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Long-Term Effects of Mistletoe Removal on Radial Growth of Semi-Arid Aleppo Pine Forests

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Abstract: Mistletoes are hemiparasites that modify how trees cope with drought by impairing the relationships between water, carbon, and nutrients within the tree. Thus, mistletoes endanger the vitality and persistence of trees in drought-prone regions, such as the Mediterranean Basin. Here, we evaluated radial growth patterns and drought sensitivity of Aleppo pine (*Pinus halepensis* Mill.) trees from which mistletoe was removed ca. two decades ago (MRTs) with control; currently infested trees (MCTs) from a semi-arid region in NE Spain. Growth showed negative trends in both tree classes since the 1980s concurrent with progressive aridification and aggravated by mistletoe infestation, as indicated by the positive effect of mistletoe removal on the growth of MRT trees. Water availability during the previous autumn and winter and current spring and early summer drove growth. Climate–growth correlations were similar between tree classes before treatment, but after mistletoe removal, precipitation became significant in MCT trees but not in MRT trees. Likewise, the impact of drought on growth changed through time: it increased until the late 20th century and then decreased in the MRT trees, which showed higher resistance and resilience against post-treatment droughts. This study provides evidence of the long-term positive effect of mistletoe removal on radial growth in semi-arid pine forests.

Keywords: drought; forest management; Mediterranean region; *Pinus halepensis*; *Viscum album* spp. *austriacum*

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1. Introduction

Mistletoes are the predominant group of hemiparasitic plants distributed in boreal and temperate forests, tropical rain forests, and semi-arid and arid woodlands [1]. Mistletoes are a diverse group that encompasses nearly 1600 species distributed among five families in the Santalales order [2]. Mistletoes are keystone species for maintaining biodiversity, providing nesting sites and food resources for forest-dependent species, and promoting nutrient cycling by fertilizing the soil with nutrient-enriched litter [3,4]. However, they can also accelerate canopy dieback, trigger growth decline, and amplify tree mortality, particularly in areas with pronounced water deficits [5,6]. Mistletoes are xylem-tapping hemiparasites that derive water and nutrients from the host's xylem solution [7], thus increasing the drought stress and compromising the carbon and nutrient balance of the host tree [8]. Hence, mistletoes may foster drought-induced forest die-off considering the tight interdependencies between water, carbon, and defenses [9].

The European pine mistletoe (*Viscum album* ssp. *austriacum* L.) is the most widespread hemiparasitic plant in Europe [10]. This mistletoe species is capable of colonizing several pine species, including Aleppo pine (*Pinus halepensis* Mill.) [11], which is the most important tree species in the western Mediterranean Basin, where it predominates in the driest and warmest areas covering ca. 3.5 million hectares in reforestation and natural stands [12]. Some of these seasonally dry stands account for the highest proportion of mistletoe-colonized forests in Mediterranean regions [13] and represent the xeric limit

of the mistletoe distribution [10,14]. Therefore, the impact of mistletoe is compounded by abiotic stress caused by increased aridification in these drought-prone Mediterranean regions, particularly under semi-arid conditions [15,16]. However, to our knowledge, no evaluations of the impact of mistletoe on the performance of Aleppo pine have yet been made. Thus, a better understanding of mistletoe impacts on semi-arid Mediterranean pine stands is essential to improving projections of their performance in the face of climate change and can provide insights into the future effects on cold-wet pine forests under warming climate scenarios.

Mistletoes have a lower water potential than host leaves, which allows them to maintain high stomatal conductance and transpiration rates [17], representing the passive mechanism by which these hemiparasites extract water and nutrients from the xylem of the tree [2,7]. As a consequence, decreases in stomatal conductance [18], losses of hydraulic conductivity [19], reductions in non-structural carbohydrate concentrations [20], morphological and physiological modifications of needles [21], decreases in essential nutrient content [22,23], and alteration of metabolic processes [24] have been reported in severely mistletoe-infested trees. The result of all these impacts of mistletoes on tree physiology translates into growth declines [6,8,25] and increases in sensitivity to water availability [26,27], which ultimately may lead to growth decline, canopy dieback, and tree death [5].

Consequently, mistletoes cause significant productive and economic losses [4,6] and several management options have been practiced to mitigate mistletoe infestation. They include mechanical methods by removing the affected host parts, chemical and biological controls using trunk injection with herbicides or fungi, and sylvicultural approaches, such as thinning of severely infested trees, breeding programs of resistant hosts, and promotion of mixed forests [4,28,29]. Mechanical control, such as pruning of infested branches or removing infested trees, is the primary and most effective control for European mistletoe [30,31]. For instance, Yan et al. [32] found that mistletoe removal from Scots pine branches resulted in increased tree-ring width, shoot growth, and leaf size due to improved carbon assimilation and nutrition. However, such direct methods have elevated time and economic costs, which limit their application to only local, small, and high-value areas and/or single interventions [28]. So, the assessment of the long-term impacts of mistletoe removal is needed in order to design ecologically and economically sustainable management plans to alleviate the mistletoe menace.

Here, we analyzed the legacy effects of mistletoe removal on the long-term radial growth patterns and sensitivity to climate in semi-arid Aleppo pine stands. For that purpose, we used a dendrochronological approach. Measurements of tree-ring width provide retrospective, long-term records of tree growth variability [33]. Moreover, radial growth is considered a sensitive indicator of tree carbon–water balance, and it is highly dependent on environmental conditions [34]. We compared pine stands in which mistletoe was removed ca. two decades ago with control stands without previous treatments. Our study stands were located in a dry and continental region of NE Spain at the xeric distribution limit of the mistletoe. We expected (i) a short- and medium-term enhancement of growth after mistletoe removal but a dilution of the positive effect in the long-term, and (ii) a reduced climatic sensitivity of mistletoe-removed trees that remains significant only a few years after treatment.

2. Materials and Methods

2.1. Study Sites and Climatic Data

Our study region was located in the Middle Ebro Basin (Aragón, NE Spain; Figure 1a; Table 1) near the thermophilic limit for Aleppo pine and at the xeric boundary for mistletoe in Europe (Figure 1b). We sampled two different sites: Alcañiz (AL; Teruel province) and Mequinenza (ME, Zaragoza province). Common understory species are *Juniperus phoenicea* L., *Juniperus communis* L., *Quercus coccifera* L., *Pistacia lentiscus* L., *Salvia rosmarinus* Spenn., *Rhamnus lycioides* L., *Globularia alypum* L., *Genista scorpius* (L.) DC., *Cistus* sp. L., *Fumana* sp.

(Dunal) Spach, and *Helichrysum* sp. Mill. The lithology of the area is limestone, and the soils are rocky and basic. The average height of the sampled Aleppo pines was 7–10 m.

