental drivers of tree canopy defoliation, an indicator of forest health. We examined the relationship between tree defoliation and Basal Area Increment (BAI), a dimension of tree growth related to wood biomass increment and carbon sequestration and therefore to the climate change mitigation potential of forests. We analysed data from mostly even-aged, single-species permanent monitoring plots in France over two growing periods (1995–2004: 47 plots, 2008 trees; 2000–2009: 63 plots, 3116 trees) and for which precipitation deficit was identified as the main environmental driver of defoliation. Trees from ten different species were assessed annually for defoliation and measured periodically for growth, from which we derived periodical (10-year) BAI (BAI_{period}). We investigated (i) direction and significance of defoliation-BAI_{period} relationships and (ii) occurrence, size and significance of BAI deviation of progressively defoliated trees in proportion to the BAI of undefoliated trees (BAI_{rel}). Analyses were first carried out at the level of individual plots, with results subsequently evaluated using meta-analysis and further aggregated at different levels (all species, functional groups, individual species). BAI_{period} resulted negatively and significantly related to defoliation, with a significant reduction detected already at slight (15%) defoliation level. A generalized statistically significant reduction of BAI_{rel} was obvious, leading to an estimated reduction of 0.7–0.8% per 1% increase in defoliation for conifers and 0.9% for broadleaves. Considering the observed distribution of trees along the defoliation range, our results indicate an overall growth reduction of ca. 42% in comparison to a theoretical population of undefoliated trees. Shifts in such a distribution can result into loss or gain of growth, which in turn may have cascading effects on carbon sequestration and therefore on land-climate interactions. In the context of the significant increase in defoliation observed in Europe in recent decades, our results suggest that even slight and moderate variations in defoliation may have had a significant impact on tree and forest growth.

1. Introduction

Forests are an essential component of the residual terrestrial carbon sink of 3.2 ± 0.8 GtC yr^{-1} (Le Quéré et al., 2018; Friedlingstein et al., 2019) and play a key role in land-climate interactions (Anderegg et al., 2013; Jia et al., 2019; Peters et al., 2020). Trees use carbon dioxide, water and mineral raw materials, light, oxygen and favourable temperature for several growth processes (e.g., foliage growth, stem growth and production of defence compounds, reproductive growth – Kozlowski & Pallardy, 1996; Dobbertin, 2005; Waring, 1987). The climate change mitigation potential of forests, however, rests largely on the ability of trees to sequester carbon into their woody tissues and therefore stem growth has a primary role (Rogiers et al., 2015). The potential impact of poor forest health on tree growth and carbon sequestration and cycle of forests has been studied in relation to pests, fire and other devastating events, i.e. those able to impair the ability of forest to survive, grow and sequester carbon at least for a certain time (e.g., Kurz et al., 2008; Langström et al., 2001; Kurkela et al, 2005; Eyles et al., 2009; 2011;

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Jacquet et al., 2012; Palacio et al., 2012) and in relation to drought-induced tree mortality (e.g. Allen et al., 2010; Anderegg et al., 2012; 2013; 2015; Neumann et al., 2017; Senf et al., 2018; Margalef-Marrase et al., 2020). Much less has been done in relation to subtle shifts from optimal condition, which may occur in response to a myriad of stressors affecting forests at any time (e.g. Brzostek et al., 2014). Such a subtle deterioration of tree- and forest health and its cascade effects on forest growth can be potentially more pervasive than mortality for the growth and carbon sequestration potential of forests. In Europe, for example, while between 2000 and 2012 "mean annual mortality rate (the average percentage of trees dying per year across all plots) was 0.50% per year in Europe's forests" (Neumann et al., 2017, p. 4791), the frequency of trees showing moderate-to-severe defoliation averaged 20.8%, i.e. ca. 42 times higher (see reports under http://icp-forests.net/page/icp-forests-technical-report). More recent figures show a similar pattern: in 2017, 0.50% (ca. 510 trees) out of the 101,779 trees observed across the ICP Forests Level I network were dead and ca. 24% (ca. 25,000 trees) showed moderate to severe reduction of foliage density (Michel et al., 2018; 2020).

Here we investigate canopy defoliation, a popular term used to indicate any deviation of foliage density on tree's crown in comparison with a reference tree assumed with full foliage density. As such, defoliation does not refer only to an active, ongoing process of loss of foliage between e.g. two subsequent times in the same season. Rather, it is intended to describe the general condition of foliage density on tree crown at a certain point in time (usually in summer, when the foliage development is expected to be complete) and determined by several, often concurring agents and processes. Under the reasonable assumption that trees with fully foliated canopies are "healthier" than trees with progressively reduced foliage, defoliation is adopted as an indicator of tree- and forest health (e.g., FOREST EUROPE, 2020). We concentrate on the possible relationship between defoliation and Basal Area Increment (BAI), i.e. an important indicator of wood growth in a tree (Bowman et al., 2013) directly related to above-ground wood volume increment, thus to biomass and carbon sequestration. Despite some contrasting results (see the review by Dobbertin, 2005), several studies reported evidence of relationships between defoliation and growth (e.g. Innes and Neumann, 1991; Söderberg, 1993; Solberg, 1999; Solberg and Tveite, 2000; Juknys et al., 2003; Drobyshev et al., 2007; Linares and Camarero, 2012). These studies were carried out in different countries (from North to South Europe) on species from both functional groups (broadleaves and conifers), adopted various defoliation thresholds to contrast defoliated and undefoliated trees (from $< 10\%$ to 50%), different investigation methods (from multi-annual and annual diameter measurements to tree-ring analyses) and covered different spatial scales (from few sites on a regional basis to large national monitoring networks). In general, however, their results suggested that – whatever the defoliation threshold adopted – trees with higher defoliation exhibit comparatively lower growth. More recent studies showed defoliation to be a significant predictor of annual growth of beech in France (although with significant regional differences – see Tallieu et al., 2020) and across the border between France and Spain (Oddou-Muratorio et al., 2019) and associated to significant growth reduction in Switzerland (Rohner et al., 2021).

Recent annual changes and/or trends in defoliation have been frequently related to drought stress and biotic stressors (e.g. Carnicer et al., 2011; Ferretti et al., 2014; Sousa-Silva et al., 2018; Pollastrini et al., 2019; Walthert et al., 2021; Rohner et al., 2021; Brun et al., 2020). Both are predicted to increase (e.g. Jakobi et al., 2019) and this may imply an upward shift in defoliation. Reduced foliage density and functionality of tree canopy may have *per se* substantial environmental impacts, e.g. on forest microclimate (e.g., Zellweger et al., 2020) and on atmosphere composition (e.g. Lin et al., 2020). If changes in foliage density on trees and forest canopy can be associated to changes in tree growth, it may also reveal a reduced ability of progressively defoliated trees and forests to produce wood and sequester carbon (two key provisioning and regulating ecosystem services) with potential further effects on land-climate interaction.

While previous individual studies on defoliation-growth relationship mostly focussed on individual species and/or on rather limited range of site conditions and/or broad categories of defoliation, here we hypothesize that progressive defoliation, even at low (>10–25%) and moderate (>25–60%) level (Eichhorn and Roskams, 2016), is more generally (i.e., across species / functional groups and site condition) associated to growth reduction in temperate, mostly single-species and even-aged European high forests. To test this hypothesis, we considered ten important European forest trees species distributed across the RENECOFOR (French acronym for National Network for Long-term Forest Ecosystem Monitoring) network of permanent plots that spans over large latitudinal (ca. 9°), longitudinal (ca. 14°), elevation (ca. 1800 m elevation range) and therefore climate gradients in metropolitan France (Tables 1 and 2, Fig. 1). Trees at these plots showed a significant increase in defoliation over the period 1995–2009 mostly related to current and previous-year precipitation deficit (Ferretti et al., 2014). Here we (i) studied the possible relationship between defoliation and tree growth expressed as BAI on ten important European forest species; (ii) tested whether, and to what extent, a significant reduction of BAI occurs at increasing defoliation levels; and (iii) evaluated whether a defoliation threshold exists for significant BAI reduction. We further calculated the relative growth of the entire tree population examined in relation to the observed and three simulated distributions along the defoliation range, from 0 to 100%. Deliberately, we did not enter into the question of causal relationship between defoliation and growth, which is very complex (e.g. Dobbertin, 2005) and unlikely to be disentangled by means of observational studies. Such a question, however, is marginal in the present study, which is centred around the association between defoliation and growth and the possibility offered by defoliation and its change to reveal possible negative effects on tree growth across the population examined.

