



How do mixing tree species and stand density affect crown defoliation after heat-drought events?

Théo Javoy, Sandrine Perret, Thomas Perot

► To cite this version:

Théo Javoy, Sandrine Perret, Thomas Perot. How do mixing tree species and stand density affect crown defoliation after heat-drought events?. Forest Ecology and Management, 2025, 586, pp.122684. <10.1016/j.foreco.2025.122684>. <hal-05035548>

HAL Id: hal-05035548

<https://hal.science/hal-05035548v1>

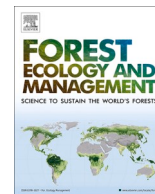
Submitted on 15 Apr 2025

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons CC BY 4.0 - Attribution - International License



How do mixing tree species and stand density affect crown defoliation after heat-drought events?

Théo Javoy^{*}, Sandrine Perret, Thomas Perot[✉]

INRAE, UR Ecosystèmes Forestiers (EFNO) - UR1455, Domaine des Barres, Nogent-sur-Vernisson 45290, France

ARTICLE INFO

Keywords:

Forest dieback
Defoliation
Sessile oak
Scots pine
Mixed forest
Tree size
Stand composition
Stand density
Drought
Heatwave

ABSTRACT

Severe droughts and heat waves have increased over the last decades, leading to forest dieback worldwide. In this context, reducing stand density and mixing tree species are two silvicultural options being investigated by forest managers to limit the impact of climate change on forest health and productivity. We studied tree size effect and stand composition and density effects on crown defoliation in adult trees belonging to two species: sessile oak (*Quercus petraea*, Matt. (Liebl.)) and Scots pine (*Pinus sylvestris*, L.). We monitored tree crown defoliation at 18 experimental plots located in central France for five consecutive years following the extreme heat wave of 2019. Our results highlight two different dynamics for crown defoliation in the two tree species. For Scots pine, we observed an abrupt severe increase in defoliation followed by a significant decrease in 2024, while sessile oak, crown defoliation continued to increase steadily after 2020. For both species, larger trees had significantly less crown defoliation than small trees. We found higher defoliation for sessile oak in mixtures and conversely, higher defoliation for Scots pine in pure stands. Finally, we found no difference in crown defoliation between low-density and medium-density stands for either species.

1. Introduction

Forest dieback is a complex and evolving multifactorial phenomenon generally characterized by tree crown defoliation and sometimes tree death (Manion, 1981; Sinclair, 1965; Vennetier, 2012). Climate change has an impact on forest dynamics, and is increasing forest dieback events linked to droughts and high temperatures (Allen et al., 2010; Gazol and Camarero, 2022; Hammond et al., 2022). Choat et al. (2012) have shown that drought-induced forest dieback is occurring not only in arid regions but also in wet forests not normally considered to be at risk of drought. In this context, more than 1300 forest dieback events linked to high temperatures and droughts have been studied worldwide since 1970, with 46 % of all the tree mortality events studied occurring between 2010 and 2018 (Hammond et al., 2022). Long-term forest monitoring reveals that tree mortality has doubled in Europe's temperate forests over the last three decades (Senf et al., 2018). Climate change can intensify the physiological stress undergone by forest ecosystems, leading to modifications in their carbon and water economies (McDowell et al., 2008), and in their structure and composition (Anderegg et al., 2013).

In this context, forest managers are wondering how to adapt their

management practices to limit the consequences of climate change. Reducing stand density and mixing tree species are two management options thought to limit forest dieback events and their impact on future forest dynamics (Sohn et al., 2016; Puettmann, 2011). Tree species diversity generally improves forest stand resistance to natural disturbances (Jactel et al., 2017) because mixing tree species can promote positive interactions (i.e. niche complementarity) among species for resource acquisition (Ammer, 2019; Forrester and Bauhus, 2016). Moreover, Porté et al. (2004) have shown that forest composition has an effect on microclimatic conditions. Tree health status is also likely to be sensitive to the presence of an accompanying species in the stand. For instance, a tree surrounded by heterospecific neighbors may be subject to different microclimatic conditions, and hence to different hydric and thermic stresses, compared to a tree surrounded by conspecific neighbors. For oak-pine mixtures, it has been shown that mixing reduces drought vulnerability and influences tree physiological mechanisms for both species (Steckel et al., 2020). The temperature perceived by the leaves could be different depending on stand composition, given that high temperatures on the leaf surface (i.e. > 40°C) increase hydraulic failure and alter photosynthesis and respiration processes (Billon et al., 2020; Cochard, 2021; Schuldt and Ruehr, 2022). To summarise, mixing

^{*} Corresponding author.

E-mail address: theo.javoy@inrae.fr (T. Javoy).

species can modify canopy microclimate, root competition for water resources and could be an appropriate silvicultural management option to limit forest dieback (Iacopetti et al., 2019).

To our knowledge, stand density effect has never been studied in relation to tree crown health status, rather only in relation to tree mortality. Even so, some results show that reducing stand density is an effective way to maintain tree growth and to reduce drought-induced tree mortality (Moreau et al., 2022; Sohn et al., 2016). Stand basal area is the main driver of stand evapotranspiration and thinning appears to help to increase water availability at a tree level; however, thinning could also increase transpiration due to higher temperatures (Bachofen et al., 2023). Pardos et al. (2021) also showed that stands with greater basal area could be more resistant and resilient to drought in terms of growth than stands with lower basal area. On the basis of this result, we can hypothesize that trends for crown defoliation over time may also differ according to stand density. Moreover, we should keep in mind that the stand density effect could be species-dependent, as has been demonstrated for tree growth in response to heat-drought events (Bello et al., 2019b).

There are also contrasting results in the literature on how tree social status affects tree sensitivity to drought. Some studies have found large trees to be more sensitive while, in other studies, they appear to be less affected than small trees (Zang et al., 2012). To give an example, Merlin et al. (2015) showed that small Scots pine have a better response to drought than do large ones and that the difference in response to drought between small and large sessile oaks is still unclear. In any case, we know that tree size could be an important factor in explaining drought-induced tree dieback, given that some studies have already shown that drought-induced tree mortality, and even tree mortality through competition, predominantly eliminate small trees (Bose et al., 2024; Pretzsch et al., 2022).

In order to better define forest management options that could help to limit the impacts of climate change on forest dieback, there is a need for results concerning the effect of mixing tree species and the role stand density and tree social status play in tree health for species with contrasting traits.

Herein, we analyse tree size, stand density and stand composition effects on tree health status for a deciduous (sessile oak (*Quercus petraea* L.)) and an evergreen (Scots pine (*Pinus sylvestris* L.)) species, both of which are particularly important economically in Europe. After being hit by several heat waves in recent years, Europe experienced another severe heat wave in 2019 (Xu et al., 2020). In July 2019, an air temperature of 42.8°C was recorded at the weather station close to our study site (INRAE, Nogent-sur-Vernisson, France); it was the highest temperature recorded over the last thirty years. Following this series of heat-drought events, we monitored tree crown defoliation for sessile oak and Scots pine from 2020 to 2024 in the experimental OPTMix network located in central France (Korboulewsky et al., 2015). We compared oak and pine defoliation on trees growing in pure stands and in an oak-pine mixture, for both low-density and medium-density stands. We asked the following research questions:

- 1) How did tree crown defoliation for sessile oak and Scots pine change during the 2020–2024 period? We hypothesized that crown defoliation would increase steadily from 2020 for both species in response to the extreme heatwaves of 2018 and 2019.
- 2) Did relative tree size affect the crown defoliation for either species? Due to a competition disadvantage, we hypothesized that smaller trees would experience more severe crown defoliation in response to heat-drought events.
- 3) Did stand composition and stand density influence tree crown defoliation in sessile oak and Scots pine? Changes in stand composition and stand density lead to changes in microclimates and relationships between individuals. These modifications can potentially have opposite consequences on crown defoliation depending on the considered species. We therefore hypothesized that these factors

would have an effect on tree species defoliation, without specifying the direction.