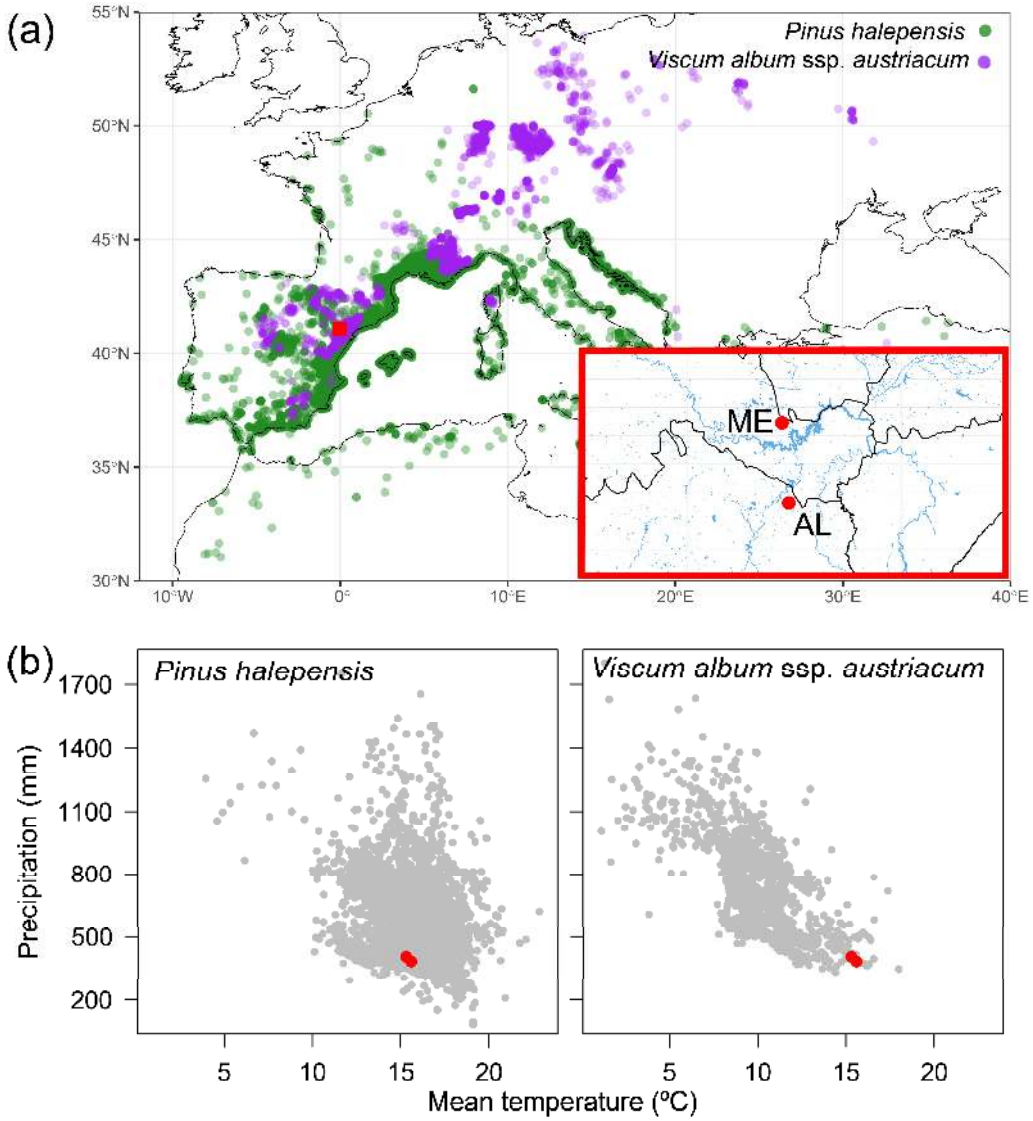


Figure 1. Distribution (**a**) and climate envelopes (**b**) of Aleppo pine (*Pinus halepensis*) and European pine mistletoe (*Viscum album* ssp. *austriacum*) on the European scale. In (**a**) circles indicate species occurrence according to GBIF database, and the red square represents the location of the study region. The bottom right inset indicates the location of Alcañiz (AL) and Mequinenza (ME) study sites; black lines are provincial boundaries and blue lines represent the main watercourses. In (**b**), the climate variables are mean annual temperature and total annual precipitation averaged over the period 1991–2020 and downloaded from TerraClimate dataset [35]. Grey symbols represent climate at the locations of occurrences of (**a**), and red symbols represent the study sites.

The climate is Mediterranean, with a pronounced period of drought during summer and rainfall in spring and autumn (Figure S1a). We obtained monthly climate data from the 4 km gridded TerraClimate dataset [35] due to the lack of homogeneous, long-term records in the study area. Climatic variables were mean maximum temperature (Tmax), mean minimum temperature (Tmin), and total precipitation (Ppt) for the period 1950–2021. Conditions in ME are slightly more xeric than in AL, with a higher mean temperature (ME: 15.0 ± 0.1 °C; AL: 14.7 ± 0.1 °C) and lower annual precipitation (ME: 399 ± 12 mm; AL: 419 ± 11 mm), although the differences are minor. The month with the lowest minimum temperature was December (ME: 1.3 °C; AL: 1.0 °C), and the maximum temperatures were

recorded in July (ME: 31.0 °C; AL: 30.8 °C). July was the driest month (ME: 12 mm; AL: 15 mm), and the wettest months were May (ME: 49 mm; AL: 51 mm) and October (ME: 48 mm; AL: 49 mm) (Figure S1a).

Table 1. Characteristics (mean ± standard error) of sampled sites and *Pinus halepensis* trees for mistletoe-control trees (MCTs) and mistletoe-removed trees (MRTs). Different letters indicate significant ($p < 0.05$) differences between NR and R trees, according to Kruskal-Wallis χ^2 tests.

Variable	Alcañiz (AL)		Mequinenza (ME)	
Mistletoe treatment	MCTs	MRTs	MCTs	MRTs
Latitude	41°4′45″ N	41°3′50″ N	41°22′21″ N	41°20′44″ N
Longitude	0°3′05″ W	0°1′35″ W	0°02′41″ E	0°3′30″ W
Elevation (m a.s.l.)	400	440	310	360
Aspect	SW	E	E-NE	NE
DBH (cm)	27.4 ± 1.9a	27.4 ± 1.3a	19.4 ± 0.7a	15.8 ± 1.6b
Tree age at 1.3 m (yrs.)	96 ± 7a	93 ± 6a	85 ± 3a	111 ± 9b
Mistletoe infestation degree	4.1 ± 0.2a	0.7 ± 0.3b	3.1 ± 0.2a	1.1 ± 0.3b
Crown defoliation (%)	70.1 ± 4.9a	17.6 ± 2.9b	63.6 ± 4.2a	19.1 ± 3.2b
No. sampled trees (No. radii)	16 (31)	17 (34)	21 (40)	15 (30)
TRW [1]	0.78 ± 0.06a	0.86 ± 0.05a	0.72 ± 0.03a	0.62 ± 0.04a
AC [1]	0.54 ± 0.04a	0.42 ± 0.03a	0.42 ± 0.02a	0.45 ± 0.04a
EPS [1]	0.907	0.985	0.986	0.940
Rbar [1]	0.379	0.798	0.772	0.511
MS [1]	0.526	0.522	0.599	0.576

Variables' abbreviations: diameter at breast height (DBH), expressed population signal (EPS), tree-ring width (TRW), mean inter-series correlation (*Rbar*), first-order autocorrelation (AC), and mean sensitivity (MS). [1] Calculated for the period 1950–2021 on raw (TRW, AC) or standardized (EPS, *Rbar*, MS) ring-width values.