2. Materials and methods

2.1. Study concept

All in all, we considered data collected at 91 out of the 102 permanent monitoring plots of the French monitoring program RENECOFOR (see below under 2.2) which is part of the UNECE ICP Forests intensive (Level II) monitoring network (Lorenz and Fischer, 2013).

Eleven of the 102 plots were not included in this study because data collection was stopped after severe damage caused by storms in 1999 (nine plots) or because growth measurements were systematically affected by anomalies (removals of bark at measurement height between periodical growth surveys that may have altered the second measurement - two plots) or because of financial reasons. With few exceptions (four oak plots; one spruce plot; and three Silver fir plots), plots were single-species and even-aged.

Four steps were undertaken and for each dataset we always considered the mean periodical defoliation (averaged over ten years) and the cumulated periodical growth, i.e. the growth over 10-year. Firstly, we investigated relationship between individual periodical mean tree defoliation and periodical BAI measured on the same trees. We did it for each plot: individual plots were considered as individual case studies where a population of trees was subject to a "treatment" (defoliation) and measured for response in terms of BAI. Results from individual plots were then subject to meta-analysis (see below) to describe the general effect size based on the results of the observed defoliation-BAI relationships. We also considered other levels of aggregation: all species, functional groups of species (conifers and broadleaves) and individual species.

Secondly, we studied whether a defoliation threshold can be associated to significant BAI reduction. To do so, the median periodical BAI of trees classified into defoliation categories >10% (15, 20, 25, …100%,

Table 1

The RENECOFOR network. Main tree species, total number of plots, number of plots considered in this study (in brackets) and range of main site, stand, climate (precipitation, temperature) and soil (exchangeable base cations, an indicator of soil nutrient availability). A. Broadleaves; B. Conifers (modified after Ferretti et al., 2014). [1] data from 1971 to 2000 (Aurelhy model, MeteoFrance).

A. Broadleaves Main tree species	*Quercus robur*	*Quercus petraea*	*Fagus sylvatica*	*Q. robur and Q. petraea*
Abbreviation	CHP	CHS	HET	CPS
Plots, n	9 (9)	19 (18)	20 (16)	2 (1)
Elevation (m)	20–370	55–330	50–1400	80–350
Stand age in 1995 (years)	35–134	55–139	41–160	76–113
Mean DBH of dominant trees in 1995 (cm)	22–49	28–43	22–49	32–47
Stand density in 1995 (trees · ha^{-1})	240–2781	296–1338	222–961	583–1079
Annual precipitation (mm) [1]	651–1163	663–1102	736–1894	698–920
Annual Tmin (°C) [1]	4.5–8.1	4.2–7.5	1.9–7.8	5.2–6.2
Annual Tmax (°C) [1]	13.7–18.6	13.5–17.3	7.6–18.7	14.3–15.4
Exchangeable base cations (cmolc kg^{-1}), mineral soil (0–40 cm)	0.5–17.9	0.2–2.2	0.3–48.7	0.3–0.5

B. Conifers Main tree species	*Abies alba*	*Picea abies*	*Pinus nigra* ssp. *laricio*	*Pinus pinaster*	*Pseudotsuga menziesii*	*Pinus sylvestris*
Abbreviation	SP	EPC	PL	PM	DOU	PS
Plots, n	11 (11)	11 (10)	2 (2)	7 (7)	6 (6)	14 (11)
Elevation (m)	400–1360	480–1700	140–1100	5–850	375–700	38–1670
Stand age in 1995 (years)	41–168	23–182	45–173	15–62	20–48	39–94
Stand density in 1995 (trees · ha^{-1})	396–806	371–1258	314–806	511–947	243–1188	510–885
Mean DBH of dominant trees in 1995 (cm)	34–54	23–51	34–55	20–40	27–52	27–38
Annual precipitation (mm) [1]	925–1564	1043–1987	743–1566	775–1328	906–1522	699–1144
Annual Tmin (°C) [1]	1.2–5.1	0.1–6.3	5.1–5.8	6.4–10.2	4.9–7.7	1–7.4
Annual Tmax (°C) [1]	10.1–15.4	10.3–14.6	14.1–15.9	15.6–18.1	13.2–17.2	12.8–16.4
Exchangeable base cations (cmolc kg^{-1}), mineral soil (0–40 cm)	0.3–22.2	0.2–26.6	0.2–3.2	0.4–4.8	0.3–2.3	0.1–1.7

Table 2

Summary of data resources, basic statistics for the variables considered by the study and correlation between individual trees defoliation and BAI. Number of plots, number of trees, mean periodical defoliation (D), periodical BAI expressed in cm^2, Spearman Rho and slope of the first order linear model (b) (with significance level: ns, not significant; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$).

Species	Growth period considered											
	1995–2004						2000–2009					
	plot, n	trees, n	D, %	BAI, cm^2	Rho	b	plot, n	trees, n	D, %	BAI, cm^2	Rho	b
Abies alba	11	520	11.3	333.6	−0.40***	−5.39***	6	298	14.4	384.7	−0.38***	−4.18***
Picea abies	10	466	7.8	249.5	−0.11*	−1.72*	4	195	6.4	284.6	−0.17*	−3.72**
Pinus nigra ssp. *laricio*	2	90	15.1	273.5	−0.32**	−5.44**	1	52	26.3	188.2	−0.44**	−0.44*
Pinus pinaster	7	290	18.1	272.7	−0.31***	−5.62***	4	192	22.7	289.1	−0.52***	−9.87***
Pinus sylvestris	11	419	12.2	202.6	−0.09 ns	−1.36 ns	3	132	19.4	251.1	−0.40***	−9.73***
Pseudotsuga menziesii	6	223	11.4	535.0	−0.33***	−5.87***	1	52	3.5	603.2	−0.19 ns	−11.47 ns
Conifers	*47*	*2008*	*11.8*	*297.6*	*−0.24****	*−4.09****	*19*	*921*	*15.2*	*325.7*	*−0.39****	*−5.80****
Fagus sylvatica	0	0	–	–	–	–	16	817	20.3	274.6	−0.01 ns	−0.06 ns
Quercus petraea	0	0	–	–	–	–	18	896	24.3	269.7	−0.23***	−2.48***
Quercus robur	0	0	–	–	–	–	9	435	25.7	257.9	−0.27***	−4.45***
Quercus robur + Q. petraea	0	0	–	–	–	–	1	47	35.3	295.8	−0.60***	−5.82***
Broadleaves	0	0	–	–	–	–	*44*	*2195*	*23.3*	*269.8*	*−0.15****	*−1.98****
Total	*47*	*2008*	*11.8*	*297.6*	*−0.24****	*−4.09****	*63*	*3116*	*20.9*	*286.3*	*−0.26****	*−3.83****

measured in 5% steps – see below under 2.2) was tested against the median BAI of trees in defoliation categories 0, 5 and 10% (merged together), traditionally classified as “healthy” trees in forest condition monitoring (see Eichhorn and Roskams, 2016).

Thirdly, we investigated the overall pattern of BAI deviations along the entire defoliation range, from 0 to 100%. To do so, we considered the relative BAI (see below) of trees of each individual defoliation category and regressed it against the corresponding defoliation value. In this case, defoliation categories were not merged and the BAI of trees with no defoliation (0%) was assumed as reference.

Fourth, we attempted to estimate the relative growth of the tree population examined in relation to its observed and simulated distribution on the entire defoliation range. To do so, we considered the same reference as above (BAI of trees with defoliation 0%).