2. Materials and methods

2.1. Study site and plot description

Data were collected on the OPTMix long-term experimental site (Oak Pine Tree Mixture, <https://www.optmix.efno.fr>, (Korboulewsky et al., 2015) located in the Orléans National Forest (France, 47°49' N, 2°29' E) (Fig. 1), which is the largest forest managed by the National Forest Office (ONF) in metropolitan France, covering 35,000 ha. Elevation ranges from 107 m to 174 m above sea level. The area has a temperate climate with an oceanic influence: the mean annual temperature is 10.8 °C and the mean annual rainfall is 729 mm (based on 1981–2010 data from the SAFRAN and ISBA analytical platforms, Météo-France, (Durand et al., 1993)). All the plots were set up on the same soil type, characterized by an upper layer of sandy loam and a clay layer appearing at around 40–70 cm in depth, which leads to temporary waterlogged conditions in winter and spring. These soils are derived from lacustrine and alluvial deposits and are chemically poor, acidic and relatively unproductive (C/N < 20, pH = 4.5) (Brêthes, 1993). The soils are classified as Planosols (IUSS-Working-Group-WRB, 2015). These characteristics limit plant water availability during the growing season (summer). Two main species were studied: sessile oak (*Quercus petraea* Matt. (Liebl.)) and Scots pine (*Pinus sylvestris* L.). These species are very common in French forests in both pure and mixed stands. The OPTMix experiment consists of 0.5-ha plots of mature forest (70–80 years old on average) with three replicates of each stand type: pure oak, pure pine, and oak-pine mixture, in both low and medium stand densities (Fig. 1, Table 1). In each site, the two 0.5-ha plots with different densities are defined by the Relative Density Index, RDI (Reineke, 1933): the low-density plot thinned in winter 2017 (target RDI = 0.4), and the medium-density plot (target RDI = 0.7). The distance between repetitions of a triplet is at least a few kilometers.

2.2. Sampling design and tree crown observations

Following severe drought-heat wave events (Appendix A, B, C), tree crown defoliation monitoring started in 2020 on the OPTMix experimental plots. We chose the tree crown defoliation because the parameter is the most widely used to indicate tree health status (Bussotti et al., 2024). For each year from 2020 to 2024, one visual observation of tree crowns per year was carried out during June or July on the same sample of trees. Defoliation was monitored through binoculars on at least fifteen trees per species. The trees were randomly selected in three diameter classes and in three zones at each plot. The same sample trees were monitored over the entire five-year period considered in this study. If a sample tree died between 2020 and 2024, the corresponding data between 2020 and its death were included in the statistical analysis (Table 2).

We followed the European protocol defined by the ICP-Forests network (Eichhorn et al., 2016) to estimate tree crown defoliation. For each assessable tree crown, the percentage of defoliation relative to a healthy reference tree was visually estimated and classified in 5 % classes: from 0 % for a healthy tree with no defoliation to 100 % indicating a dead tree. This indicator integrates microphylls and the proportion of dead branches.

To limit observer effects, every effort was made for one and the same person to conduct all the observations for each one-year period and, as far as possible, for several consecutive years. Two main observers were involved: one conducted the observations from 2020 to 2022 and the other one joined the first observer to assess tree crown defoliation in 2023 and 2024. The two observers calibrated their observations together at the beginning of the season to guarantee continuity in the measurements.

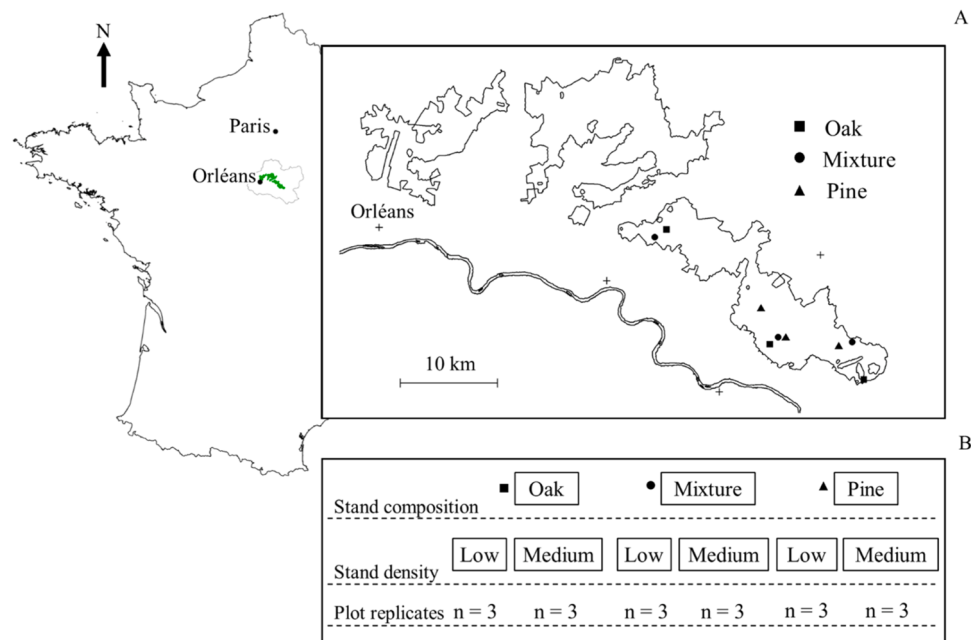


Fig. 1. (A) Location of the OPTMix experimental study sites. Stands of each type (Oak, Pine, Mixture) are spread over nine forest sites in the Orléans State Forest (green area) (France, 47° 49'N, 2° 29'E). (B) Experimental design at the plot level (N = 18). Each site corresponds to two experimental plots with the same stand composition but different densities, a low and a medium stand density.

Table 1
Plot characteristics at the end of the 2020 growing season. N.ha⁻¹ = Number of stems per hectare. BA tot. = total stand basal area. Dg = quadratic mean diameter. Ho = dominant height. oak = sessile oak. pine = Scots pine.

