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EDITED BY
Juan A. Martin,
Universidad Politecnica de
Madrid, Spain

REVIEWED BY
Diego Gallego,
University of Alicante, Spain
Andrea Battisti,
University of Padua, Italy

*CORRESPONDENCE
Fernando Castedo-Dorado
✉ fcasd@unileon.es

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The impact of the Asian chestnut gall wasp (*Dryocosmus kuriphilus*) on chestnut tree growth may be mediated by site resources

Fernando Castedo-Dorado ^{1*}, Pedro Álvarez-Álvarez ²
and María Josefa Lombardero ³

¹DRACONES Research Group, Department of Engineering and Agricultural Sciences, School of Agricultural and Forestry Engineering, University of León, León, Spain, ²Department of Organisms and Systems Biology, Polytechnic School of Mieres, University of Oviedo, Mieres, Spain, ³Unit for Sustainable Forest and Environmental Management, University of Santiago de Compostela, Lugo, Spain

Introduction: The Asian chestnut gall wasp (*Dryocosmus kuriphilus*) is a major pest of chestnut trees worldwide, seriously affecting chestnut cultivation. Information concerning the effects of gall wasp attack on diameter growth of chestnut trees is currently scarce and limited to coppice stands and to use of the growth of a non-target control species (unaffected by the pest) for reference purposes. The effects of the pest on widely-spaced plantations (grown at a much lower density than chestnut coppices) and the use of explicitly-observed annual infestation rate data remain to be explored.

Methods: In the present study, we analyzed the impact of the chestnut gall wasp on the diameter growth of chestnut trees, using data from 16 experimental plots established in widely-spaced plantations located in good quality sites. Two of the plots are in plantations where a susceptible hybrid chestnut clone and a chestnut clone resistant to the gall wasp coexist, whereas the remaining 14 plots are in *Castanea sativa* plantations where the level of gall wasp infestation varies across trees and years. The plots were surveyed to determine the diameter growth of the trees and the level of infestation during 5 years (2017–2021).

Results: The infestation level corresponding to the theoretical damage threshold was surpassed in most plots during the study period. Nevertheless, there were no differences in the growth of attacked and unaffected plants in the two plots planted with hybrid clones with contrasting susceptibility to the gall wasp. The attack had a modest effect in *C. sativa* plots, with a mean reduction in annual basal area increment of 9.9%.

Discussion: These findings apparently contradict previous reports of a marked reduction in radial growth of chestnut coppice trees due to gall wasp attack. The difference in findings may be related to increased compensation for herbivory with increasing levels of resources (especially light) in the plantations under study,

which were less dense than previously studied stands. The study outcomes add to existing knowledge on the impact of chestnut gall wasp on wood formation and may have implications regarding planting site recommendations and subsequent stand management.

KEYWORDS

chestnut tree pest, infestation level, compensation for herbivory, high forest, basal area increment

1. Introduction

In Europe almost 1.8 million hectares of chestnut forest, which corresponds to two-thirds of the total chestnut-growing area (Manetti et al., 2020), is devoted to timber production. Most of this forest (around 80%) is managed using the coppice system, characterized by relatively short rotations and sparse silvicultural treatments (e.g., thinning). In Spain, the existing 100,000 ha of stands managed for timber production is divided approximately equally between coppice and high forest (Conedera et al., 2004).

In NW Spain, numerous chestnut tree plantations have been established in the last 20 years. Moreover, new plantations are currently being established, with more than 400,000 chestnut trees presently produced annually (Xunta de Galicia, 2020). Approximately half of these trees are sweet chestnut (*Castanea sativa* Mill.) and the other half are Euro-Japanese hybrid clones. Clonal forestry techniques have been applied to chestnut plantations in order to produce plants that are resistant to ink disease and also to generate certain productive traits such as vigorous growth, stem form and apical dominance (Fernández-López, 2011). The main objective of the plantations is usually to produce high quality round-wood at intermediate rotation ages, so that plantation density is usually low (280–625 trees per hectare).