2.2. Data resources, data quality and measurement methods

Data on the indicators defoliation and growth (BAI) were collected at the permanent monitoring plots of the RENECOFOR program in France. Two datasets including paired defoliation and BAI data relevant to growing periods 1995–2004 and 2000–2009 were considered. These two different periods were chosen to maximize the total number of plots for the study (n = 91), with conifer plots only (n = 47) in the 1995–2004 period and both broadleaves (n = 44) and conifers (n = 19) in the 2000–2009 period. In particular, the 1995–2004 dataset includes data from 47 plots (with 16–52 trees each; 2008 trees in total) where the main tree species (MTS) were conifers (Table 2): silver fir (*Abies alba* Mill.), Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) H. Karst.). Plots with broadleaves were also measured in this period, but not included in the present analysis because concerns about “a shift in the severity of the defoliation scoring” (Ferretti et al., 2014) for broadleaves between 1994 and 1997 that may had potentially affected the consistency of defoliation data. In the 2000–2009 dataset there was a large prevalence of broadleaved species (Table 2) with a total of 3116 trees in 63 plots: European beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* Liebl.) were the most frequent species. Nineteen conifer

1995-2004

2000-2009

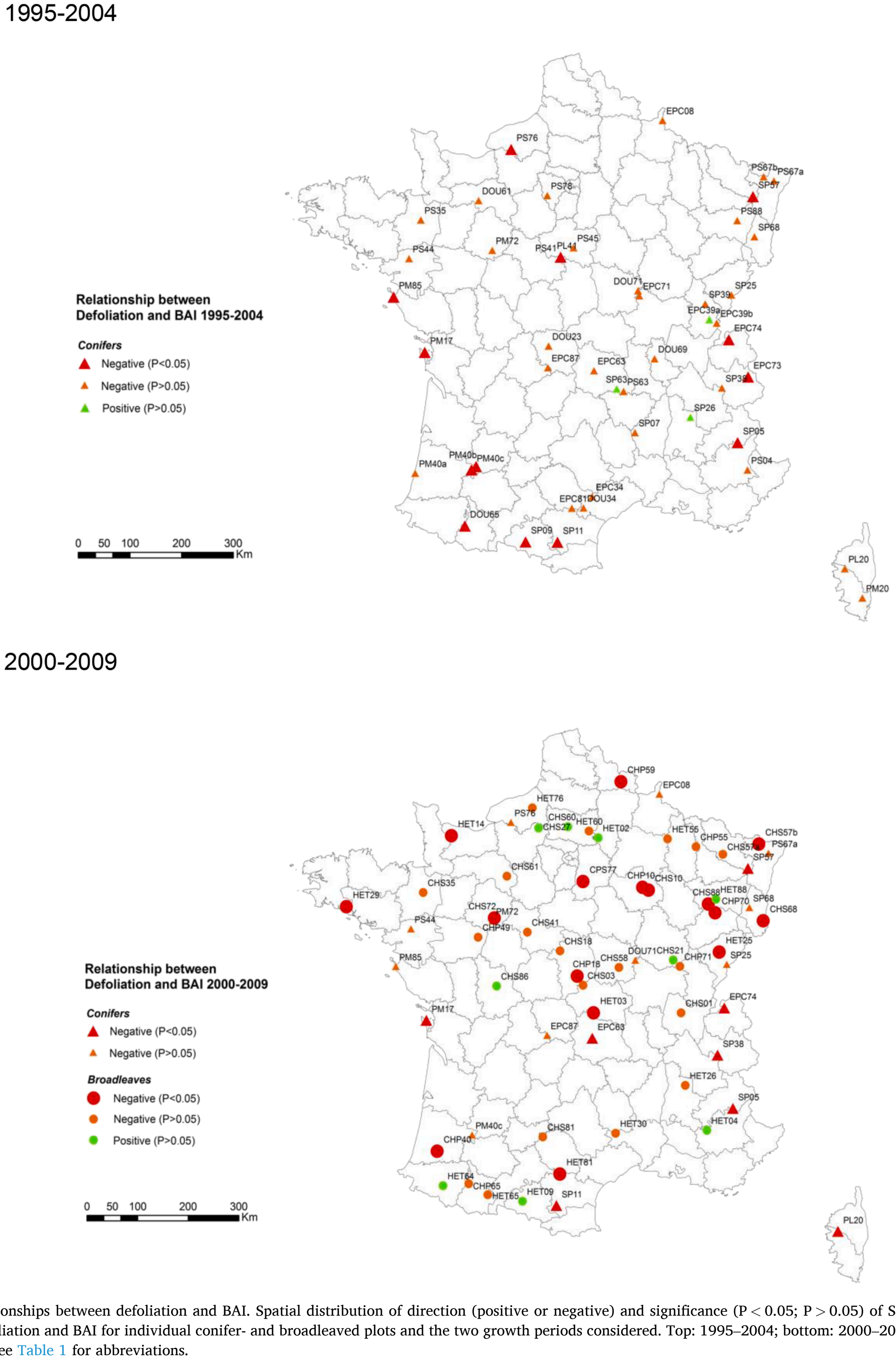

Fig. 1. Relationships between defoliation and BAI. Spatial distribution of direction (positive or negative) and significance ($P < 0.05$; $P > 0.05$) of Spearman Rho between defoliation and BAI for individual conifer- and broadleaved plots and the two growth periods considered. Top: 1995–2004; bottom: 2000–2009. Codes are the plot ID. See Table 1 for abbreviations.

plots were present in both datasets. The rest of the 102 plots were not measured in 2009 because of financial constraints.

The number of trees per plot was in general greater than 40 and trees were haphazardly selected from those belonging to the dominant and codominant layer. Raw data consisted of tree defoliation (in 5% steps) and tree circumference (in cm). "Defoliation" is used to describe deviation of foliage density on a tree in comparison with a reference tree assumed with full density. Here, the reference tree adopted was always a local one and this implies that reported defoliation values account for the site condition. While it is known to be prone to observer errors (e.g. Innes et al., 1993), the quality of defoliation assessments can be controlled by adequate training and field checks (Ferretti et al., 1999; Bussotti et al., 2009; Eickenscheidt & Wellbrock, 2014). The quality of defoliation data used in this study was evaluated by Ferretti et al. (2014). They found high data completeness (>98%) and, in terms of consistency, "data from field checks carried out between 2001–2005 and 2008–2009 on 16 plots and 697 trees revealed that 76% of the defoliation scores attributed were within ±5% difference between field crew and control team and 92% within ±10%". Further, observer effect and turnover was proven to be a non-significant factor in explaining defoliation trends in France (Ferretti et al., 2014). Annual defoliation scores for each tree were then averaged over the same periods considered for growth (1995–2004 and 2000–2009).

Entry data for calculating Basal Area (BA) were measurements of tree circumferences, customary carried out every 4–5 years according to the ICP Forests Manual (Dobbertin and Neumann, 2016). Additional measurements were carried out on a less regular basis, before and after management operations. The time period of ten years was chosen to reduce the relative importance of the uncertainties in circumference measurements in the calculated growth, especially for slowly-growing trees and/or at high elevation sites. Original circumference data were inspected to evaluate possible measurements anomalies. All in all, the overall frequency of reported anomalies for individual tree measurements was 1.1% (Fig. A1) and these measurements were discarded. Circumference data were subsequently transformed into basal area, BA, and then into periodical (ten years) Basal Area Increment (BAI_{period}) for the examined growth periods.

A summary of data resources for both growth periods is reported in Tables 1 and 2.

2.3. Data processing

2.3.1. Relationships between defoliation and growth

After testing different models (see Appendix A, Tables A1 and A2), first-order linear model and simple non-parametric correlation between periodical BAI (BAI_{period}) and defoliation were used. Such a solution provided also a proper effect size for the meta-analysis (see below). The slope, the significance and the root mean square error (RMSE) were computed for linear model, Spearman Rho and its significance were calculated. These analyses have been carried out for different data aggregation: all trees, functional groups of species (conifers, broadleaves), individual species and individual plots. Model's goodness of fit was evaluated on the basis of RMSE for all trees, which provides immediate information about the performance of the model. Moreover it is easy to interpret as it is expressed in the same unit as the response variable of the model itself (BAI_{period}).

The results of the correlation analysis between defoliation and BAI carried out for individual plots were summarized by means of meta-analysis, with Spearman Rho adopted as effect size (Harrison, 2011; Stewart, 2010; Hillebrand, 2008). We used both fixed- and random/mixed- effects models (Berkey et al., 1995; van Houwelingen et al., 2002) after the adopted effect sizes were tested with respect to normality by using the Shapiro-Wilk test (1995–2004: W = 0.96, P = 0.108; 2000–2009: W = 0.98, p = 0.572). See Ferretti et al. (2014) for details.

Under the R statistical environment (R Core Team, 2020), meta-analyses were conducted by using the metafor package (Viechtbauer, 2010), the package ggplot2 (Wickham, 2016) was used for graphing, while the R base package was used for linear modelling and correlation analyses.

2.3.2. Defoliation threshold for growth reduction and growth reduction pattern

To identify whether a defoliation threshold exists at which BAI starts to be significantly reduced, mean periodical defoliation data were aggregated on a 5% defoliation basis and the relevant median BAI was computed for each 5% class. The median BAI value of trees with 0, 5, 10% defoliation (traditionally considered "healthy"; Eichhorn and Roskams, 2016) was adopted as reference BAI (BAI_r). The three defoliation categories were merged to obtain a sufficient sample size and to account for observer errors (see above under 2.2). The effect of increasing defoliation d ($d = 15, 20, 25, \dots 100\%$) on BAI was evaluated against such a reference. The absolute deviation between median BAI of trees in each defoliation category d (BAI_d) with respect to the reference BAI_r were computed and tested by means of the non-parametric Wilcoxon Mann-Whitney U test. The threshold for significant growth reduction has been defined as the lowest defoliation value for which a significant (negative) difference between BAI_d and BAI_r starts to occur.