To characterize drought severity in the study area during the period 1950–2021, 0.5°-gridded monthly data of the Standardized Precipitation Evapotranspiration Index (SPEI) were obtained from the SPEI Global Drought Monitor webpage (https://spei.csic.es, accessed on 24 April 2024). The SPEI is a multi-scalar index used as a proxy of soil moisture, which is calculated as cumulative water balances estimated using temperature and precipitation data, in which positive and negative values indicate wet and dry conditions, respectively [36]. We retrieved SPEI at temporal resolutions from 1 to 24 months.

2.2. Mistletoe Treatment and Field Sampling

The Regional Forest Service (Aragón Govt., Zaragoza, Spain) completely removed all mistletoe individuals from Aleppo pine in the two study stands in 1998 (AL) and in 2001 (ME). In order to eliminate the haustoria, the perennial endophytic system by which mistletoe taps into the host xylem [7], the branches colonized by mistletoe were pruned. Those trees were defined as mistletoe-removed trees (MRTs). To evaluate the effect of mistletoe removal by comparison with stands of similar characteristics, we selected two other plots in the vicinity of the previous plots, under similar climate and soil conditions, where no mistletoe treatments were carried out. These trees with all mistletoes intact were referred to as mistletoe-control trees (MCTs).

Field sampling was conducted in the summer and autumn of 2022. In total, we selected 69 dominant trees (15–20 trees per plot). Two cores at 1.3 m height were extracted from each selected tree using 5 mm Pressler increment borers (Haglöf, Långsele, Sweden) for dendrochronological analysis. We estimated the mistletoe infestation degree of the selected trees using a modified version of the Hawksworth scale [37]. The tree crown was divided into three similar vertical parts, and each third was scored with 0 (absence of mistletoe), 1 (moderate presence of mistletoe), or 2 (high presence of mistletoe), and finally, the contribution of each third was summed to obtain a tree-level value [27]. Therefore, the infestation degree ranged between 0 and 6. We also assessed crown defoliation (%)

by visual assessment of crown transparency as an estimate of tree vitality [38]. For each selected tree, we measured diameter at breast height (DBH) using tapes.

2.3. Dendrochronological Methods

Extracted wood cores were air-dried, glued onto wooden mounts, and polished until the xylem cellular structure was visible [33]. All samples were visually cross-dated, and tree-ring width (TRW) was measured with a 0.001 resolution using scanned images (resolution 2400 dpi) and the CooRecorder-CDendro software (v. 9.8.1, Saltsjöbaden, Sweden) [39]. The visual cross-dating was statistically checked using the COFECHA software, which calculates moving correlations between individual series of ring-width values and the mean sites series [40].

To compute climate–growth correlations, all individual TRW chronologies were detrended using a spline of two-thirds of the growth series length and a 0.5 response cut-off. Afterwards, an autoregressive model was applied to each detrended series to remove the first-order autocorrelation, therefore building residual, pre-whitened ring-width index chronologies. Tree-level series were averaged by bi-weight robust mean to develop mean chronologies for each site and mistletoe treatment. Dendrochronological statistics were calculated over the best-replicated period (1950–2021), including the first-order autocorrelation (AC), the expressed population signal (EPS) that estimates the quality and reliability of the chronologies, the mean correlation among indexed ring-width series (*Rbar*), and the mean sensitivity (MS), which measures relative changes in width between consecutive years [33,41].

To assess radial growth patterns of trees from different sites and mistletoe treatments, we transformed individual tree TRW series into the basal area increment (BAI) series to account for geometrical constraints [42]. The BAI series were calculated using the following equation and assuming concentric rings:

$$\mathrm{BAI} = \pi\,(R^2{}_t - R^2{}_{t-1}), \tag{1}$$

where $R^2{}_t$ and $R^2{}_{t-1}$ are the cumulative radii corresponding to the years t and $t - 1$, respectively.

We evaluated the radial growth response of trees to severe drought episodes (1994–1995, 2005, 2012) by calculating resilience indices [43]. Resistance (Rt) characterizes the ability of the tree to absorb the stress situation induced by the drought event; recovery (Rc) reflects the extent of growth increase or decrease after the drought event; and resilience (Rs) indicates a tree's ability to revert to pre-drought growth levels. The indices based on the ratios of pre-drought, drought, and post-drought growth BAI values were calculated as follows:

$$\mathrm{Rt} = \mathrm{BAI_D}/\mathrm{BAI_{preD}}, \tag{2}$$

$$\mathrm{Rc} = \mathrm{BAI_{postD}}/\mathrm{BAI_D}, \tag{3}$$

$$\mathrm{Rs} = \mathrm{BAI_{postD}}/\mathrm{BAI_{preD}}, \tag{4}$$

where $\mathrm{BAI_D}$ is the growth during the drought event and $\mathrm{BAI_{preD}}$ and $\mathrm{BAI_{postD}}$ are the mean BAI of the three years preceding and following, respectively, the drought when no drought conditions occurred. Pre- and post-drought periods of three years were established based on previous studies [15]. Index calculations for the two-year drought of 1994–1995 were performed, including, in the drought period, the average of 1994 and 1995 BAIs.

2.4. Statistical Analysis

We used the Kruskal–Wallis tests to evaluate differences in tree characteristics (DBH, tree age, mistletoe infestation degree, crown defoliation, mean TRW, and resilience indices) between treatments within sites. Climate–growth relationships were assessed by calculating bootstrapped correlations between RWI chronologies and monthly Tmax, Tmin, Ppt, and SPEI (considering 1- to 24-month long time scales) for the 1950–2021 period. The window

of analysis spanned from the previous September to September of the year of tree-ring formation. To quantify potential instabilities in the climate–growth relationships, we computed correlations for two comparable periods before (1980–1999) and after mistletoe removal (2000–2021).