Plot	Stand composition	Stand density	N.ha ⁻¹	BA tot. (m ² .ha ⁻¹)	BA oak (m ² .ha ⁻¹)	BA pine (m ² .ha ⁻¹)	Dg oak (cm)	Dg pine (cm)	Ho oak (m)	Ho pine (m)
O12.2	Oak	Low	292	14.2	14.2	0	24.9	-	20.7	-
O214.2	Oak	Low	281	14.1	14.1	0	25.2	-	19.1	-
O593.2	Oak	Low	191	13.8	13.8	0	30.3	-	22.6	-
O12.3	Oak	Medium	485	22.8	22.8	0	24.4	-	22.1	-
O214.1	Oak	Medium	577	20.8	20.8	0	21.4	-	19	-
O593.1	Oak	Medium	416	22.8	22.8	0	26.4	-	21.4	-
O216.1	Mixture	Low	245	16.6	7.3	9.3	25.3	34.4	18.7	19.4
O57.3	Mixture	Low	205	16.2	7.1	9.1	25.4	41.9	20	22.9
O598.1	Mixture	Low	178	16.6	7.3	9.3	30.2	39.5	20.4	20.7
O216.4	Mixture	Medium	397	25.2	12.3	12.8	24.8	33.7	19.8	22.3
O57.1	Mixture	Medium	417	28.6	12	16.7	23.1	40.1	20.3	23.1
O598.4	Mixture	Medium	328	27.3	9.7	17.6	26.8	37.9	21.2	22.6
O200.2	Pine	Low	173	19	0	19	-	37.2	-	21.7
O333.2	Pine	Low	197	19.6	0	19.6	-	35.5	-	24.2
O83.2	Pine	Low	194	19.9	0	19.9	-	36.2	-	25.1
O200.1	Pine	Medium	343	31.1	0	31.1	-	33.9	-	22.5
O333.3	Pine	Medium	334	31.3	0	31.3	-	34.5	-	23.8
O83.1	Pine	Medium	283	31.2	0	31.2	-	37.4	-	24.9

Table 2
Number of trees observed per species for each year according to stand density and composition.

Species	Stand composition	Stand density	2020	2021	2022	2023	2024
<i>Quercus petraea</i>	Pure	Low	75	75	75	75	75
		Medium	82	82	82	82	81
	Mixture	Low	66	66	66	66	66
		Medium	77	76	76	76	76
<i>Pinus sylvestris</i>	Pure	Low	77	78	77	76	75
		Medium	78	77	77	77	75
	Mixture	Low	68	68	62	62	62
		Medium	73	72	68	68	68

2.3. Statistical analysis of stand characteristics effects on tree crown defoliation during the 2020–2024 period

For each tree species, we fitted a linear mixed effects model with stand composition, stand density, relative tree size and year as fixed effects (global model). The objective of this global model for each species was to identify differences in crown defoliation dynamics over the 2020–2024 period according to the stand characteristics. Year was a numerical variable from 0 to 4, with 0 corresponding to the first survey year (2020). The year effect was tested with a linear and a quadratic term for each species. Relative tree size was calculated for each species based on tree circumference at breast height (1.3 m), and was defined as the difference between the tree circumference and the mean species circumference divided by total mean species circumference in the plot where the tree was located. We fitted our models with tree and plot as nested random effects. The tree and plot random effects allowed us to properly estimate stand composition and stand density effects while varying crown defoliation class over repeated observations from 2020 to 2024. A plot random effect was added on the intercept to take into account varying plot factors such as soil characteristics in our experimental network. A plot random effect was also added to the model for the year effect because we assumed that crown defoliation dynamics could be different for each plot. We verified this assumption by comparing models with random effects on the intercept only and models with random effects on both the intercept and the year effect. We assumed that stand composition, stand density and relative tree size effects could vary over time. We therefore tested whether there was any interaction between these factors and the year effect. We also tested whether there was an interaction between stand composition, stand density and relative tree size.

For each species, we also fitted separate linear mixed effects models for each year (annual models) in complementary analyses. In these models, relative tree size, stand composition and stand density were added as fixed effects and plot was added on the intercept as a random effect. The objective of these annual models for each species was to identify specific differences in crown defoliation for a given year according to stand characteristics.

Data analysis were performed with the R software version 4.2.3. All the linear mixed effects models were fitted with the lmer function of the lme4 package (Bates et al., 2015). We performed pairwise post-hoc multiple comparisons with the emmeans package according to the Sidak method (Lenth, 2017). Estimated marginal means and predictions from the linear mixed effect models were also computed with the emmeans package (Lenth, 2017).

3. Results

3.1. Defoliation dynamics during the 2020–2024 period

For both species, tree crown defoliation increased significantly over the 2020–2024 period (Fig. 2, Table 3). Sessile oak defoliation increased steadily from 34 % to 55 % over the period. Scots pine defoliation increased abruptly from 26 % in 2020 to 43 % in 2021, then continued to increase slightly from 43 % in 2021 to 50 % in 2023, and finally, decreased to 45 % in 2024 (Fig. 2). In 2020, defoliation was higher for sessile oak; however, both species reached a similar defoliation percentage in 2023 (50 %) (Fig. 2).

3.2. Relationship between tree crown defoliation and relative tree size for sessile oak and Scots pine

For both species, our results show a negative relationship between tree crown defoliation and relative tree size (p -value < 0.001 for sessile oak and Scots pine, Table 3). Larger trees suffered less from defoliation than did smaller trees (Fig. 3). Relative tree size effect was stronger for Scots pine than for sessile oak (Table 3) in pure stands: as relative tree

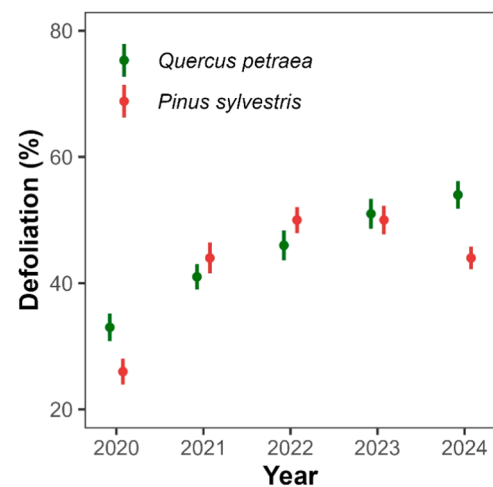


Fig. 2. Tree crown defoliation for sessile oak and Scots pine over the 2020–2024 period. Each point represents the average observed for each tree species and all stand types. Error bars show the standard errors of the observed values.

size changed from 0 to 1, 18.99 % less defoliation for oak and 31.6 % less defoliation for Scots pine. For example, smaller pines (Relative size = -0.25 , circumference = 90 cm) had 54 % defoliation while larger pines (Relative size = $+0.25$, circumference = 140 cm) had 38 % defoliation in 2024.

For sessile oak, the results show a significant interaction between stand composition and the relative tree size (p -value = 0.01, Table 3). In pure stands, small oaks (relative size = -0.25 , circumference = 60 cm) had 55 % defoliation while larger oaks (relative size = $+0.25$, circumference = 100 cm) had 46 % defoliation in 2024. In mixed stands, defoliation was similar in 2024 for larger oaks (relative size = $+0.25$, defoliation = 61 %) and smaller oaks (relative size = -0.25 , defoliation = 63 %). Large and medium-sized oaks had significantly higher defoliation in mixed stands than in pure stands (Fig. 3).

3.3. Stand composition effect on tree crown defoliation for sessile oak and Scots pine

For sessile oak, the results show a slight but significant interaction between the stand composition effect and the year effect (p -value = 0.04, Table 3), which means that changes in defoliation were significantly different between mixed and pure stands (Fig. 4). We systematically observed higher defoliation in mixed stands than in pure stands after 2020 (for the same stand density) and defoliation increased faster in the mixed stands than in pure stands over the period 2020–2024 (24 %). The defoliation increase in mixed stands was slightly higher than defoliation increase in pure stands for sessile oak (Table 3, sessile oak: Est. pure stands = $4.33 \text{ \%} \cdot \text{year}^{-1}$ and Est. mixed stands = $5.96 \text{ \%} \cdot \text{year}^{-1}$). Post-hoc mean comparisons with our global model showed that crown defoliation was not significantly different between pure and mixed stands for sessile oak in 2020 and 2021. However, defoliation became significantly higher in the mixed stands from 2022 to 2024: the difference in defoliation between mixed and pure stands was 7.6 % in 2022, 9.2 % in 2023 and 10.9 % in 2024.