The pattern of BAI deviation at increasing levels of defoliation was also investigated. Unlike the previous analysis, we considered all individual defoliation categories (no merging) and the reference value adopted for growth was the periodical BAI of the least defoliated trees (0% for most of species). We calculated the relative BAI for each defoliation category d (BAI_{rel_d}) as the percent ratio between the median BAI of trees in each defoliation category d and the median BAI of trees with no defoliation (0%) (Equation 1):

$$BAI_{rel_d} = \frac{BAI_d}{BAI_0} \cdot 100$$

where

BAI_d is the median BAI observed for the trees in each defoliation category d (see Table 4 B)
BAI_0 is the median BAI observed for trees with $d = 0$.

The deviation between BAI_{rel_d} and the BAI of non-defoliated trees was regressed against the defoliation values for the main groups: all trees, broadleaves and conifers and individual species. For each group, we calculated the coefficient of determination, regression equation and significance. The R base package was used for testing median differences and correlation analyses.

2.3.3. Defoliation and growth of the whole tree population examined

We calculated the relative growth of the tree population examined in 2000–2009 (the most complete of the two datasets examined) as percent of the growth of a theoretical population of trees with null defoliation: with all trees in defoliation category 0%, the growth of the entire population is assumed to be 100%. This population is purely theoretical, but is convenient for comparison purposes. In our hypothesis (increasing defoliation associated to increasing growth reduction), we expect a progressive and negative deviation from 100% relative growth as soon as the distribution of trees shift towards higher defoliation categories.

The relative growth of the population is directly related to the observed proportion of trees in the various defoliation categories (from 0 to 100%) and on their BAI_{rel_d} (see above). The percent contribution of trees in each defoliation category d to the relative growth of the entire tree population can be calculated as follows (Equation 2):

$$Contribution\ to\ Relative\ Growth_d = \frac{1}{N}\left(n_d\ BAI_{rel_d}\right) \cdot 100$$

where

N is the total number of trees of the population examined. For the 2000–2009 dataset it amounts to 3116 (Table 4 B).

Table 3

Meta-analysis for the two growing periods. τ^2: estimate of total amount of heterogeneity; τ: square root of the estimate of total heterogeneity; I^2: percent of total variability due to heterogeneity; H^2: total variability / within-study variance. Significance level: ***, $p < 0.001$.

Model		1995–2004		2000–2009	
		Value	95% CI negative-positive	Value	95% CI negative-positive
Random	*Estimated r (back transformed)*	−0.263 ***	−0.313; −0.213	−0.229 ***	−0.279; −0.179
	τ^2	0.011	0; 0.023	0.023	0.011; 0.038
	τ	0.102	0; 0.145	0.153	0.106; 0.196
	I^2	34.804	0; 50.96	58.475	40.481; 69.709
	H^2	1.533	1; 2.093	2.408	1.68; 3.301
Mixed with continuous moderators	*Intercept*	−0.925	−2.301; 0.45	−0.878	−2.452; 0.696
	Elevation	0	0; 0.002	0.0001	−0.0001; 0.0003
	Latitude	0	0; 0	0	0; 0
	Longitude	0	0; 0	0	0; 0
	τ^2	0.011	0; 0.022	0.023	0.01; 0.01
	τ	0.106	0.019; 0.148	0.151	0.104; 0.196

Table 4

BAI and defoliation. Median BAI for each 5% defoliation class, difference between BAI of each defoliation class (BAI_d) and the median BAI value of trees with 0, 5, 10% defoliation (assumed as reference, BAI_r) for the two growing period considered (A: 1995–2004; total number of trees: 2008; B: 2000–2009; total number of trees: 3116), broadleaves and conifers and the entire tree population examined. NA: not assessed.

	Broadleaves				Conifers				All			
D, %	Trees, n	BAI median, cm^2	BAI_d-BAI_r cm^2	*U* test, P-value	Trees, n	BAI median, cm^2	BAI_d-BAI_r cm^2	*U* test, P-value	Trees, n	BAI median, cm^2	BAI_d-BAI_r cm^2	*U* test, P-value
A. 1995-2004												
0	0	–	–	–	163	388.7	–	–	163	388.7	–	–
5	0	–	–	–	424	315.3	–	–	424	315.3	–	–
10	0	–	–	–	327	255.1	–	–	327	255.1	–	–
15	0	–	–	–	485	247.5	−41.7	0.0000	485	247.5	−41.7	0.0000
20	0	–	–	–	307	212.8	−76.4	0.0000	307	212.8	−76.4	0.0000
25	0	–	–	–	151	260.4	−28.9	0.0001	151	260.4	−28.9	0.0001
30	0	–	–	–	67	233.5	−55.8	0.0012	67	233.5	−55.8	0.0012
35	0	–	–	–	40	227.4	−61.8	0.0223	40	227.4	−61.8	0.0223
40	0	–	–	–	20	185.7	−103.5	0.0021	20	185.7	−103.5	0.0021
45	0	–	–	–	11	287.2	−2.1	0.2319	11	287.2	−2.1	0.2319
50	0	–	–	–	6	186.5	−102.7	0.1054	6	186.5	−102.7	0.1054
55	0	–	–	–	3	225.0	−64.2	NA	3	225.0	−64.2	NA
60	0	–	–	–	0	NA	NA	NA	0	NA	NA	NA
65	0	–	–	–	1	181.0	−108.2	NA	1	181.0	−108.2	NA
70	0	–	–	–	1	41.4	−247.8	NA	1	41.4	−247.8	NA
75	0	–	–	–	1	85.6	−203.6	NA	1	85.6	−203.6	NA
80	0	–	–	–	1	15.0	−274.2	NA	1	15.0	−274.2	NA
85	0	–	–	–	0	NA	NA	NA	0	NA	NA	NA
90	0	–	–	–	0	NA	NA	NA	0	NA	NA	NA
95	0	–	–	–	0	NA	NA	NA	0	NA	NA	NA
100	0	–	–	–	0	NA	NA	NA	0	NA	NA	NA
B. 2000-2009												
0	0	–	–	–	74	490.1	–	–	74	490.1	–	–
5	35	307.4	–	–	178	392.3	–	–	213	379.4	–	–
10	127	265.1	–	–	111	365.8	–	–	238	326.9	–	–
15	282	268.0	−16.0	0.1927	126	328.1	−47.5	0.0002	408	300.1	−55.9	0.0000
20	439	250.5	–33.6	0.0132	115	294.8	−86.7	0.0000	554	279.8	−80.4	0.0000
25	485	255.7	−28.3	0.0212	121	264.4	−127.7	0.0000	606	272.1	−83.6	0.0000
30	374	241.9	−42.2	0.0012	104	248.9	−139.2	0.0000	478	263.3	−94.5	0.0000
35	214	217.4	−66.6	0.0000	51	202.8	−174.3	0.0000	265	242.4	−123.2	0.0000
40	119	215.4	−68.6	0.0001	21	225.9	−181.3	0.0002	140	246.3	−119.9	0.0000
45	64	203.6	−80.5	0.0007	10	286.0	−112.9	0.0529	74	250.8	−128.7	0.0000
50	28	172.4	−111.6	0.0000	3	369.3	20.8	NA	31	206.2	−152.9	0.0000
55	19	126.6	−157.5	0.0000	3	169.1	−168.0	NA	22	174.4	−206.7	0.0000
60	3	178.8	−105.2	NA	0	NA	NA	NA	3	151.2	−155.6	NA
65	3	98.7	−185.3	NA	1	53.1	−310.0	NA	4	83.0	−258.5	NA
70	0	NA	NA	NA	1	53.0	−310.0	NA	1	53.0	−281.3	NA
75	0	NA	NA	NA	1	428.4	65.4	NA	1	428.4	94.0	NA
80	2	79.9	−204.2	NA	0	NA	NA	NA	2	79.9	−254.5	NA
85	1	80.2	−203.8	NA	0	NA	NA	NA	1	80.2	−254.2	NA
90	0	NA	NA	NA	1	30.6	–332.5	NA	1	30.6	−303.8	NA
95	0	NA	NA	NA	0	NA	NA	NA	0	NA	NA	NA
100	0	NA	NA	NA	0	NA	NA	NA	0	NA	NA	NA

n_d is the number of trees observed in each defoliation category d (see Table 4 B).

BAI_{rel_d} is the median relative BAI observed for the trees in each defoliation category d (Equation 1; see also Table 4 B for entry data).