We used generalized additive mixed models (GAMMs) [44] to describe temporal changes in the tree growth response to soil moisture. Individual log-transformed BAI was modelled as a function of tree size (DBH), calendar year, and SPEI as:

$$\log (BAI_i + 1) = \beta_0 + s (DBH_i) + s (\text{calendar year}_i \times SPEI_i) + Z_i B_i + \varepsilon_i \quad (5)$$

where the BAI of a tree i is modelled as smooth functions (s) of DBH and the interaction between calendar year and SPEI. The selection of the month and time scale of SPEI was based on previously calculated climate–RWI correlations. The smooth terms were represented using thin plate regression splines with a maximum of five degrees of freedom [45]. Trees (Z_iB_i) were regarded as random effects to account for repeated measures over the same individual. We also included in the model an error term (ε_i) with a first-order [AR(1)] correlation structure. The goodness of fit of models was evaluated with the coefficient of determination proposed by [46]: marginal (R^2m) and conditional (R^2c) R^2 values, which account for the effects of fixed and fixed plus random factors, respectively. Finally, we explored BAI residuals, which characterize the year-to-year growth variation after removing the effect of soil moisture variability, to assess whether trees grew more or less than predicted by GAMMs.

All statistical analyses were performed within the R software (version 4.3.3) [47]. Processing of radial growth series and calculation of dendrochronological statistics were conducted using the R package *dplR* [48]. Relationships between radial growth series and climate were calculated using the R package *treeclim* [49]. Calculation of drought resilience indices was conducted with *pointRes* package [50]. The GAMMs were fitted using the R package *mgcv* [51].

3. Results

3.1. Differences in Radial Growth Patterns between Mistletoe Treatments

The mean DBH of MRTs was similar to that of MCTs in AL, but lower in ME (Table 1). Similarly, the tree age of AL pines did not differ between mistletoe treatments, but MCTs were younger than MRTs in ME. We found no differences in mean TRW between treatments during the period 1950–2021 at any study site. MCTs at both sites exhibited a higher degree of mistletoe infestation and crown defoliation than MRTs (Table 1).

In AL, MRTs grew less than MCTs in the mid-20th century, but after mistletoe removal, BAI trends became slightly positive and negative in MRTs and MCTs, respectively (Figure 2a). In ME, both tree classes showed similar BAI patterns throughout most of the 20th century, but MCT growth trends turned negative during the 21st century, while MRTs showed no trend (Figure 2b). Growth rates of MCTs were lower than those of MRTs a few years after mistletoe removal at both sites.

3.2. Long- and Short-Term Growth Responses to Climate and Drought

Significant climate–RWI correlations were more frequent for precipitation than temperature variables (Figure S2). In the site ME, MCTs responded more to May–July precipitation than MRTs. June and July Tmax had negative effects on the RWI of trees in ME, whereas April Tmin showed a consistent positive effect on growth at both sites. Previous winter, spring, and early summer precipitation presented positive correlations with RWI at both sites (Figure S2). Consistently, we found that the strongest correlations between RWI and the drought index were found with March SPEI calculated at a 6-month-long scale (SPEI6.March: AL: $r_{MCT} = 0.543$, $r_{MRT} = 0.539$; ME: $r_{MCT} = 0.449$, $r_{MRT} = 0.559$) and with July SPEI calculated at a 9-month scale (SPEI9.July: AL: $r_{MCT} = 0.519$, $r_{MRT} = 0.530$; ME: $r_{MCT} = 0.556$, $r_{MRT} = 0.538$) (Figure 3). These results highlight the importance of soil

moisture during the previous fall and winter and current spring and early summer on growth variability.

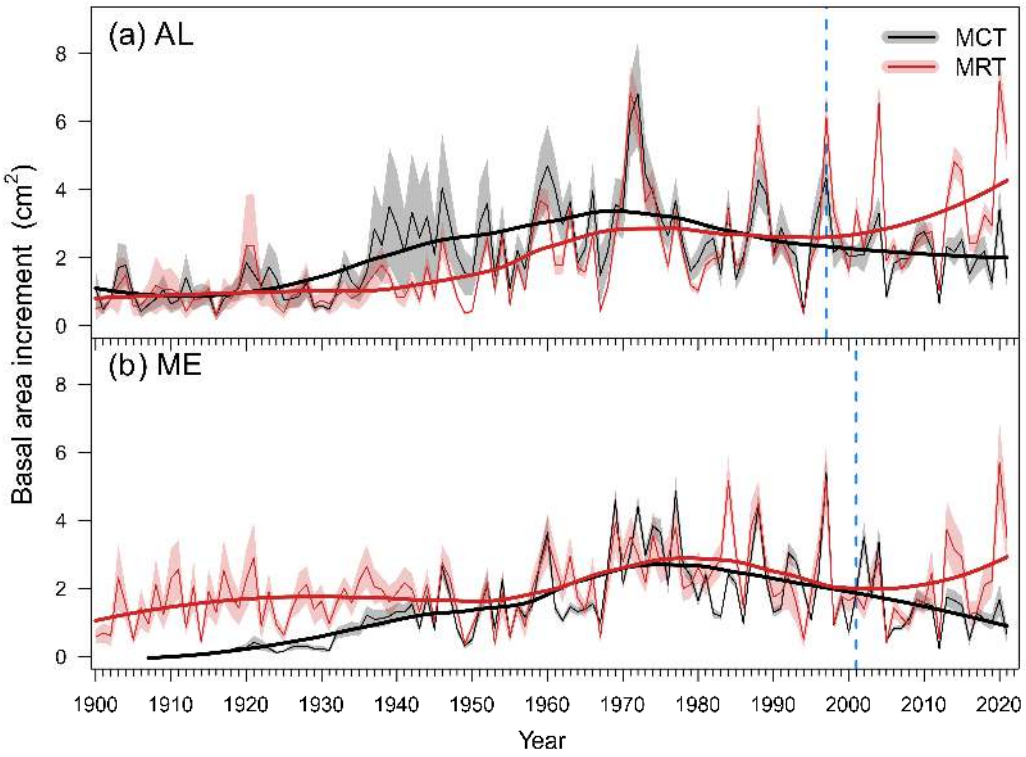


Figure 2. Interannual variation of basal area increment (BAI) of Aleppo pine. Thin lines represent the means, and shaded areas around them the standard error of the mean. Thick lines indicate the nonlinear model fitted using the LOESS smoothing method. Blue dashed lines represent years of mistletoe removal.

Tree growth responses to the most severe droughts from the last three decades differed between mistletoe treatments. Rt was higher in MRTs than in MCTs with respect to the 2005 and 2012 droughts in AL, and against 2012 drought in ME. MRTs showed better recovery capacity (Rc) after the 2005 drought and greater Rs against the 2005 and 2012 droughts than MCTs at both sites (Figure 4). Therefore, the impact of decreasing soil moisture on the growth of mistletoe-infested Aleppo pine trees appeared to be attenuated several years after mistletoe removal.