For Scots pine, defoliation was similar in pure and mixed stands in 2020 (Fig. 4) but our results show a significant interaction between the stand composition effect and the year effect ($P < 0.001$, Table 3). Stand type (mixed or pure) significantly influenced changes in defoliation over the 2020–2024 period for Scots pine. In the pure stands, the trees experienced slightly more severe and brutal crown defoliation from 2020 to 2022 (Fig. 4). Nevertheless, post-hoc mean comparisons with our global model showed no significant difference between the two stand compositions dependent on year. The models fitted separately for each year also showed that defoliation was not significantly higher in

Table 3
Estimated parameter values of the linear mixed effects model fitted for *Quercus petraea* and *Pinus sylvestris* defoliation (%). The models were fitted according to the REML method. Nb obs. = number of observations. AIC = Akaike information criterion. RMSE = Root-mean-square error. Est. = Estimate. SE = standard error. Df = Satterthwaite degree of freedom. The intercept of the model represents the defoliation percentage for an average-sized tree in a pure stand in 2020 (2020 was set as the origin $t = 0$).

Species	Nb obs.	AIC	RMSE	Parameter	Est.	SE	Df	t value	p-value
<i>Quercus petraea</i>	1495	12098	9.88	Intercept	32.53	2.82	10	11.53	< 0.001
				Relative size	−18.99	4.25	284	−4.47	< 0.001
				Year	4.55	0.49	10	9.32	< 0.001
				Stand composition (mixture)	4.33	4.01	10	1.08	0.31
				Year: Stand composition (mixture)	1.63	0.7	10	2.35	0.04
				Relative size: Stand composition (mixture)	14.64	5.69	284	2.57	0.01
<i>Pinus sylvestris</i>	1438	11663	9.78	Intercept	24.02	2.82	10	8.53	< 0.001
				Relative size	−31.6	4.64	250	−6.82	< 0.001
				Year	24.72	1.3	43	18.97	< 0.001
				Stand composition (mixture)	4.97	4.01	11	1.24	0.24
				Year ²	−4.68	0.24	1077	−19.82	< 0.001
				Year ² : Stand composition (mixture)	1.81	0.35	1078	5.24	< 0.001
				Year: Stand composition (mixture)	−9.42	1.88	47	−5.01	< 0.001

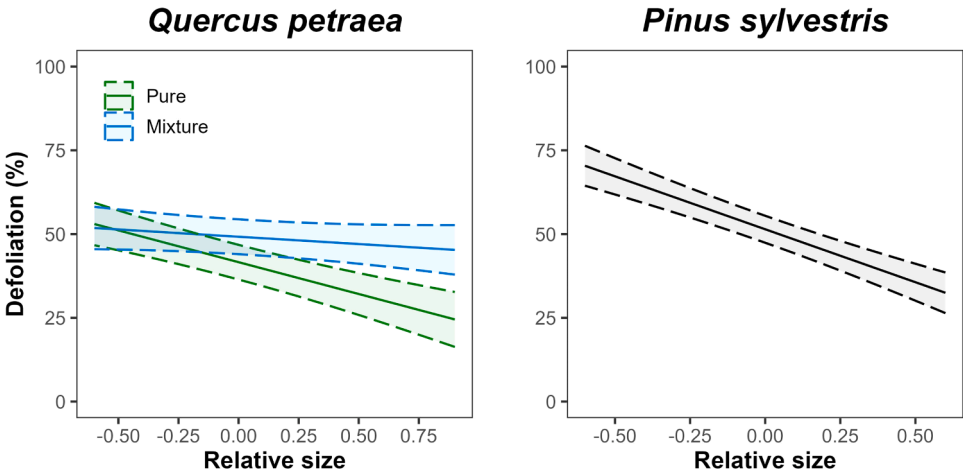


Fig. 3. Sessile oak and Scots pine defoliation in pure and mixed stands during the 2020 – 2024 period according to relative tree size. The solid line corresponds to the predicted values of the linear mixed-effects model (Table 3). The year was fixed at mid-period (2022, year = 2). For each species, we predicted defoliation for average stand density conditions. For Scots pine, we predicted defoliation for an average stand composition. The dashed line corresponds to the confidence interval of the fitted values.

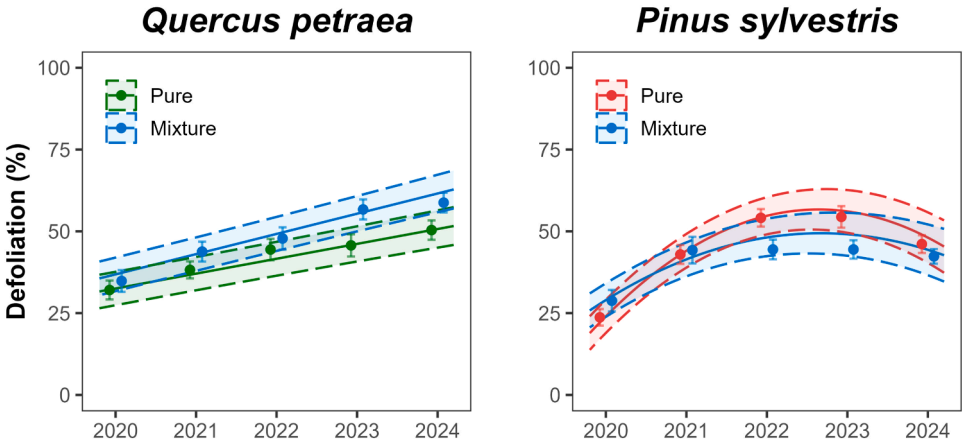


Fig. 4. Changes in defoliation during the 2020 – 2024 period for sessile oak and Scots pine in pure and mixed stands. Solid lines correspond to the values predicted by the linear mixed-effects model (Table 3). Dashed lines correspond to the confidence interval of the fitted values. Each point represents the average observed according to the stand composition (pure or mixed). Error bars represent standard errors of the observed values. Relative tree size is fixed to 0, which corresponds to the average-sized tree. For each species, we predicted defoliation for average stand density conditions.

pure stands than in mixed stands (see [Appendix D](#) for statistical values).

3.4. Stand density effect on tree crown defoliation for sessile oak and Scots pine

Our global models showed that stand density had no significant effect on defoliation for either species during the period 2020 – 2024, whether in pure or mixed stands ([Table 3](#)) (see [Appendix E](#) for statistical values). For both species, we observed approximately the same level of crown defoliation in both the low-density and medium-density plots over the period 2020 – 2024 ([Fig. 5](#)); furthermore, our models fitted separately for each year confirmed that stand density had no effect on defoliation in any given year during the period, whether for pure or mixed stands (see [Appendix D](#) for statistical values).

4. Discussion

With data collected over five consecutive years following the extreme heat waves in 2018 and 2019 from pure and mixed stands of Scots pine and sessile oak, we used linear mixed effect models to study the effects of tree size, stand composition and stand density on crown defoliation.