The relative growth of the entire population (P) over the period examined is then the sum of contributions of each defoliation category d (0, 5, 10, …100) and is expressed in percent of the growth of a theoretical population of trees with null defoliation. It can be written as follows (Equation 3):

$$Relative\ Growth_P = \sum_{d=0}^{d=100} \frac{1}{N}\left(n_d BAI_{rel_d}\right) \cdot 100$$

Notation are the same as in Equation 2.

3. Results

3.1. Defoliation and Basal Area Increment (BAI)

The 1995–2004 dataset included only conifers (Table 2). Mean species defoliation was in general low over the period examined and varied between 7.8% (Norway spruce) and 18.1% (Maritime pine, *Pinus pinaster* Ait.) (Table 2). Periodical BAI was larger for Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) (535 cm^2 on average, ca. + 64% with respect to the beginning of the growth period examined) than for the other species (200–330 cm^2, ca. + 20–40%). The 2000–2009 dataset included both conifers and broadleaves. For conifers, defoliation was below 20%, with the exception of Maritime pine and Corsican pine (*Pinus nigra* ssp. laricio). Periodical BAI was again larger for Douglas fir (603 cm^2 on average, ca. + 62% with respect to the beginning of the period). BAI_{period} for other conifer species varied between 190 and 400 cm^2, i.e. + 7–40%. As for broadleaves, defoliation was higher than 20% and periodical BAI between 250 and 300 cm^2, which corresponds to a 15–25% increase with respect to the beginning of the investigated growth period.

We found a negative relationship between defoliation and BAI_{period} for the majority of plots (Fig. 1). In particular, 14 plots in 1994–2005 and 25 plots in 2000–2009 showed significant ($P < 0.05$) negative correlation (Fig. 1). The random *meta*-analysis model revealed a significant amount of the total heterogeneity ($\tau^2 = 0.011$; $\tau^2 = 0.023$; $Q_{test\ (46d.f.)} = 66.72$, $P = 0.025$; $Q_{test\ (62d.f.)} = 154.92$, $p < 0.001$), with a significant effect across the plots examined in both growing periods (1995–2004: estimated r: −0.263, Confidence Interval, 95%: −0.313, −0.213; 2000–2009: estimated r: −0.229, Confidence Interval, 95%: −0.279, −0.179) (Table 3).

To test whether the relationship between defoliation and BAI was influenced by geographical factors (which at the scale of the study can be also indicative of different climatic conditions) we included latitude, longitude and elevation in the mixed-effect model as continuous moderators. They were not significant and the amount of residual heterogeneity (τ^2) was the same as in the random model (Table 3).

Highly significant ($P < 0.001$) negative correlation was found between BAI_{period} and defoliation for conifers (both periods) and for broadleaves in 2000–2009 ($P < 0.001$) (Table 2). At the level of individual species, the correlation was almost always negative and significant regardless the species and the growing period, with three exceptions: Scots pine in 1995–2004 and Douglas fir and beech in 2000–2009 (Table 2). In general, conifers showed more pronounced negative correlation coefficients than broadleaves, in particular for Silver fir and Maritime pine. Beech was the broadleaved species with the slightest relationship between defoliation and BAI_{period}.

3.2. BAI deviation in relation to defoliation level

Table 4 reports the difference between the median BAI of trees in defoliation classes 0, 5, 10% (BAI_r) and the median BAI of increasingly defoliated conifers and broadleaved trees (BAI_d with $d = 15, 20, 25,\ldots 100\%$), and its statistical significance after the U test. In some cases the analysis is influenced by the small sample size for individual defoliation classes (especially in the upper range of defoliation) and this limitation should be considered when examining the results. There is, however, a distinct progressive reduction of growth with increasing defoliation: differences between BAI_d and BAI_r were generally negative and significant ($P < 0.05$) with $d = 15\%$ for conifers (both growing periods) and with $d = 20\%$ for broadleaves (Table 4). This resulted into an overall (conifers + broadleaves) significant BAI reduction from 15% defoliation level on.

When individual species are concerned (Supplementary material, Tables A3 and A4), analysis were influenced by the small range of defoliation values observed for some species: for example, there was no Corsican pine tree with defoliation <15% and there was only one Douglas fir tree with defoliation >10%. Yet, a significant reduction was observed starting in the range of 15–25% defoliation level in conifers, while for broadleaves the pattern was less clear: BAI of sessile oak is significantly reduced from 30% defoliation on, while no clear threshold can be observed for pedunculate oak (perhaps due to a small sample size, see Table S4) and beech.

Fig. 2 shows the percent deviation of BAI (BAI_{rel}) assuming the BAI of the trees in the lowest defoliation level (0% defoliation) as reference value. Reduction in BAI_{rel} occurred even at low defoliation level (<15%) and progress in an almost linear way up to 80%. However, beyond 35% (conifers) and 45% defoliation (broadleaves), sample size becomes small (see Table 4) and individual observation can influence the results (see for example the data point corresponding to defoliation 75% and growth still high in Fig. 2 – top: it corresponds to only one Silver fir tree in this class). To account for small sample sizes in individual defoliation classes, regressions were computed considering data points arising from defoliation categories with >30 trees (main graph) and all the data points (inset) (see Table 4 for the number of trees for each defoliation level). When only defoliation categories with $n > 30$ trees are considered, a linear decrease in BAI_{rel} per 1% increase of defoliation can be observed, and amounts to 0.9 – 1.5% (conifers, two growing periods), 0.7% (broadleaves) and 0.9% (all species). This pattern remains valid when all defoliation categories are considered, although with some changes in slope values for conifers (−0.7; −0.8) and broadleaves (−0.9) (Fig. 2, insets). This applies also for the majority of the species considered (see Appendix A, Tables A3, A4, A5).

Table 5 summarizes our main findings for the two datasets, individual species, functional groups and in total.

3.3. Defoliaton and forest growth

Fig. 3 shows four different defoliation scenarios (A: observed; B, C, D: arbitrary simulations) and the relative growth for the resulting population expressed in percent of a theoretical population of trees with 0% defoliation. Coupling the frequency distribution of trees along the defoliation range observed in 2000–2009 (grey columns in Fig. 3 A; see original data in Table 4 B) and the observed BAI_{rel_d} (black dashes in Fig. 3 A, see original data in Table 4 B), we calculated that such a distribution (modal defoliation: 25%; 82% of trees with defoliation ≤ 30%) resulted into an overall relative growth of 58% as compared to a theoretical population of undefoliated (defoliation 0%) trees (Fig. 3), i.e. a 42% reduction of relative growth. Fig. 3 shows three additional arbitrary simulated defoliation scenarios and shows that, when the the same BAI_{rel_d} is assumed, shifts of tree distribution towards higher defoliation levels (C, moderate increase: mode: 50%; 82% of trees with defoliation ≤55%; D, strong increase: mode: 75%; 86% of trees with defoliation ≤85%) will result into further reduction of relative BAI, up to 70% as compared to the reference (theoretical) population of undefoliated trees. Conversely, a shift towards lower defoliation (B, moderate decrease: mode: 0%; 82% of trees with defoliation ≤20%) will limit the reduction of relative BAI to 29%.