3.3. Changes in Climate–Growth Relationships Related to Mistletoe Removal

We found that climate–growth associations changed through time. Comparable periods before and after mistletoe removal showed differences in climate–RWI associations (Figure 5). The few temperature variables with significant impacts in the 1980–1999 period disappeared in 2000–2021 period. However, in site AL, the negative effect of the prior September Tmax on RWI during the period 2000–2021, which probably reflects late summer drought stress, was significant in MCTs but not in MRTs. On the other hand, many precipitation variables from the previous autumn, winter, and growing season become significant. Importantly, the stronger effect of precipitation was detected only in MCTs (Figure 5). Consistently, the relationship between RWI and May, June, and July precipitation did not differ between tree classes before mistletoe removal, but it was much steeper in MCTs than in MRTs during the period 2000–2021 (Figure S3).

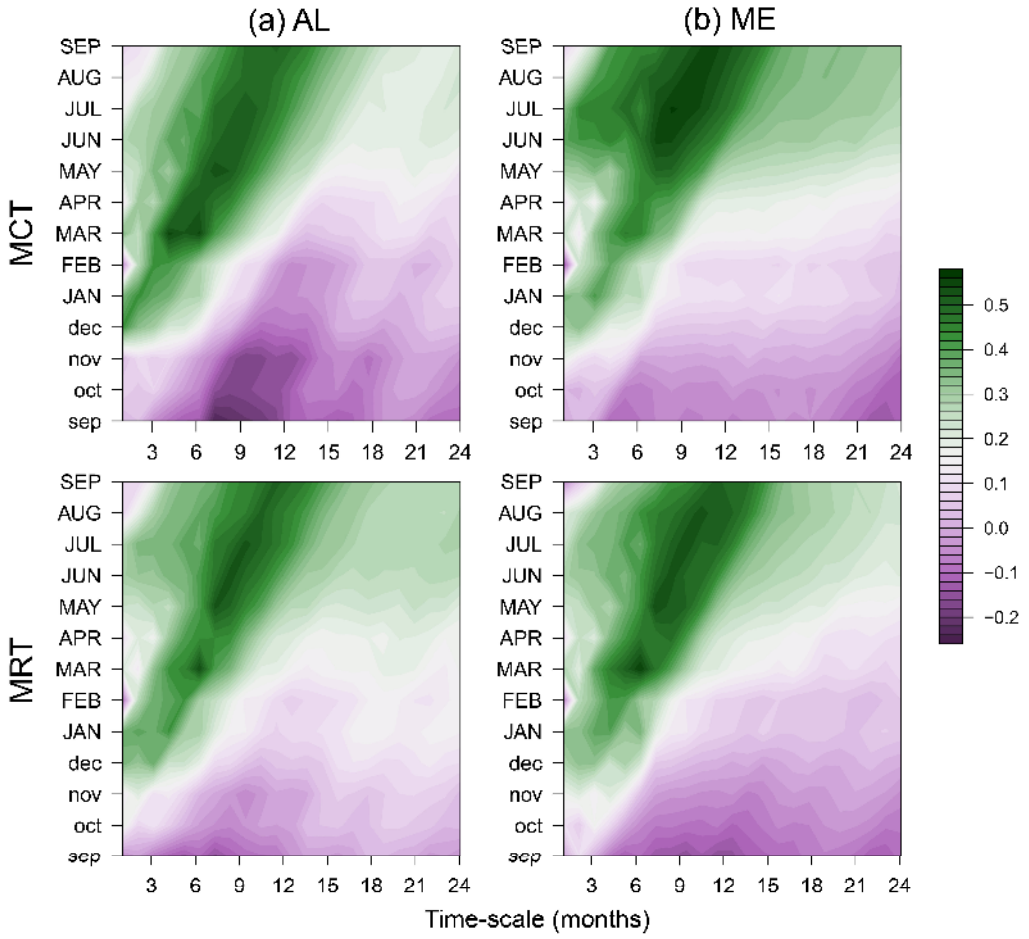


Figure 3. Relationships between RWI chronologies and the SPEI drought index for mistletoe-control trees (MCTs, upper panels) and mistletoe-removed trees (MRTs, lower panels). The color scales show bootstrapped correlation coefficients obtained for the common period 1950–2021 by relating monthly SPEI values (y axes) calculated at 1- to 24-month long scales (x axes). Months indicated in lowercase and uppercase letters on the y-axis represent the year prior to ring formation to the current year of tree ring formation, respectively.

The impact of soil moisture on radial growth was not constant over time, as shown by the results of the GAMMs (Table 2). It is noteworthy that the higher R^2m values found in ME than in the AL site indicating a higher explanatory power of the fixed factors. The effect of SPEI6.March initially diminished in both tree classes and sites until the 1970s–1980s, and later, the drought sensitivity of growth of MRTs exceeded that of MCTs. The impact of SPEI6.March on the MCTs' growth increased steadily during the 21st century, but after mistletoe removal, this impact decreased and ceased increasing in MRTs from AL and ME sites, respectively (Figure 6a). The impact of SPEI9.July on BAI followed similar patterns at both sites. It increased in both MCTs and MRTs until the late 1990s and early 2000s, when it began to decline, although the decrease was more pronounced in MRTs (Figure 6b).