4.1. Changes in sessile oak and Scots pine tree crown defoliation during the 2020–2024 period

The defoliation we observed in 2023 in the pure stands was 55 % for sessile oak and 45 % for Scots pine. These defoliation rates are much higher than those observed for Europe in 2023 by the International Cooperative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests) (30 % and 35 % for sessile oak and Scots pine, respectively). The more severe defoliation we observed is probably because our study site has particularly poor, acidic and relatively unproductive soils ([Brêthes, 1993](#)). In any case, overall, tree health is deteriorating in European forests due to climate change; several studies have confirmed the increase in defoliation over the past 20 years for sessile oak (+2.6 %) and Scots pine (+4.3 %) growing in temperate regions ([Michel, 2022](#)). For sessile oak, [Michel \(2022\)](#) highlighted that the largest positive deviation from the otherwise gradually increasing trend in defoliation occurred in 2019, possibly due to the effects of heat-drought events both in 2018 and 2019, then the increasing trend in defoliation continued in 2021. For Scots pine, [Michel \(2022\)](#) also showed that mean defoliation values were consistently above the trend line after 2015, with the highest value recorded in 2019.

In our study, the annual changes in defoliation between 2020 and 2024 differ for the two species. For sessile oak, there was a linear increase in tree crown defoliation with an annual increase of 5 % per year ([Fig. 2](#)). For Scots pine, annual changes in defoliation followed a quadratic curve. Between 2020 and 2023, Scots pine foliage health first deteriorated rapidly, then stabilized, and finally, after 2023, improved with a 5 % decrease in defoliation. The crown defoliation we observed at our study site occurred after several severe heat waves and droughts ([Appendix B, C](#)) observed in recent years in Europe ([Xu et al., 2020](#)). [Knutzen et al. \(2025\)](#) demonstrated a significant increase in defoliation due to the heat and drought events from 2018 to 2022 for broadleaves and conifers in French forests. We can assume that these events also triggered an increase in crown defoliation at our study site.

For Scots pine, our results show that the increase in crown defoliation after 2019 was limited over time, with some indications of crown resilience in 2024 ([Fig. 2](#)). Scots pine crown resilience corresponded to regained favorable growing-season conditions with lower maximum temperatures and higher precipitation rates after 2020 ([Appendix A, B, C](#)). For sessile oak, our results show a steady increase in defoliation. We observed that some oaks adapted their crown morphology with sprout growth on the main branches and along the trunk but this phenomenon could not be assessed with the defoliation protocol we applied.

For the 2020 – 2024 period, we were therefore able to assess two different crown dieback patterns following heat-drought events for two tree species. We found particularly abrupt and severe crown defoliation followed by a slight crown recovery for Scots pine, while sessile oak crown defoliation increased steadily.

4.2. Tree crown defoliation is less severe in large trees than in small trees

Our results show a negative correlation between tree crown defoliation and tree size for both sessile oak and Scots pine. For Scots pine, we found a strong negative correlation between tree size and tree crown defoliation. Relative tree size was the most important explanatory effect for crown defoliation in Scots pine ([Table 3](#)). For sessile oak in pure stands, the relative tree size effect was much weaker ([Table 3](#)). For both species, crown defoliation was higher for smaller trees than for larger ones ([Fig. 3](#)). This may indicate that competition was among the main drivers of crown defoliation, as it is for tree mortality; indeed, higher mortality rates in smaller trees have been widely observed for Scots pine ([Bose et al., 2024](#)). Our results are consistent with some research demonstrating that recent temperatures and rainfall trigger over-mortality for small trees but not for dominant trees ([Taccoen et al., 2021](#)). Dominant trees are usually taller and have deeper coarse roots

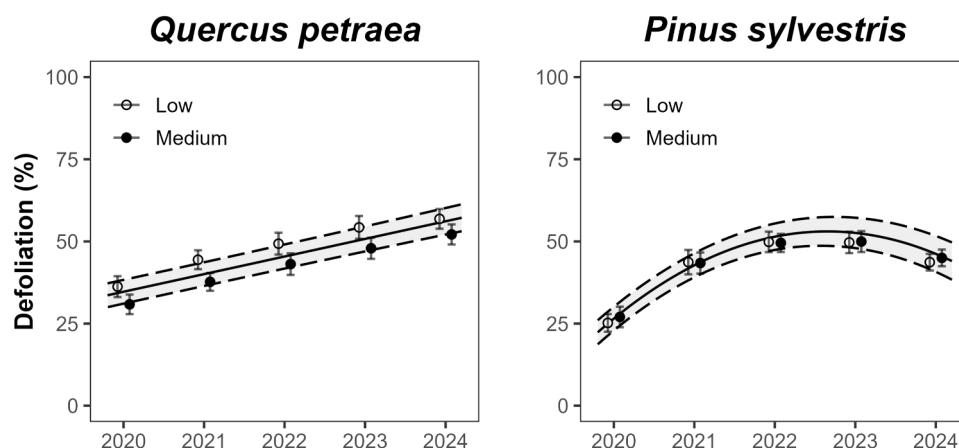


Fig. 5. Changes in defoliation during the 2020 – 2024 period for sessile oak and Scots pine in low-density and medium-density stands. Solid lines correspond to the predicted values of the linear mixed-effects model ([Table 3](#)). Dashed lines correspond to the confidence interval of the fitted values. Points represent the average observed according to the stand density (low or medium). Error bars represent standard errors of the observed means. Relative tree size is fixed to 0, which corresponds to the average-sized tree. For each species, we predicted defoliation for average stand composition conditions.

and a greater fine-root biomass than do suppressed trees, thus giving them better access to water and potentially delaying water stress (Grote et al., 2016). In our study, crown defoliation was higher for smaller trees than for larger ones suggesting that competition between individuals was the main process involved for both species.

4.3. Stand composition effect for Scots pine and sessile oak during the 2020 – 2024 period

For both species, our results show a weak effect of stand composition on changes in tree crown defoliation between 2020 and 2024 (Table 3). Scots pine experienced more severe and more brutal crown defoliation in pure stands (Fig. 4). For sessile oak, our results show only a slight stand composition effect on defoliation after 2020 with a steeper slope for mixed stands than for pure stands (Fig. 4). Moreover, we found a significant interaction between stand composition and relative tree size for sessile oak. The tree size effect was weaker in mixtures than in pure sessile oak stands: small, medium and large sessile oaks all had similar defoliation levels in mixed stands (Fig. 3).

Tree crown morphology could explain our results because canopy filling and crown plasticity could modify light interception, productivity and growth in response to stress in mixed stands (Pretzsch, 2014). The presence of an accompanying species in a stand modifies the temperatures perceived by the leaves of the target tree, and this affects crown defoliation. Oak tree crowns received more light and more heat in our mixed stands than in their corresponding pure stands because Scots pine foliage intercepts less solar radiation than does sessile oak foliage (Perot et al., 2017). Oaks surrounded by pines also benefit much less from a cooling effect of the canopy, especially if the transpiration activity of the pines decrease due to heat-drought events. Oaks surrounded by conspecific neighbors benefit from more favourable thermic conditions due to the cooling effect of oak transpiration. Therefore, the canopy temperature may reach critical levels more quickly in mixed stands than in pure oak stands during severe heatwaves like the one in July 2019 (Xu et al., 2020). This could explain why medium-sized and large oaks had higher tree crown defoliation rates in the oak-pine mixtures; and why the increase in oak defoliation was greater in mixtures.