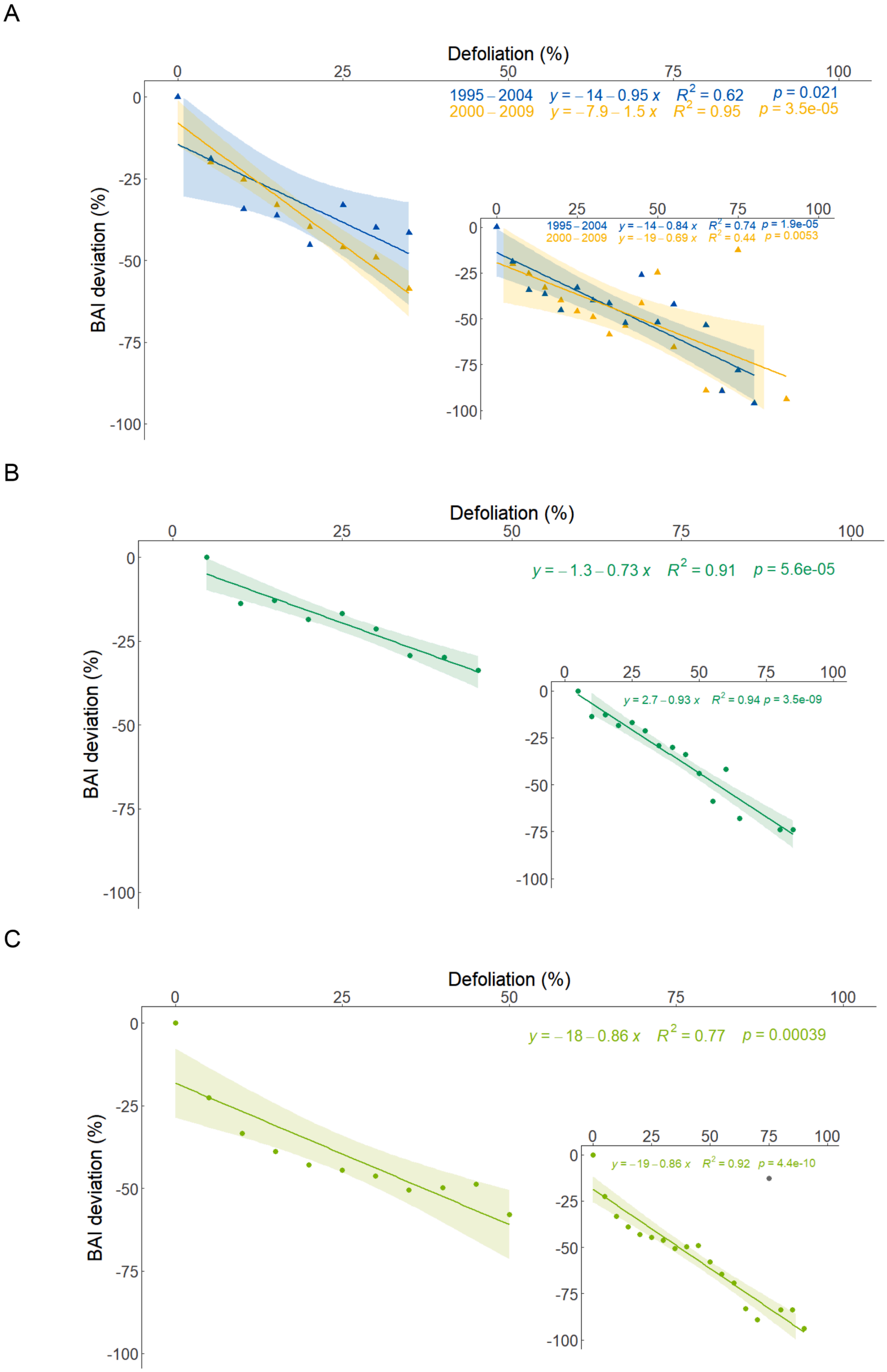

Fig. 2. BAI deviation for increasing defoliation. BAI deviation (in relative terms with respect to undefoliated trees) of trees for increasing defoliation level. Large graphs: defoliation categories with more than 30 trees per class; inset: all defoliation classes. Top: Conifers (1995–2004: yellow triangles; 2000–2009: blue triangles); Middle: broadleaves (2000–2009); Bottom: all species (2000–2009). Coefficient of determination, regression equation and P levels are reported. The shaded areas represent the 95% confidence interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 5

Summary of results at the level of individual species, functional groups, the entire tree population and for the two growing periods considered. Number of trees examined, defoliation threshold for which a significant and consistent growth reduction was identified (*U* test, see Table 4 A, B) and estimated reduction in BAI_{rel} per unit (1%) increase in defoliation (Figure 2) are reported. NA: not assessed due to low number of trees.

Species	1995–2004			2000–2009		
	Trees, n	Defoliation threshold for significant reduction of BAI	Estimated % reduction of BAI_{rel} per 1% increase of defoliation	Trees, n	Defoliation threshold for significant reduction of BAI	Estimated % reduction of BAI_{rel} per 1% increase of defoliation
Abies alba	520	15	−0.89	298	15	−0.56
Picea abies	466	25	−1.30	195	20	−0.97
Pinus nigra ssp. *laricio*	90	none	−1.55	52	NA	−1.47
P. pinaster	290	20–30	−1.34	192	25	−1.44
P. sylvestris	419	none	−1.66	132	20	−2.49
Pseudotsuga menziesii	223	25–40	−1.15	52	NA	−2.00
Conifers	2008	15	−0.84	921	15	−0.69
Fagus sylvatica	0			817	none	−0.63
Quercus petraea	0			896	30	−1.16
Q. robur	0			435	unclear	−1.33
Q. robur + *Q. petraea*	0			47	NA	−1.27
Broadleaves	0			2195	20	−0.93
Total	2008	15	−0.84	3116	15	−0.86

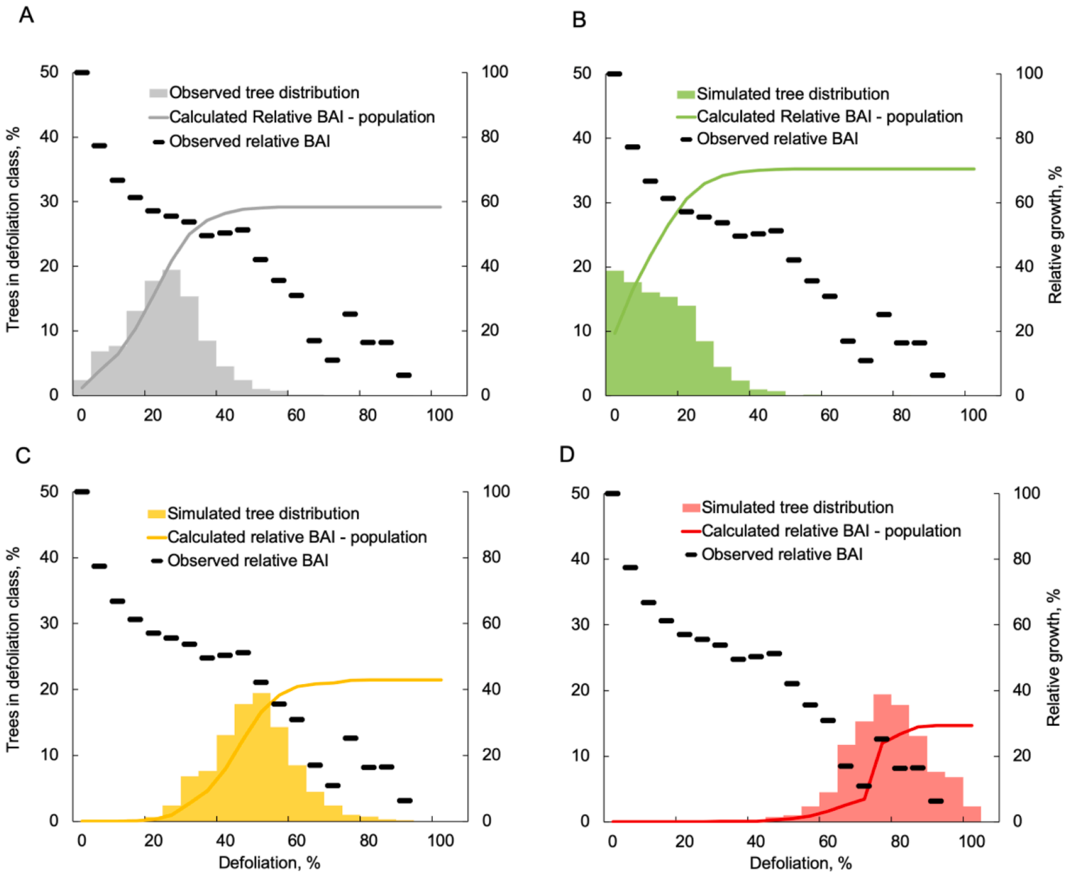

Fig. 3. Shifts in defoliation and forest growth. Observed and simulated percent frequency of trees for each defoliation class (columns) and relative BAI of the population (lines) in percent of a theoretical population of undefoliated trees. A: observed values in 2000–2009; B, C, and D: simulated distributions of trees arising from an arbitrary shift towards lower (B, moderate decrease) and higher (C: moderate increase; D: strong increase) defoliation ranges (left y axis) and corresponding relative BAI for the resulting populations (in % with respect of a theoretical population of undefoliated trees) (right y axis). Black dashes: observed BAI_{rel_d} per each defoliation class (right y axis). See text under 2.3.2 and 3.3 for details.

While simulations reported in Fig. 3 are arbitrary in terms of distribution shifts and based on median BAI deviations observed in our study, signals that a shift in defoliation is actually associated to change in growth can be detected in our dataset. Fig. 4 presents results from the 19 coniferous plots for which data were available for both 1995–2004 and 2000–2009 periods: despite the partial overlap of the two periods, we observed a significant negative relationship between changes in defoliation and relative BAI, especially when defoliation change is >5% in absolute values (Fig. 4).