Dryocosmus kuriphilus Yasumatsu (Hymenoptera, Cynipidae) is one of the major key insect pests in chestnut orchards and forests (e.g., Fernandes et al., 2022). This pest, commonly known as the Asian chestnut gall wasp, is native to China and can affect species of the genus *Castanea* and hybrid clones. Nevertheless, a wide range of variability among clones regarding the level of infestation by *D. kuriphilus* has been reported, suggesting a genotype-dependent variation in susceptibility (Sartor et al., 2015; Míguez-Soto et al., 2018; Castedo-Dorado et al., 2021; Lombardero et al., 2022). The same applies to the European populations of *C. sativa*, suggesting that the differences are due to specific features of individual trees within the populations (Bombi et al., 2018).

D. kuriphilus galling activity prevents or inhibits the development of normal shoots and leads to the production of abnormal plant structures (Maltoni et al., 2012). In the long term, the decreased capacity of developing buds can

result in malformation of the branch architecture and general deterioration of the crown (Gehring et al., 2018a). As a result of the reduction in the leaf area of the affected trees, a gradual loss of the photosynthetic biomass and a decrease in tree vigor are expected to occur (Kato and Hijii, 1997). Additionally, the replacement of plant tissue damaged by insects requires plant resources, influencing plant allocation patterns, which in turn can affect radial growth (Waring, 1987; Cipollini et al., 2014).

Different studies have quantified the effect of the gall wasp attack on the yield of chestnut products. The gall wasp can reduce nut production by up to 80% in heavily infested trees (Battisti et al., 2014) and can also reduce the chestnut component of honey (Gehring et al., 2018b). Regarding timber yield, the pest has been found to cause a marked reduction in radial growth, although studies of the impact of the gall wasp are scarce (but see Mariotti et al., 2013; Marcolin et al., 2021).

These studies (*op. cit.*) focused on coppice stands, in which stand density is much higher (stem density >600 trees ha^{-1} , with some plots surpassing 3,000 trees ha^{-1}) than in chestnut plantations. As tree responses to herbivores are mediated by resource conditions (e.g., light, water and nutrients) (e.g., Maschinski and Whitham, 1989; Hawkes and Sullivan, 2001), it can be hypothesized that widely spaced high forest stands, where there is less competition for these resources, will be less impacted by the pest. The quality of the site, related to nutrient availability, may also play a role in compensating for herbivory (Coley et al., 1985; Maschinski and Whitham, 1989; Lombardero et al., 2016).

Furthermore, Marcolin et al. (2021) indirectly assessed both the gall wasp outbreak evolution and the effect of the pest on tree growth. In order to assess the former, these researchers used the time since the gall wasp and its specific parasitoid (*Torymus sinensis* Kamijo) arrived at each site, whereas for the latter they used the growth of a non-target control species (unaffected by the pest) as a baseline reference to account for the effect of the local environment. Therefore, the effects of the explicitly observed annual infestation rate relative to healthy reference chestnut trees remain to be explored.

Here, we used data from manual band dendrometers to determine the effects of Asian chestnut gall wasp on annual basal area increment of chestnut trees from low density plantations established in good quality sites. We sought to evaluate the following hypotheses: (i) the insect activity has less impact

in widely spaced high forest stands (i.e. under conditions of reduced intraspecific competition), opposite to the high competition in coppice stands, and (ii) the site quality may also play a role in compensating for the pest-induced damage.

2. Materials and methods

2.1. Study area

Sixteen study plots were established in spring 2017 in an inland area of Galicia (NW Spain) to monitor the damage caused by *D. kuriphilus* to chestnut trees. The plots were relatively close to each other: the mean distance between each plot was 15 km and the maximum distance between the two most widely separated plots was 55 km. The climatic conditions were therefore similar in all plots (Figure 1). The climate diagrams for the years under study for the weather station of Campus de Lugo, in the vicinity of one of the study plots (see Figure 1; data available at <https://www.meteogalicia.gal/observacion/estacioneshistorico/historico.action?idEst=10053>) is shown in Supplementary Figure 1.

The plots were established in plantations for wood production or both wood and fruit production, with a wide plant spacing ranging from 4×4 to 8×8 m. There were no grafted trees and no treatments for fruit production (e.g., irrigation, fertilization or crown formation pruning) had been carried out. All of the plots were established in private chestnut plantations, and the forest owners provided some information about the plantation history. The plantations were carried out since the turn of the century and were established on former agricultural land.

The presence of *D. kuriphilus* was first reported in the center of the study area (the surroundings of the city of Lugo) in 2014 (Pérez-Otero and Mansilla, 2014). We estimate that the wasp arrived in the plots in 2015 and 2016, although this is not certain. In spring 2017, *D. kuriphilus*-induced galls were present in all 16 of the study plots.