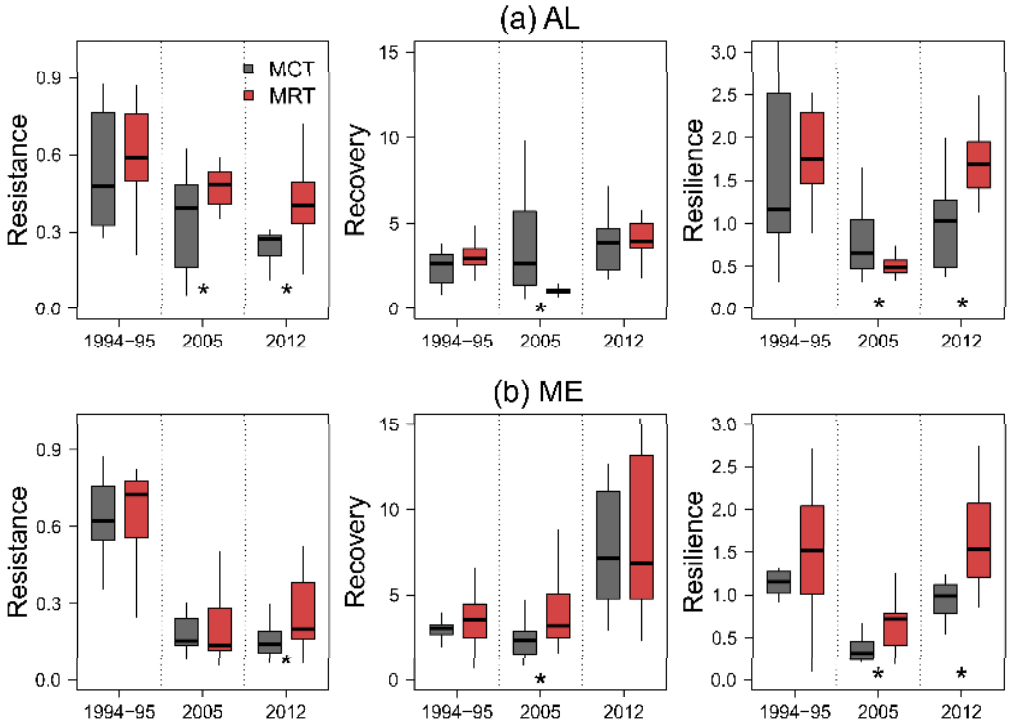


Figure 4. Resistance, recovery, and resilience against 1994–1995 (before mistletoe removal), 2005 and 2012 droughts (after mistletoe removal). Grey and red bars represent mistletoe-control trees (MCTs) and mistletoe-removed trees (MRTs), respectively. Significant differences ($p < 0.05$) between MCTs and MRTs, according to Kruskal–Wallis test, are indicated with asterisks.

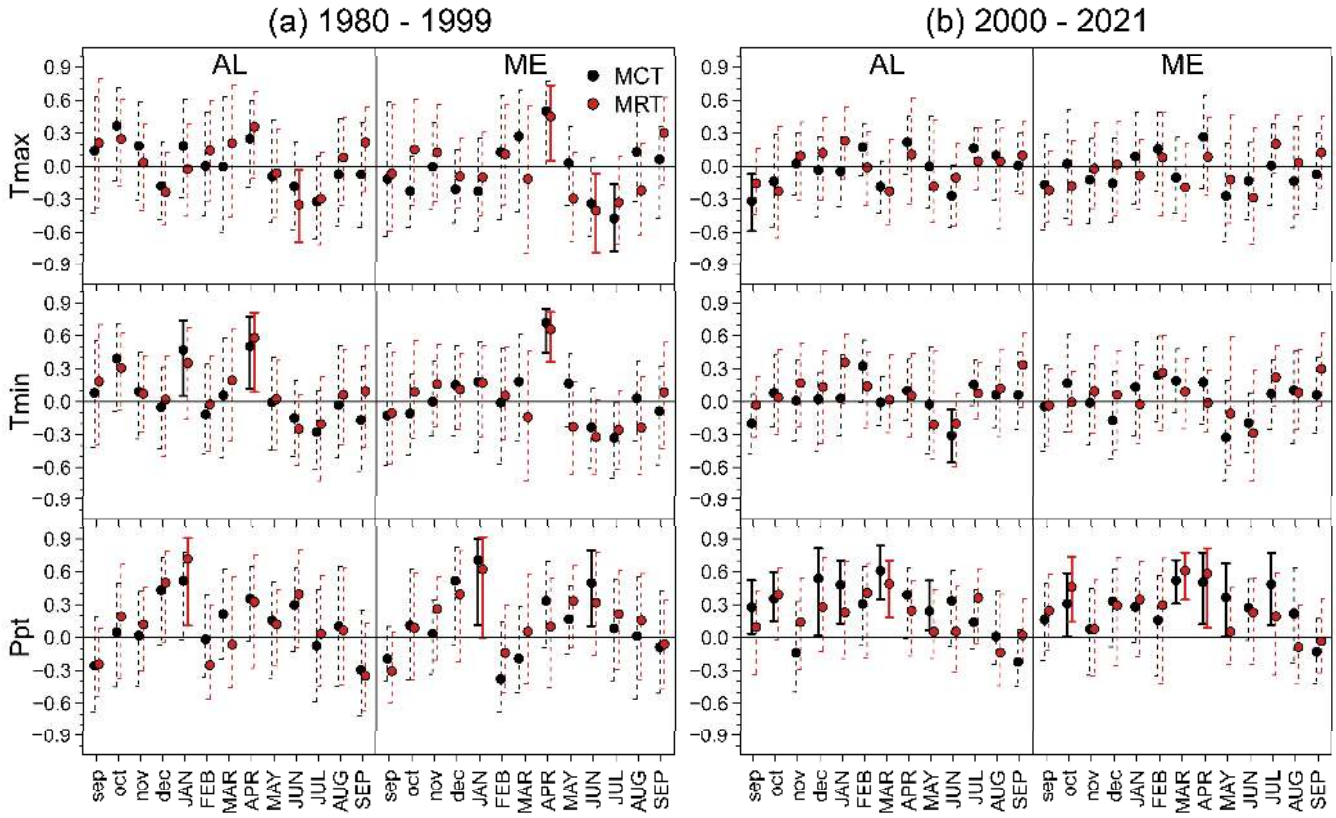


Figure 5. Bootstrapped correlation coefficients between RWI and monthly maximum (Tmax) and minimum temperatures (Tmin), and total precipitation (Ppt) in Aleppo pine during the periods

(**a**) 1980–1999, and (**b**) 2000–2021. Error bars are 95% confidence intervals, and significant and non-significant effects are represented by solid and dashed lines, respectively. Months indicated in lowercase and uppercase letters on the x-axis represent the year prior to ring formation to the current year of tree ring formation, respectively.

Table 2. Generalized additive mixed models (GAMMs) fitting radial growth (BAI) chronologies against tree size (DBH), calendar year, and its interactions with drought index (SPEI).

Variable	**AL**				**ME**			
	MCTs		MRTs		MCTs		MRTs	
	Edf	*F*	*Edf*	*F*	*Edf*	*F*	*Edf*	*F*
DBH	1.000	3.843*	1.000	31.480***	1.000	16.180***	1.000	267.70***
Year x SPEI6.Mar	3.509	21.951***	4.926	53.200***	2.976	52.180***	4.762	39.580***
Year x SPEI9.Jul	3.943	14.455***	4.913	23.130***	4.851	16.180***	4.871	31.180***
R^2m	0.239		0.270		0.491		0.406	
R^2c	0.545		0.966		0.887		0.946	

Abbreviations: effective degrees of freedom (*Edf*), *F*-statistic (*F*), basal area increment (BAI), diameter at breast height (DBH), Standardized Precipitation Evapotranspiration Index (SPEI), marginal (R^2m), and conditional (R^2c) coefficients of determination.