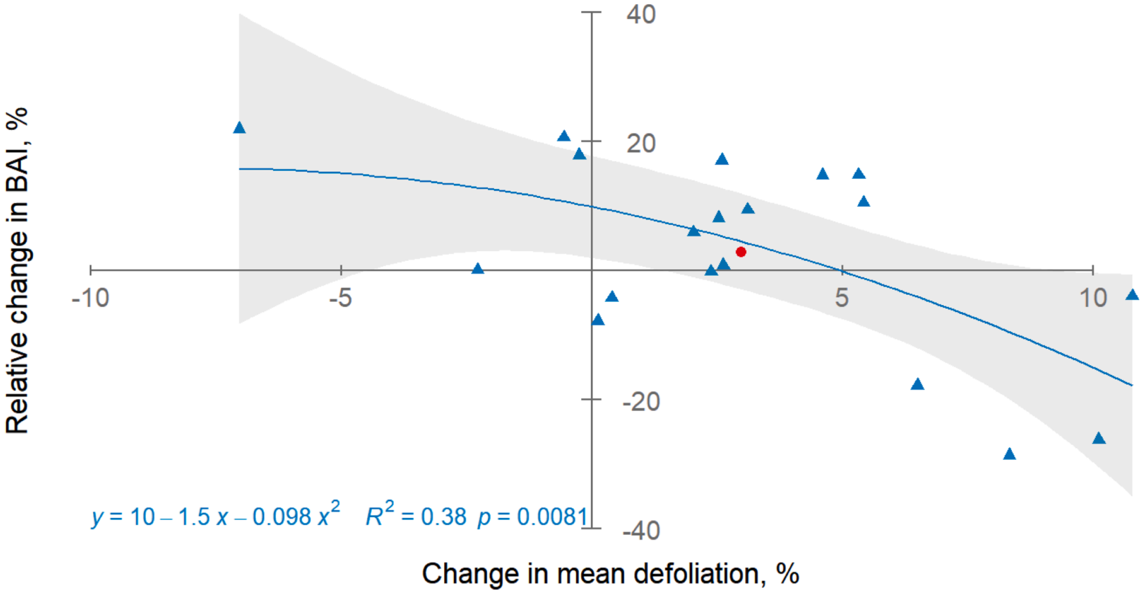

Fig. 4. Observed changes in defoliation and growth on re-measured plots. Changes in mean defoliation and BAI between 1994 and 2005 and 2000–2009 for plots covered in both measurement periods (n = 19). The red dot represents the average difference between the two periods for both defoliation (+3.0%) and BAI (+2.8%). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

We observed a generalized, significant negative correlation between mean periodical tree defoliation and periodical BAI. Here we discuss our results in the context of previous studies, in relation to the role of possible confounding factors and in view of their ecological significance and potential impact.

4.1. Context

Several studies showed that defoliation is associated to growth reduction. In particular, Solberg (1999) found that “considerable growth depressions were already found at slight levels of defoliation and discoloration. Growth approached zero as defoliation and discolouration increased towards 100%”. In another study on Norway spruce, Solberg & Tveite (2000) argued that “the various relationships consistently indicated that approximately 1% change in crown density corresponded to 1% change in growth.” These estimates are very close to our results: we found that there is a 0.9% change of BAI (in relative terms with respect to undefoliated trees) per 1% change in defoliation. Some more recent studies showed that – besides periodical growth - also annual growth can be affected by defoliation. Tallieu et al. (2020) compared annual defoliation and annual radial growth of beech across France. They found that, despite substantial regional differences, defoliation is a significant predictor of annual radial growth at the national level in France (i. e., the same scale and geographical domain of our study). Rohner et al. (2021) found that beech trees affected by severe defoliation (>60%) after the 2018 drought had significantly lower BAI than unaffected trees. A simultaneous, partial recovery of canopy defoliation and BAI occurred in 2019 after favourable weather. This is supported by our results presented in Fig. 4, where changes in defoliation (increase and decrease) are correlated to changes in BAI.

Several authors questioned the appropriateness of the 25% defoliation threshold used by international monitoring programs (e.g. ICP Forests) for identifying “damaged” trees because of its lack of connections with trees’ physiological and productive performance (e.g. Tallieu et al., 2020; Bussotti et al., 2018; but see also Ferretti, 1997). As almost any other threshold in ecology (e.g. Munson et al., 2018), also a defoliation-related one needs to be considered with caution and mostly as having an indicative value. Studies carried out since the late 1990s, however, showed that relationships between defoliation and growth exist. More recent studies found consistent patterns between defoliation and damage symptoms on trees (e.g. Ferretti et al., 2014; 2018) and defoliation and other indicators of tree condition and photosynthesis efficiency (e. g., Gottardini et al., 2016; 2020). Our results show that a significant reduction of growth can occur in the defoliation range of 15–30% for many species, thus providing evidence that the 25%-defoliation threshold adopted by international monitoring programs can be a reasonable approximation for tree classification.

While our results show an overall consistent relationship between defoliation and growth, there were cases where such a pattern was less obvious, namely for Scots pine in 1995–2004 and Douglas fir and beech in 2000–2009 (Table 2). In these cases, relationships were negative, but not significant. For Scots pine in 1995–2004 and Douglas fir in 2000–2009, the lack of significance likely depends on the distribution of observations along the defoliation scale: 92% of the 419 Scots pine trees in 1995–2004 and all Douglas fir trees in 2000–2009 (from only one plot) concentrated in the lower defoliation range (0–20%, see Tables A3 and A4). The case of beech is more complex. Beech trees were distributed mostly in the defoliation range 5–35% and we actually observed a significant negative relationship with BAI at several plots (Fig. 1) and an overall significant BAI reduction already at 15 and 20% defoliation. This pattern, however, flattened down, and the overall negative relationship BAI-defoliation was not significant. This likely depends on species-specific behaviour of beech: several studies pointed out that the growth of beech trees is strongly driven by fruiting and masting years (e. g. Lebourgeois et al., 2018), which had much more limited impact on leaf biomass (Eichhorn et al., 2008). In a more recent study involving also some of the plots considered in this paper, Nussbaumer et al. (under revision and personal communication) found similar results: while oak’s growth and foliage biomass were not affected by fruiting and masting years, beech displayed a distinct impact of fruiting on growth, accompanied by a much less consistent effect on leaf production. Masting years have been reported to occur with a frequency ranging from 2.6 to 5.5 years in beech plots from several European countries (Nussbaumer et al., 2016). At the beech monitoring plots examined in this paper, masting years occurred several times during the 2000–2009 growing period (i.e. 2000, 2002, 2004, 2006, see Lebourgeois et al., 2018) and this may have impacted tree growth and affected defoliation-BAI relationships.

4.2. *Confounding factors*

Several confounding factors can be considered: site and stand influence, method of assessment, observer and measurement errors, the influence of tree age and the aggregation of data over 10-year growing periods. Site influence can be discussed together with methods of assessment because defoliation assessment is based on the reference standard adopted which is in turn also related to the site. In general, there are two main options to identify a standard reference for defoliation assessment: a local reference tree, i.e. a real tree growing in/nearby the site and considered fully foliated, taking into account the site condition; and an absolute reference, often depicted as a photo in defoliation photoguides (e.g. Müller & Stierlin, 1990; Innes, 1990; Ferretti, 1994). The question about absolute and local reference tree is a long-lasting one in tree defoliation assessment (e.g. Ferretti, 1997, 1998; Redfern & Boswell, 2004) and all solutions have pros and cons. At the RENECOFOR plots, defoliation was always assessed in relation to local, real reference tree, thus accounting for local site and stand characteristics. The adoption of local reference tree permits to interpret increasing defoliation levels as progressive deviation from the local optimum canopy foliage status. As the comparison between BAI and defoliation in our study was always tree-wise, this permits to have always fully comparable data adjusted for site characteristics.

Stand density and competition among trees are key drivers for tree growth. It is worth noting that our data refers for the most part to even-aged, single species and relatively homogeneous forest plots and were collected on trees of the dominant and co-dominant storey only. Nevertheless, some degree of social differentiation can always occur: competition may therefore lead to reduced growth and trees that remained in less dominant condition may adjust / reduce foliage density accordingly. In such a case, it is difficult to establish a causal link between defoliation and growth. Ferretti et al. (2014) reported that the number of trees per hectare was actually one important predictor of annual changes of defoliation at the plots considered in this study, but the direction of relationship was either positive or negative, depending on individual plots and species. Here we do not find any generalized relationship between defoliation and size of individual trees, neither for the entire tree population examined (Fig. A2) nor when the consistency of relationship at the level of individual plot is considered (Fig. A3). Actually, we observed that the correlation between defoliation and growth may hide the effect of the tree size only in two instances out of the entire number of plots examined in the two growing periods. Thus, at least for the trees and plots examined in this paper, we are inclined to exclude competition as a general driver of the observed defoliation-growth relationship. As mentioned in the introduction, although the question of causal relationship between defoliation and growth is very complex (e.g. Dobbertin, 2005), it is only of marginal importance here, where the focus is on the possibility offered by defoliation to reveal changes in growth across the tree population examined.