Scots pine also showed a different rate of change in tree crown defoliation depending on stand composition (Table 3). Surprisingly, Scots pine experienced more severe and more brutal crown defoliation in pure stands (Fig. 4) than in mixed stands. We expected higher defoliation for Scots pine in mixed stands because sessile oak is known to have a competitive advantage over Scots pine for water resources during drought periods (Bello et al., 2019a). However, hotter canopy microclimates in pure pine stands could explain our results; pine crowns may be more exposed to high temperatures and strong solar radiation due to their relatively transparent crowns. Conversely, pines surrounded by oaks may benefit from more favorable microclimatic conditions due to partial shading, more transpiration activity and the higher buffering capacity of the oaks. Thus, Scots pine could be more stressed and suffer more crown defoliation in pure stands following severe heat and drought events due to higher canopy temperatures (eg. > 40°C) and increasing hydraulic failure (Billon et al., 2020; Cochard, 2021). In our study, canopy microclimate was probably the main explanatory factor for changes in crown defoliation rates related to stand composition for both species.

4.4. Why was there no stand density effect on tree crown defoliation for oak and pine?

In our study, there was no effect of stand density on tree crown defoliation over the 2020–2024 period, either for Scots pine or for sessile oak (Fig. 5). Stand densification normally increases tree mortality due to self-thinning processes (Bose et al., 2024) but at our study site, our stand densities were below the biological maximum ($RDI = 1$) for both our low-density (target $RDI = 0.4$) and our medium-density plots (target RDI

= 0.7) (Reineke, 1933). Reducing stand density decreases competition and increases the water available for each tree (Breda et al., 1995). In a drought context, we would have expected higher tree defoliation rates in medium-density stands due to higher competition for water among the roots.

Canopy temperatures can reach higher levels in low-density stands than in higher-density stands during heat-drought events (Díaz-Calafat et al., 2023). In low-density stands, excessive water losses caused by high cuticular permeability can trigger hydraulic failure due to higher canopy temperatures (approximately 40°C) (Billon et al., 2020; Cochard, 2021), and similar temperatures could have been reached at our study site. Considering the previously reported hypotheses, the lack of stand density effect for both species in our study is surprising.

Even though physiological processes involved may differ depending on stand density, crown defoliation rates have been similar in recent years. Possibly, our trees suffered from more root competition for soil water resources at the medium-density but from higher temperatures and sudden hydraulic failure at the low-density. Another explanation could be that recent heat-drought events may have been too severe to subsequently distinguish a stand density effect on tree crown defoliation. For instance, the below-canopy air temperature exceeded 42°C in summer 2019 at our study site and we can easily suggest that canopy temperature exceeded below-canopy air temperature by over 10°C (Gauthey et al., 2024). Whether stand density was low or medium, leaf critical temperature (T_{crit}) could have been exceeded for both species during the heat wave (*Pinus sylvestris*: $T_{crit} = 45^\circ\text{C}$, *Quercus petraea*: $T_{crit} = 59.5^\circ\text{C}$) (Gauthey et al., 2024, 2023). A physiological threshold may have triggered tree crown defoliation, regardless of stand density. Finally, though the range between the two density classes we studied was large from a forest management point of view, it was perhaps still too narrow to reveal any effect on tree crown defoliation. In our study, stand density was not related to tree crown defoliation. However, further investigation is needed to better understand whether reducing density can be an advantage or, on the contrary, an aggravating factor in the case of extreme heat waves or severe droughts leading to forest dieback.

5. Conclusion

Our study provides insights into forest dieback following successive, extreme heat-drought events in 2018 and 2019. Mixing species in a stand and reducing stand density are two of the strategies currently being considered to face climate change. We investigated changes in defoliation rates in Scots pine and sessile oak over the 2020–2024 period related to relative tree size, stand composition and stand density. The two species showed different changes in terms of crown defoliation. Crown defoliation first increased abruptly for Scots pine, then stabilized, and finally, decreased in 2024. For sessile oak, crown defoliation increased steadily over the study period, by approximately 5 % each year. Relative tree size was the strongest observed effect for Scots pine. Larger pines had significantly less crown defoliation than smaller ones, possibly due to greater root competition for water experienced by the smaller trees. We observed the same effect for sessile oak in pure stands but not in mixed stands, probably due to an interaction with microclimatic conditions in mixed stands. For both species, we found a slight stand composition effect on crown defoliation with higher defoliation for sessile oak in mixtures and, conversely, higher defoliation for Scots pine in pure stands. This result could be explained by higher canopy air temperatures when Scots pine is present because its foliage intercepts less solar radiation than sessile oak and because the cooling effect of Scots pine is lessened due to reduced transpiration in case of drought. Unexpectedly, we found no stand-density effect on tree crown defoliation. This may be due to opposite effects when stand density is reduced: there is a better water balance at the tree level but higher temperatures in the canopy.

Our results indicate that mixing tree species could be an interesting

strategy for forest managers to limit crown defoliation but only for Scots pine mixed with sessile oak. Further research and monitoring are needed to better understand how root competition for water and microclimatic conditions are involved in these different stand types during a forest dieback episodes following heat waves and severe droughts, and how these factors interact with the forestry scenarios (e.g. tree growth) being proposed to face climate change.

CRedit authorship contribution statement

Perret Sandrine: Writing – review & editing, Validation, Supervision, Data curation, Conceptualization. **Javoy Théo:** Writing – original draft, Visualization, Formal analysis, Conceptualization. **Perot Thomas:** Writing – review & editing, Validation, Supervision, Methodology, Data curation, Conceptualization.

Declaration of Competing Interest

None.

Acknowledgements

This work was carried out at the OPTMix (Oak Pine Tree Mixture) experimental site (<http://optmix.efno.fr/>) managed by INRAE and supported by the Centre-Val de Loire Region and the French National Forest Office (ONF) Centre-Val de Loire Region and the French National Forest Office (ONF). This research also received support under the Sycomore Programme, with the financial support of the Centre-Val de Loire Region (France) Centre-Val de Loire Region (France). Field measurements and observations were funded in part by the French National Forest Office (ONF) French National Forest Office (ONF). The site belongs to the French national research infrastructure, ANAEE-F (<http://www.anaee-france.fr/fr/>) and the GIS Coop network (<https://www6.inra.fr/giscoop/>), which is supported by the French Ministry for Agriculture and Food. We thank all the members of the OPTMix team for their technical help. We thank Victoria Moore for her assistance in correcting the English version of the manuscript.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2025.122684](https://doi.org/10.1016/j.foreco.2025.122684).

Data availability

Data will be made available on request.