In two closely located plots, “Esperante” and “O Corgo” (numbers 7 and 8 in Figure 1), we initially found trees with numerous galls and also trees without any galls. The owners reported that they had planted two hybrid chestnut clones, although they did not know which specific clones were used. Genetic analysis (identification of molecular markers) of two trees of each class, carried out by Functional Genomics and Sequencing Platform (RIAIDT) of the University of Santiago de Compostela, confirmed that the trees belong to different hybrid clones: “324” and “502” in “Esperante” and “324” and “HS” in “O Corgo.” No galls were found in trees of clone “324,” which is known to be resistant to the gall wasp (Míguez-Soto et al., 2018; Castedo-Dorado et al., 2021; Lombardero et al., 2022), whereas galls were present in trees of both “502” and “HS” clones. In the remaining 14 plots, we found that the level of gall wasp

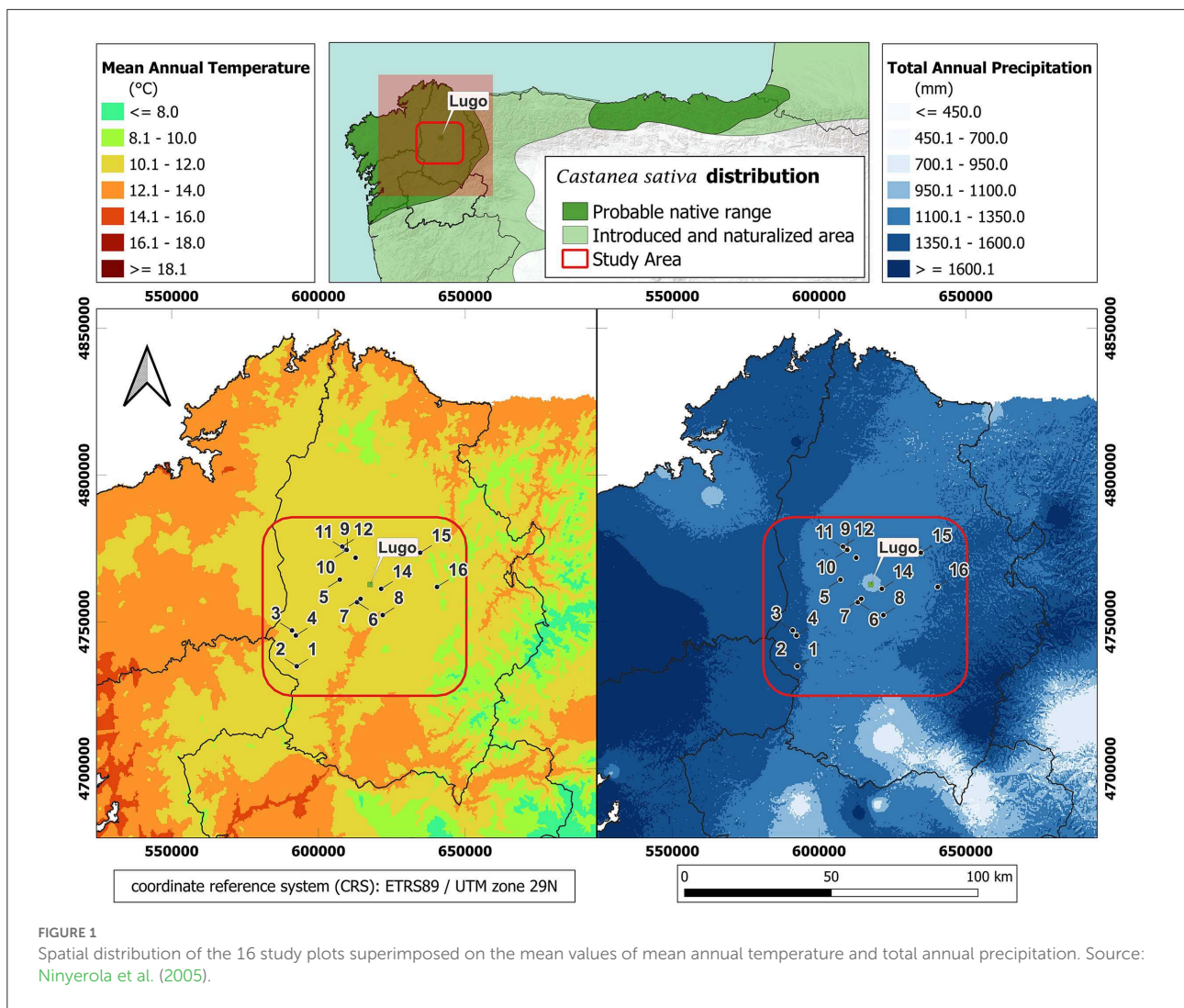
attack varied across the trees. The planted material from these plots was not analyzed for identification purposes, because the owners reported that native sweet chestnut trees (*C. sativa*) had been planted.