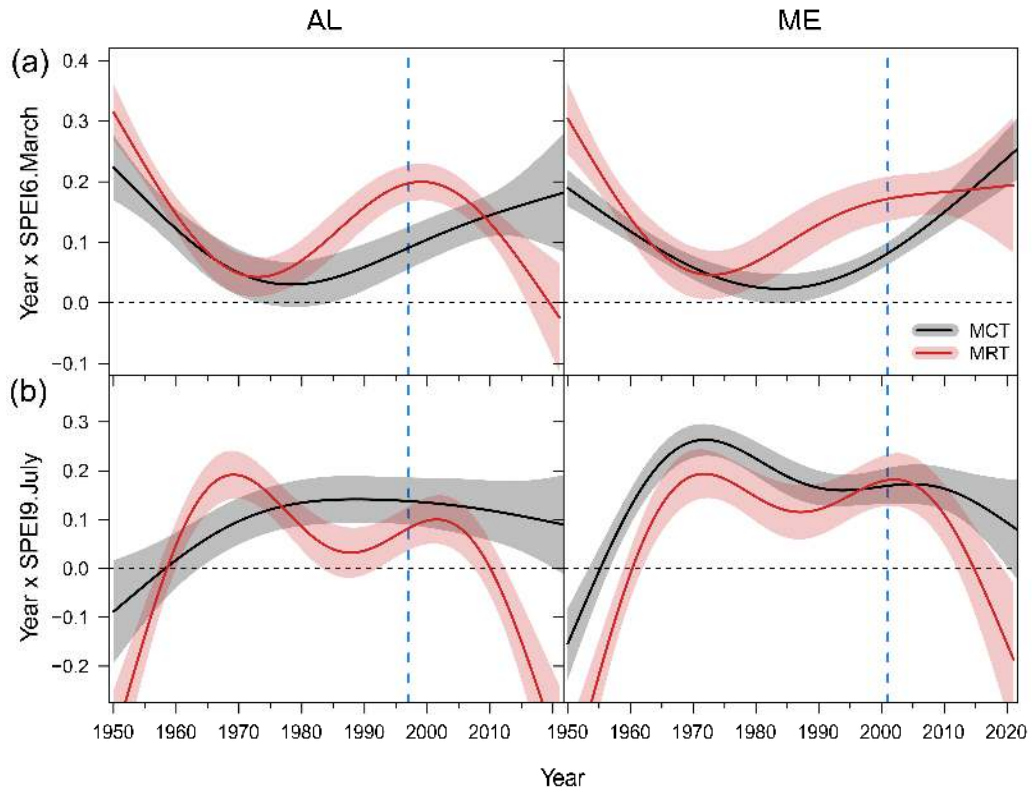


Figure 6. Estimated smoothing splines (solid lines) and their 95% confidence intervals (shaded areas) of the interaction between calendar year and the SPEI drought index from March, calculated at 6-month scale (SPEI6.March (**a**)); and from July, calculated at 9-month scale (SPEI9.July (**b**)), in radial growth (BAI) of Aleppo pine trees during the period 1950–2021, according to GAMMs. Blue dashed lines represent years of mistletoe removal.

Patterns of BAI residuals derived from GAMMs showed some differences regarding mistletoe treatment. In AL, MRTs grew lower than expected before mistletoe removal, but after 1997, residuals were clearly positive. The residuals of MCTs at this site were nearly constant and close to zero (Figure 7a). In ME, BAI residuals increased from negative to

positive values throughout the second half of the 20th century, and then declined in both tree classes. After mistletoe removal, MRTs changed to an increasing trend and adopted positive values (Figure 7b). These results agree with the patterns of raw BAI (Figure 2).

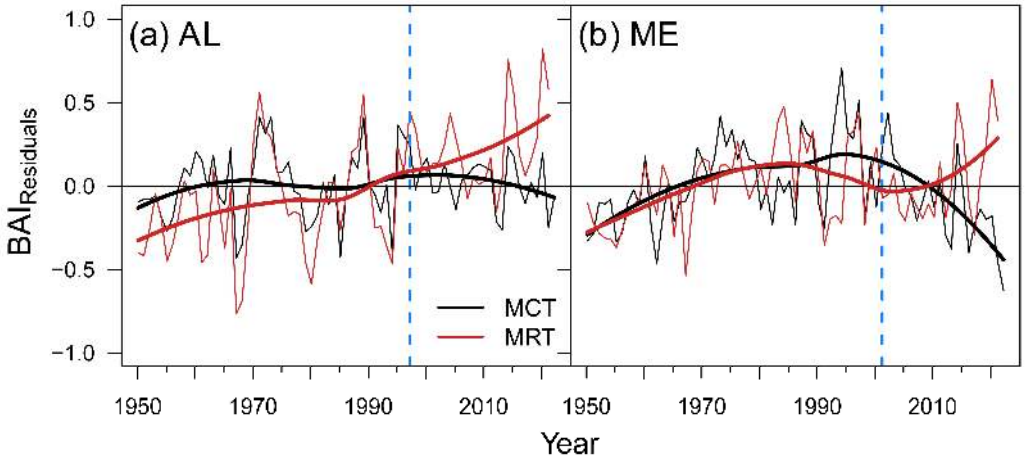


Figure 7. Year-to-year variation of radial growth of Aleppo pine after accounting for soil moisture effect. Thin lines represent BAI residuals of GAMMs (see Table 2), and thick lines indicate the nonlinear model, fitted using the LOESS smoothing method. Blue dashed lines represent years of mistletoe removal.

4. Discussion

Evidence coming from dendrochronological studies indicates consistent negative effects of European mistletoe, leading to significant reductions in growth and declining growth trends of host tree species, including the Eurosiberian Scots pine (*Pinus sylvestris* L.) [8,20,25,52] and the Mediterranean Crimean pine (*Pinus nigra* ssp. *pallasiana* (Lamb.) Holmboe) [53,54]. However, the impact of mistletoe on the growth patterns of Aleppo pine has not yet been evaluated, despite the fact that it is one of the main host species in the driest regions of the western Mediterranean Basin [11,55,56]. In this study, we provide the first dendrochronological analysis of mistletoe impact on Aleppo pine radial growth to the best of our knowledge.

Both control and mistletoe-removed trees showed declining growth trends since 1980s at the two study sites, concurrent with the onset of climate warming and drying and severe droughts (Figure S1b). Previous studies have reported similar patterns in drought-prone Mediterranean pine forests [16,57,58]. We also found low resistance and high recovery against severe droughts, in agreement with the findings of Gazol et al. [15], who found strong growth reductions of Aleppo pine stemming from the 1994–1995 drought. The growth of pines in our study was not only affected by drought stress, but also by mistletoe infestation, as indicated by positive growth trends following mistletoe pruning (Figure 2). Furthermore, mistletoe removal increased the growth resistance and resilience after the 2012 in both sites, suggesting a better growth reaction to water shortage and an improved recovery in less-infested trees (Figure 4). Mistletoe-induced reduction in crown area, as a result of leaf loss and leaf morphological and physiological alterations [8,59], is considered an important factor causing growth decline and tree mortality [5]. Therefore, elimination of the hemiparasite probably allowed trees to increase their photosynthetically active leaf area, which triggered the recovery of radial growth rates. Indeed, mistletoe removal has previously been shown to enhance the tree ring width of host trees [32,60].