References

- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H. (Ted), Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S. W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manag.* 259, 660–684. <https://doi.org/10.1016/j.foreco.2009.09.001>.
- Ammer, C., 2019. Diversity and forest productivity in a changing climate. *N. Phytol.* 221, 50–66. <https://doi.org/10.1111/nph.15263>.
- Anderegg, W.R.L., Kane, J.M., Anderegg, L.D.L., 2013. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nat. Clim. Change* 3, 30–36. <https://doi.org/10.1038/nclimate1635>.
- Bachofen, C., Poyatos, R., Flo, V., Martínez-Vilalta, J., Mencuccini, M., Granda, V., Grossiord, C., 2023. Stand structure of Central European forests matters more than climate for transpiration sensitivity to VPD. *J. Appl. Ecol.*, 1365–2664.14383 <https://doi.org/10.1111/1365-2664.14383>.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Soft.* 67. <https://doi.org/10.18637/jss.v067.i01>.
- Bello, J., Vallet, P., Perot, T., Balandier, P., Seigner, V., Perret, S., Couteau, C., Korboulewsky, N., 2019b. How do mixing tree species and stand density affect seasonal radial growth during drought events? *For. Ecol. Manag.* 432, 436–445. <https://doi.org/10.1016/j.foreco.2018.09.044>.
- Bello, J., Hasselquist, N.J., Vallet, P., Kahmen, A., Perot, T., Korboulewsky, N., 2019a. Complementary water uptake depth of *Quercus petraea* and *Pinus sylvestris* in mixed stands during an extreme drought. *Plant Soil* 437, 93–115. <https://doi.org/10.1007/s11104-019-03951-z>.
- Billon, L.M., Blackman, C.J., Cochard, H., Badel, E., Hitmi, A., Cartailleur, J., Souchal, R., Torres-Ruiz, J.M., 2020. The DroughtBox: a new tool for phenotyping residual branch conductance and its temperature dependence during drought. *Plant Cell Environ.* 43, 1584–1594. <https://doi.org/10.1111/pce.13750>.
- Bose, A.K., Gessler, A., Büntgen, U., Rigling, A., 2024. Tamm review: Drought-induced Scots pine mortality – trends, contributing factors, and mechanisms. *For. Ecol. Manag.* 561, 121873. <https://doi.org/10.1016/j.foreco.2024.121873>.
- Breda, N., Granier, A., Aussenac, G., 1995. Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus petraea* (Matt.) Liebl.). *Tree Physiol.* 15, 295–306. <https://doi.org/10.1093/treephys/15.5.295>.
- Brêthes, A., 1993. Les Types de station forestière de l'Orléanais. Office national des forêts (ONF), Paris.
- Bussotti, F., Potocić, N., Timmermann, V., Lehmann, M.M., Pollastrini, M., 2024. Tree crown defoliation in forest monitoring: concepts, findings, and new perspectives for a physiological approach in the face of climate change. *For. Int. J. For. Res.* cpad066. <https://doi.org/10.1093/forestry/cpad066>.
- Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S., Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P.J., Nardin, A., Pittermann, J., Pratt, R.B., Sperry, J.S., Westoby, M., Wright, I.J., Zanne, A.E., 2012. Global convergence in the vulnerability of forests to drought. *Nature* 491, 752–755. <https://doi.org/10.1038/nature11688>.
- Cochard, H., 2021. A new mechanism for tree mortality due to drought and heatwaves. *Peer Community J.* 1, e36. <https://doi.org/10.24072/pjournal.45>.
- Díaz-Calafat, J., Uria-Diez, J., Brunet, J., De Frenne, P., Vangansbeke, P., Felton, A., Öckinger, E., Cousins, S.A.O., Bauhus, J., Ponette, Q., Hedwall, P.-O., 2023. From broadleaves to conifers: the effect of tree composition and density on understory microclimate across latitudes. *Agric. For. Meteorol.* 341, 109684. <https://doi.org/10.1016/j.agrformet.2023.109684>.
- Durand, Y., Brun, E., Merindol, L., Guyomarc'h, G., Lesaffre, B., Martin, E., 1993. A meteorological estimation of relevant parameters for snow models. *Ann. Glaciol.* 18, 65–71. <https://doi.org/10.3189/S0260305500011277>.
- Eichhorn, J., Roskams, P., Potocić, N., Timmermann, V., Ferretti, M., Mues, V., Szepesi, A., Durrant, D., Seletkovic, I., Schroeck, H.-W., 2016. Part IV Visual assessment of crown condition and damaging agents. Manual on methods and criteria for harmonized sampling, assessment, monitoring and analysis of the effects of air pollution on forests.
- Forrester, D.I., Bauhus, J., 2016. A review of processes behind diversity—productivity relationships in forests. *Curr. For. Rep.* 2, 45–61. <https://doi.org/10.1007/s40725-016-0031-2>.
- Gauthey, A., Bachofen, C., Deluigi, J., Didion-Gency, M., D'Odorico, P., Gisler, J., Mas, E., Schaub, M., Schuler, P., Still, C.J., Tunas, A., Grossiord, C., 2023. Absence of canopy temperature variation despite stomatal adjustment in *Pinus sylvestris* under multidecadal soil moisture manipulation. *N. Phytol.*, nph.19136 <https://doi.org/10.1111/nph.19136>.
- Gauthey, A., Kahmen, A., Limousin, J., Vilagrosa, A., Didion-Gency, M., Mas, E., Milano, A., Tunas, A., Grossiord, C., 2024. High heat tolerance, evaporative cooling, and stomatal decoupling regulate canopy temperature and their safety margins in three European oak species. *Glob. Change Biol.* 30, e17439. <https://doi.org/10.1111/gcb.17439>.
- Gazol, A., Camarero, J.J., 2022. Compound climate events increase tree drought mortality across European forests. *Sci. Total Environ.* 816, 151604. <https://doi.org/10.1016/j.scitotenv.2021.151604>.
- Grote, R., Gessler, A., Hommel, R., Poschenrieder, W., Priesack, E., 2016. Importance of tree height and social position for drought-related stress on tree growth and mortality. *Trees* 30, 1467–1482. <https://doi.org/10.1007/s00468-016-1446-x>.
- Hammond, W.M., Williams, A.P., Abatzoglou, J.T., Adams, H.D., Klein, T., López, R., Sáenz-Romero, C., Hartmann, H., Breshears, D.D., Allen, C.D., 2022. Global field observations of tree die-off reveal hotter-drought fingerprint for Earth's forests. *Nat. Commun.* 13, 1761. <https://doi.org/10.1038/s41467-022-29289-2>.
- Iacopetti, G., Bussotti, F., Selvi, F., Maggino, F., Pollastrini, M., 2019. Forest ecological heterogeneity determines contrasting relationships between crown defoliation and tree diversity. *For. Ecol. Manag.* 448, 321–329. <https://doi.org/10.1016/j.foreco.2019.06.017>.
- IUSS-Working-Group-WRB, 2015. World Reference Base for Soil Resources 2014, update 609 2015. International soil classification system for naming soils and creating legends for 610 soil maps. World Soil Resources Reports. FAO, Rome, p. 192.
- Jactel, H., Bauhus, J., Boberg, J., Bonal, D., Castagneyrol, B., Gardiner, B., Gonzalez-Olabarria, J.R., Koricheva, J., Meurisse, N., Brockerhoff, E.G., 2017. Tree diversity drives forest stand resistance to natural disturbances. *Curr. For. Rep.* 3, 223–243. <https://doi.org/10.1007/s40725-017-0064-1>.
- Knutzen, F., Auerbeck, P., Barrasso, C., Bouwer, L.M., Gardiner, B., Grünzweig, J.M., Hänel, S., Haustein, K., Johannessen, M.R., Kollet, S., Müller, M.M., Pietikäinen, J.-P., Pietras-Couffignal, K., Pinto, J.G., Rechid, D., Rousi, E., Russo, A., Suarez-Gutierrez, L., Veit, S., Wendler, J., Xoplaki, E., Gliksmann, D., 2025. Impacts on and damage to European forests from the 2018–2022 heat and drought events. *Nat. Hazards Earth Syst. Sci.* 25, 77–117. <https://doi.org/10.5194/nhess-25-77-2025>.
- Korboulewsky, N., Perot, T., Balandier, P., Ballon, P., Barrier, R., Boscardin, Y., Richard, E.D., Dumas, Y., Ginisty, C., Gosselin, M., 2015. OPTMix-Dispositif expérimental de suivi à long terme du fonctionnement de la forêt mixte. *Rendez-vous Tech. De l'ONF* 60–70.