Field releases of *Torymus sinensis*, the major biocontrol agent used against the chestnut gall wasp, have been performed since 2015 in the study area, with release of small quantities in the first 3 years (2,000, 67,200 and 151,200 individuals for the whole Galicia region for years 2015, 2016 and 2017, respectively) (Pérez-Otero et al., 2017). The percentage of parasitism by *T. sinensis* in Galicia was low until 2019, probably due to the low population density of the releases (Nieves-Aldrey et al., 2019). More successful establishment was observed in 2020 and 2021, when the percentage of parasitism in the study area reached 25% in some locations (Xunta de Galicia, 2021).

2.2. Field measurements

We assessed a number of trees in each plot between spring of 2017 and November 2021. In the “Esperante” and “O Corgo” plots, 10 trees of each clone were evaluated. In the remaining 14 plots, we selected 6 trees with similar diameter at breast height and different levels of infestation at the beginning of the study period: 3 trees with a lower level and 3 trees with a higher level. The level of infestation varied notably in the following years in some trees, so that the initial classification of trees could not be used in the analysis. In some plots, the data on some trees had to be discarded because the trees had died or were severely damaged by other factors during the study period.

When the study plots were established, the diameter at breast height (d) of each tree was measured with a caliper, and total tree height (h) was measured with a digital hypsometer. In addition, from July 2017 onwards, girth at breast height growth was recorded via permanent measuring tapes marked with Vernier scales of 0.1 mm resolution (Type D1 Permanent Tree Girth, UMS, Germany). In the “Esperante” and “O Corgo” plots, the girth tapes were examined monthly between the beginning of April and the beginning of November. In the remaining plots, the tapes were revisited annually, at the end of the growing period (November). To avoid diurnal biases due to high temperatures, in summer all measurements were made early in the morning. We opted to use permanent bands instead of a caliper to characterize secondary tree growth to prevent errors in identifying the exact location of the measurement point. Moreover, the owners did not allow us take stem cores from the trees, to prevent damaging the basal log (which is the most valuable from an economic point of view) or causing wounds that could foster chestnut blight infections [*Cryphonectria parasitica* (Murrill) Barr]. Girth growth data from year 2017 was not used for analysis as we installed the band dendrometers in July and therefore we did not record the growth throughout all the growing season.



To assess secondary growth, girth increment data were transformed to diameter increments assuming a cylindrical stem shape. Annual basal area increment (BAI) was calculated from tree diameters as the difference between consecutive basal areas ($BA = \pi/4 \cdot d^2$); bark growth was assumed to be null during the 4-year interval. We used BAI instead of diameter growth because it is a more biologically meaningful descriptor of growth trends (Biondi and Qeadan, 2008). As we were dealing with only four stem growth intervals, age-detrending individual tree diameter measurement series for removing non-climatic trends was not considered.

From initial tree measurements, we estimated the dominant height of each plot (H) as the average height of the thickest trees in the plot. Subsequently, and using information on stand age provided by the owners, we estimated the site index (SI) as the dominant height of the plot at a reference age of 45 years, according to the site index curves reported by Patrício and Nunes (2017) for high chestnut forest stands in

the nearby region of Northern Portugal. In addition, we used the number of stems per hectare (N) and H to calculate the relative spacing (RS), which is a measure of stand density. The relative spacing index was calculated as the ratio of the average distance between trees and the dominant height, expressed as a percentage. Assuming a square spacing, the index can be calculated as follows: $RS (\%) = 10,000 / (\sqrt{N} \cdot H)$. As dominant height varies over years, RS was estimated for 2018–2021 by projecting annually H of each plot through the site index curves of Patrício and Nunes (2017). The main stand features of the 16 plots are shown in Table 1.