Our results also confirm that precipitation is the main limiting factor for the radial growth of Aleppo pine (Figures 3 and S2), in line with the solid body of existing knowledge [61–63]. There is also evidence that rainfall variability is the main factor influencing the growth responses of Aleppo pines to drought [15,64]. Moreover, the precipitation–growth relationship is stronger as conditions become drier [58,65,66]. Thus, our study

populations presumably show a high climatic sensitivity, as they are close to the dry edge of the species' distribution (Figure 1). Likewise, the ongoing climate aridification during the last decades would strengthen the relationships between drought severity and growth. In contrast, this pattern was only found on control, currently infested trees (Figure 5), while mistletoe-removed trees have shown reduced sensitivity to drought after pruning (Figure 6). Therefore, these findings endorse the role of mistletoe in amplifying drought stress experienced by trees [26,27]. Mistletoes alter the water relationships of their hosts due to the continuous flow of water from host xylem to the hemiparasite [7,17], leading to tree stomatal closure to prevent leaf turgor loss or stem hydraulic failure under water limitation [18,19]. Reductions of water-use efficiency caused by mistletoe infestation has also been reported in mistletoe-infested trees, likely mediated by limited photosynthesis capacity, as indicated by the lower concentration of non-structural carbohydrates measured in infested trees [27,32,59]. Reductions in leaf area and sapwood [67], low stomatal conductance [18], or decreases in chlorophyll content [21] and essential nutrient concentrations, such as N, P, and K [22,23], have been proposed as mechanisms explaining the reduction in carbon assimilation under severe mistletoe infestation. Although some mistletoe species have been demonstrated to be capable of tapping the host's phloem for carbon [7], there is no evidence of heterotrophic carbon gain by European mistletoe [68].

Mistletoe removal from severely infested trees has been shown to reverse the impairment of the water–carbon–nutrient balance caused by the hemiparasite. For instance, Yan et al. [32] found a higher concentration of non-structural carbohydrates and nitrogen in needles and greater leaf area, leading to enhanced primary and secondary growth in Scots pine trees from which mistletoe was removed compared to control trees. Consistently, our study supports that management interventions can reduce or eliminate the deleterious impact on mistletoe in semi-arid pine forests in the long-term. Therefore, our hypotheses about the positive effects of mistletoe removal in the short- and medium-term and its disappearance in the long-term are refuted, since the growth of mistletoe-removed trees remains higher than predicted by climate models more than 20 years after treatment (Figure 7). Previously, Maffei et al. [60] also found a positive effect of dwarf mistletoe (*Arceuthobium douglasii* Engelm.) removal on the growth of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) that emerged once trees recovered from pruning and remained for at least 14 years. Similarly, we found a delayed effect of mistletoe treatment on both growth patterns and climate–growth associations (Figures 2 and 6), likely reflecting the short-term impact of canopy removal along with mistletoe individuals. Management recommendations state that at least 30% of the tree crown should remain after pruning to avoid persistent declines in tree vitality and irreversible growth decline [60,69].

The main dispersers of European mistletoe seeds are birds, which play a major role in short- and long-distance seed transport from the host tree [10]. For this reason, it is difficult to avoid reintroductions, and continuous pruning is recommended despite the labor and cost-intensiveness of these interventions [4]. However, positive growth trends and reduced sensitivity to drought of pruned trees in this study hint that mistletoe reinfestation has not occurred or continues to have no significant impact on tree growth two decades later. Indeed, the degree of mistletoe infestation of the treated trees remains significantly lower than that of the control trees at the time of field sampling (Table 1). This long-term effect of mistletoe removal in dry-warm Aleppo pine stands may be related to the fact that these mistletoe populations represent the xeric edge of the species' distribution (Figure 1). This was previously illustrated by Sangüesa-Barreda et al. [14], who provided evidence of low climatic suitability of mistletoe colonizing Aleppo pine stands from the Middle Ebro Basin using species distribution models. That study also highlighted a limitation of mistletoe recruitment in drought-prone Mediterranean sites [14]. Moreover, it is projected that the potential range of European mistletoe will shift in a north-eastern direction and to higher altitudes [70]. Thus, the low fitness of mistletoe at the study sites may have prevented a successful reinfestation.

Considering the long-lasting effects on radial growth patterns, this study provides evidence of the usefulness of single mistletoe-removal treatments from semi-arid pine forests that can, therefore, represent a viable tool to preserve these Mediterranean woodlands against the combined threat of drought and mistletoe, as has been previously suggested [20]. Furthermore, mistletoe removal would reduce mistletoe seed production, which would limit mistletoe dispersal in the tree and prevent reinfestations in the lower parts of the canopy [20]. However, the distribution of mistletoe on Aleppo pine forests also depends on the neighboring land use, which is closely related to the habitat preferences of bird dispersers [13]. The wild fruits of mistletoe and olive (*Olea europaea* L.) are an important food resource for many resident and overwintering bird species during winter [10,71]. Thus, it has been shown that the proximity of olive groves is positively related to the presence of mistletoe in Aleppo pine forests in NE Spain [13,56]. Therefore, management of mistletoes may cover not only local scales by removing mistletoe individuals from infested trees but also consider measures at the landscape level by controlling the availability of nutrient-rich food sources that attract bird dispersers.

5. Conclusions

Mistletoes are the most successful group of hemiparasitic plants colonizing trees and shrubs worldwide. Mistletoes rely on tap from the host xylem to capture water and nutrients and thus modify how trees cope with water stress, thereby emerging as important co-contributors to canopy dieback and tree mortality. This can become particularly relevant in drought-prone Mediterranean regions where forests face the dual menace of drought and mistletoe. Therefore, a proper understanding of the combined effects of both stressors on tree performance is crucial, along with the design of adequate management strategies that alleviate the hemiparasite impacts.

In this study, we provide the first assessment of mistletoe impact on the radial growth of Aleppo pine by comparing mistletoe-removed trees with control trees from a semi-arid region in NE Spain. We found positive effects of mistletoe removal on growth trends and a reduced growth sensitivity to drought that persist even two decades after treatment. These long-lasting effects can be explained by the water-dependent growth or by the poor climatic suitability of mistletoe in the study region, which may constrain its recruitment and, therefore, reinfestations. Therefore, pruning of mistletoe-infested branches would be recommended to improve vitality and mitigate the negative impacts of European mistletoe in semi-arid Mediterranean pine stands at the limit of the hemiparasite's xeric distribution.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f15071113/s1.

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