Defoliation is known to be prone to observer error (e.g. Innes et al., 1993). The quality of defoliation data used in this study, however, has been already ruled out as a factor affecting defoliation trends at the observed plots (Ferretti et al., 2014). When potential problems could have affected data consistency (i.e. broadleaved plots between 1994 and 1997), we deliberately excluded the concerned plots from the analysis. Circumference measurements are also subject to measurement errors, but the overall frequency of reported measurement problems was quite low (1.1%, see Fig. A1) and – in any case –excluded from the analysis.

Tree age is a factor frequently associated with defoliation levels (e.g. Dobbertin, 2005). It is worth noting that our analyses were carried out plot-wise and the plots considered in this study were mostly even-aged, so age is not a factor that may have impacted BAI-defoliation relationships at plot level. At larger aggregation level (e.g. all trees, individual species) we did not find any relationship between defoliation and individual tree's basal area, which may be considered also as a possible proxy for tree age (Fig. A2).

The use of 10-year growing periods (with cumulated growth and mean defoliation levels) has also disadvantages because it renders unfeasible capturing signals from individual years. This is, however, hardly feasible anyway because of different timing of defoliation and growth measurements: tree defoliation is usually assessed in July-August, while growth can extend much further in the season (but see below) and it is better measured after the end of the growing season (e.g. in winter). Cumulated growth over several years has, on the other hand, the advantage to reduce the relative importance of errors that may arise from circumference measurements, given the higher signal (growth over ten years) to noise (measurement error) ratio. It permits also to focus on "average" condition and smooth the effect of sudden short-term random events/disturbances that may create further noise. Also, it helps to minimize the impact of the different timing usually adopted to evaluate canopy defoliation and compute growth: the former is usually carried out in July-August, the latter typically accounting for the entire vegetative season. Rohner et al. (2021) recently demonstrated that, depending on the timing of the climate stress occurrence, the standard crown defoliation assessment time in early- and mid-summer is not able to capture the signal of crown deterioration and its immediate (i.e., within the same growing season) effects on tree growth.

4.3. *Significance*

Intuitively, progressive reduction of foliage on tree canopy may affect growth. Besides observational studies (see above under 4.1), several manipulative experiments with induced defoliation (e.g. Langström et al., 2001; Kurkela et al., 2005; Eyles et al., 2011) and meta-analysis (e.g. Jacquet et al., 2012) provided evidence for this across a range of species in Europe and elsewhere.

Defoliation has been found to be associated with other morphological and physiological indicators of reduced tree vitality in several observational studies. The frequency of symptoms of damage recorded on different tree's compartments (foliage, branches, stem, collar) was reported closely related to defoliation for all the species considered in this study, in France and elsewhere (e.g. Ferretti et al., 2014, 2018; Gottardini et al., 2020; Carnicer et al., 2011). Gottardini et al. (2016) found a consistent pattern between crown transparency (a proxy for crown defoliation), visible damage on trees, reduction of shoot length, needle weight, photosynthetic potential and $\delta^{18}O$ (an oxygen isotope useful to evaluate plant responses to environmental variables that influence leaf stomatal functioning, see e.g. Gessler et al., 2014) in Norway spruce along an elevation gradient. In a more recent study, Gottardini et al. (2020) found also that defoliation in beech (but not in oaks) was associated with reduced photosynthetic efficiency.

The potential impact of defoliation on the growth of the entire tree population examined depends on the population's distribution along the entire 0–100% defoliation range, which is typically unimodal with positive skewness (e.g. Bussotti et al., 2003; see also Fig. 3 A). The majority of trees examined in this paper were in a defoliation range between 15 and 30%, i.e. a range where a median reduction in relative BAI of 40–50% was observed for individual trees (Fig. 2). A certain share of defoliated/unhealthy trees is as inherent to forest ecosystems as healthy trees and it is unrealistic to expect to have all trees in the lowest defoliation range. It is reasonable to assume, however, that a shift in the overall distribution of the population of trees along the defoliation range may reflect a more general shift in the condition of forest canopy. We estimated that shifts of distribution of the examined tree population along the defoliation gradient may result into considerable gain or loss of BAI, even in absence of mortality (see Figs. 3 and 4). These results can have clear relevance at the continental scale. At European level, 69.3% of trees are classified with defoliation between 15 and 60% (Michel et al., 2020), i.e. in a range where we observed a BAI reduction of 40–60% with respect to undefoliated trees. Besides, a significant increase in defoliation has been detected for most of the species considered in this paper (Michel et al., 2020). This means that, when projected at

European level, our findings point to a widespread, significant reduction of growth over a considerable share of European forest trees and that such an effect has likely increased over time due to increasing defoliation level. BAI is a key measure of wood growth in a tree (Bowman et al., 2013) and is directly related to above-ground volume increment, thus to biomass increment and carbon sequestration. In the perspective of augmented climate stress on forest, shifts in canopy defoliation induced by e.g. drought may lead to substantial impact on stem growth, wood production and the ability of forests to remove and sequester carbon from the atmosphere, with possible feedback into land-climate interactions. For example, an immediate response of beech trees in Switzerland and central Europe after the 2018 megadrought was identified in terms of crown condition (Brun et al., 2020; Schuldt et al., 2020; Rohner et al., 2021; Walthert et al., 2021) and this was reflected by reduced BAI, volume increment and carbon sequestration (Rohner et al., 2021). This feedback may pile up with other effects connected to reduced canopy coverage and functionality already detected on e.g. forest microclimate, leading to a termophilisation of the understorey vegetation (Zellweger et al., 2020) and on diminished gas exchange, leading to exacerbate ozone air pollution (Lin et al., 2020). In this respect, all management actions that can augment forest resilience against climate stressors and biotic agents (the two, often interconnected, most important drivers of defoliation), like managing for more diverse forests (e.g. Sousa-Silva et al., 2018; Brockerhoff et al., 2017; but see Bussotti et al., 2018) need to be considered.

5. Conclusions

We examined two datasets referring to two 10-year growing periods (1995–2004 and 2000–2009) and including 2008 and 3116 trees (respectively) for which paired defoliation (an indicator of forest health) and BAI (and indicator of forest growth) data were available from long-term monitoring in France. We observed that growth, expressed in terms of periodical BAI, is negatively and significantly related to mean defoliation regardless of the model adopted to describe such a relationship. This pattern occurred consistently for the growing periods examined, the geographical domain considered, across functional groups and for most of the individual tree species considered. Over the tree population examined, it resulted in an overall significant average reduction in relative BAI of 0.9% per unit increase of defoliation. The difference in BAI with undefoliated trees becomes significant at 15% (overall) and 15–30% (individual species) defoliation levels, thus providing evidence that the 25%-defoliation threshold adopted by international monitoring programs can be a reasonable approximation for tree health classification.

We conclude that considerable and significant BAI reduction can be expected even in the absence of severe defoliation and tree mortality, and – given the statistics about tree defoliation in Europe – such an effect can be widespread and substantial. Given that BAI is a key component of volume and biomass increment, this effect can indicate altered wood production (a key provisioning ecosystem service) and a potential impact of sub-optimal forest health on land-climate interactions via reduction of carbon sequestration (a key regulating ecosystem service) by progressively defoliated trees. Since density and functionality of tree canopy is important also for forest microclimate and gas exchange with atmosphere, protecting and improving the health of European forests (e.g. through proper management actions) may lead to considerable benefits in terms of several ecosystem services (economic production, air quality, carbon sequestration) and protection of biodiversity.

CRediT authorship contribution statement

Marco Ferretti: . **:** Conceptualization, Supervision, Methodology, Writing - review & editing. **Giovanni Bacaro:** Formal analysis, Writing - review & editing. **Giorgio Brunialti:** Data curation, Writing - review & editing. **Marco Calderisi:** Formal analysis, Writing - review & editing. **Luc Croisé:** Data curation, Writing - review & editing. **Luisa Frati:** Data curation, Writing - review & editing. **Manuel Nicolas:** Conceptualization, Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.107749.

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