- Lenth, R.V., 2017. emmeans: Estimated Marginal Means, aka Least-Squares Means. <https://doi.org/10.32614/CRAN.package.emmeans>.
- Manion, P.D., 1981. Tree disease concepts. Tree disease concepts.
- McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., Yepez, E.A., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *N. Phytol.* 178, 719–739. <https://doi.org/10.1111/j.1469-8137.2008.02436.x>.
- Merlin, M., Perot, T., Perret, S., Korboulewsky, N., Vallet, P., 2015. Effects of stand composition and tree size on resistance and resilience to drought in sessile oak and Scots pine. *For. Ecol. Manag.* 339, 22–33. <https://doi.org/10.1016/j.foreco.2014.11.032>.
- Michel, A.K., 2022. Forest Condition in Europe: The 2022 Assessment; ICP Forests Technical Report under the UNECE Convention on Long-range Transboundary Air Pollution (Air Convention). Johann Heinrich von Thünen-Institut, DE.
- Moreau, G., Chagnon, C., Achim, A., Caspersen, J., D'Orangeville, L., Sánchez-Pinillos, M., Thiffault, N., 2022. Opportunities and limitations of thinning to increase resistance and resilience of trees and forests to global change. *For.: Int. J. For. Res.*, cpac010 <https://doi.org/10.1093/forestry/cpac010>.
- Pardos, M., del Río, M., Pretzsch, H., Jactel, H., Bielak, K., Bravo, F., Brazaitis, G., Defosse, E., Engel, M., Godvot, K., Jacobs, K., Jansone, L., Jansons, A., Morin, X., Nothdurft, A., Oreti, L., Ponette, Q., Pach, M., Riofrío, J., Ruíz-Peinado, R., Tomao, A., Uhl, E., Calama, R., 2021. The greater resilience of mixed forests to drought mainly depends on their composition: analysis along a climate gradient across Europe. *For. Ecol. Manag.* 481, 118687. <https://doi.org/10.1016/j.foreco.2020.118687>.
- Perot, T., Mårell, A., Korboulewsky, N., Seigner, V., Balandier, P., 2017. Modeling and predicting solar radiation transmittance in mixed forests at a within-stand scale from tree species basal area. *For. Ecol. Manag.* 390, 127–136. <https://doi.org/10.1016/j.foreco.2017.01.023>.
- Porté, A., Huard, F., Dreyfus, P., 2004. Microclimate beneath pine plantation, semi-mature pine plantation and mixed broadleaved-pine forest. *Agric. For. Meteorol.* 126, 175–182. <https://doi.org/10.1016/j.agrformet.2004.06.001>.
- Pretzsch, H., 2014. Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. *For. Ecol. Manag.* 327, 251–264. <https://doi.org/10.1016/j.foreco.2014.04.027>.
- Pretzsch, H., Bravo-Oviedo, A., Hilmers, T., Ruiz-Peinado, R., Coll, L., Löf, M., Ahmed, S., Aldea, J., Ammer, C., Avdagić, A., Barbeito, I., Bielak, K., Bravo, F., Brazaitis, G., Cerný, J., Collet, C., Drössler, L., Fabrika, M., Heym, M., Holm, S.-O., Hylen, G., Jansons, A., Kurylyak, V., Lombardi, F., Matović, B., Metslaid, M., Motta, R., Nord-Larsen, T., Nothdurft, A., Ordóñez, C., den Ouden, J., Pach, M., Pardos, M., Ponette, Q., Pérot, T., Reventlow, D.O.J., Sitko, R., Sramek, V., Steckel, M., Svoboda, M., Uhl, E., Verheyen, K., Vospernik, S., Wolff, B., Zlatanov, T., del Río, M., 2022. With increasing site quality asymmetric competition and mortality reduces Scots pine (*Pinus sylvestris* L.) stand structuring across Europe. *For. Ecol. Manag.* 520, 120365. <https://doi.org/10.1016/j.foreco.2022.120365>.
- Puettmann, K.J., 2011. Silvicultural challenges and options in the context of global change: “simple” fixes and opportunities for new management approaches. *J. For. Reineke, L.H.*, 1933. Perfecting a stand-density index for even-aged forests. *J. Agric. Res.* 46, 627–638.
- Schuldt, B., Ruehr, N.K., 2022. Responses of European forests to global change-type droughts. *Plant Biol.* 24, 1093–1097. <https://doi.org/10.1111/plb.13484>.
- Senf, C., Pflugmacher, D., Zhiqiang, Y., Sebal, J., Knorn, J., Neumann, M., Hostert, P., Seidl, R., 2018. Canopy mortality has doubled in Europe’s temperate forests over the last three decades. *Nat. Commun.* 9, 4978. <https://doi.org/10.1038/s41467-018-07539-6>.
- Sinclair, W.A., 1965. Comparisons of Recent Declines of White Ash, Oaks and Sugar Maple in Northeastern Woodlands.
- Sohn, J.A., Saha, S., Bauhus, J., 2016. Potential of forest thinning to mitigate drought stress: a meta-analysis. *For. Ecol. Manag.* 380, 261–273. <https://doi.org/10.1016/j.foreco.2016.07.046>.
- Steckel, M., del Río, M., Heym, M., Aldea, J., Bielak, K., Brazaitis, G., Černý, J., Coll, L., Collet, C., Ehbrecht, M., Jansons, A., Nothdurft, A., Pach, M., Pardos, M., Ponette, Q., Reventlow, D.O.J., Sitko, R., Svoboda, M., Vallet, P., Wolff, B., Pretzsch, H., 2020. Species mixing reduces drought susceptibility of Scots pine (*Pinus sylvestris* L.) and oak (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.) – Site water supply and fertility modify the mixing effect. *For. Ecol. Manag.* 461, 117908. <https://doi.org/10.1016/j.foreco.2020.117908>.
- Taccoen, A., Piedallu, C., Seynave, I., Gégout-Petit, A., Nageleisen, L.-M., Bréda, N., Gégout, J.-C., 2021. Climate change impact on tree mortality differs with tree social status. *For. Ecol. Manag.* 489, 119048. <https://doi.org/10.1016/j.foreco.2021.119048>.
- Vennetier, M., 2012. Climate change and forest decline: causes and consequences. *Cah. D. Etude* 50, 60.
- Xu, P., Wang, L., Liu, Y., Chen, W., Huang, P., 2020. The record-breaking heat wave of June 2019 in Central Europe. *e964 Atmos. Sci. Lett.* 21. <https://doi.org/10.1002/asl.964>.
- Zang, C., Pretzsch, H., Rothe, A., 2012. Size-dependent responses to summer drought in Scots pine, Norway spruce and common oak. *Trees* 26, 557–569. <https://doi.org/10.1007/s00468-011-0617-z>.