The level of infestation by the gall wasp on each tree was evaluated in July in four of the 5 years under study (2017, 2018, 2020, and 2021) (the trees were not able to be examined in 2019). In 2017 and 2018, the infestation level was evaluated in two different ways. First, the same observer (MJL) visually estimated the percentage of crown affected by *D. kuriphilus* at 10% intervals and then assigned a severity index (from 0 to 5)

TABLE 1 Stand characteristics of the 16 study plots.

Plot name	ID	Tree host	Age (years)	Dm (cm)	H (m)	SI (m)	N (trees ha ⁻¹)	RS (%)
Verin I	1	<i>C. sativa</i>	20	26.6	12.00	23.03	494	37.5
Verin II	2	<i>C. sativa</i>	20	28.4	14.70	25.45	400	34.0
Carballal	3	<i>C. sativa</i>	15	25.3	11.10	25.58	556	38.2
Rumin	4	<i>C. sativa</i>	16	20.5	12.20	25.84	556	19.1
Torible	5	<i>C. sativa</i>	21	30.1	13.90	24.21	444	34.1
Calde	6	<i>C. sativa</i>	21	21.6	12.60	23.00	333	43.5
Esperante	7	Hybrid clones	14	18.3	8.40	23.60	400	59.5
O Corgo	8	Hybrid clones	9	12.9	8.30	28.17	156	96.4
Uriz I	9	<i>C. sativa</i>	17	29.7	13.50	26.25	333	40.6
Uriz II	10	<i>C. sativa</i>	21	33.7	15.50	25.55	278	38.7
Casa Laranxa	11	<i>C. sativa</i>	21	27.9	12.20	22.61	278	49.2
Gaioso	12	<i>C. sativa</i>	14	22.3	10.10	25.42	500	44.3
Robra	13	<i>C. sativa</i>	22	26.1	12.40	22.21	625	32.3
Buratai	14	<i>C. sativa</i>	21	31.2	13.30	23.66	333	41.2
Castroverde	15	<i>C. sativa</i>	11	14.0	9.30	27.19	625	43.0
Masoucos	16	<i>C. sativa</i>	16	11.7	10.80	24.57	400	53.8

Identification (ID) numbers refer to the plot locations shown in Figure 1. Dm is the average breast height diameter of the plot. The values of age, Dm, H and RS refer to the time of plot establishment (July 2017).

based on the level of damage (number of galls). In the largest trees, the galls were observed with the aid of binoculars. The level of attack (LoA) was calculated by dividing the percentage of crown affected by *D. kuriphilus* by 100 and multiplying the value thus obtained by the severity index. Subsequently, four small branches were randomly selected in each tree, although where possible each faced a different direction within the tree crown. We used 4 m telescopic pruning shears to cut the branches, thus allowing access to branches that were 6–7 m above the ground. Branches in the sunlit tree crown were thus able to be sampled in all cases. In each branch, we located and examined the shoot that had grown in the previous growing season. We counted both the number of newly developed buds (i.e., developed in the current growing season) and the number of galls on these buds along the length of the old shoot. We used these data to calculate two commonly used infestation indices for each tree: (i) the ratio between the number of galls and the number of buds in 2019 (GpB; e.g., Sartor et al., 2009, 2015); and (ii) the ratio between the number of attacked buds (i.e. buds with the presence of galls) and the total number of buds (AB; Kotobuki et al., 1985). LoA was strongly correlated with both GpB and AB (Supplementary Figure 2), and therefore in 2020 and 2021 we chose to assess the level of infestation by using only the latter two indices. During the last diameter growth survey, in November 2021, we remeasured tree height in the “Esperante”

and “O Corgo” plots in order to estimate the primary tree growth during the study period.

2.3. Statistical analysis

The annual BAI measurements were square-root transformed prior to analysis to improve normality and homoscedasticity. As the growth data series is short (4 years) and only 2 plots included unaffected trees, the relationship between climate variables and diameter growth could not be established. The Standardized Precipitation Index (SPEI) (Vicente-Serrano et al., 2010) was considered a climate covariate to assess the impact of climate on the diameter growth in all annual BAI models. Given the sensitivity of chestnut to summer climate conditions, SPEI was calculated over a period of 3 months and averaged across the summer months (June, July, August; SPEI_{JJA}) (Marcolin et al., 2021). We assumed that the hybrid clones and *C. sativa* will behave the same way in response to climate because no specific information is available on the topic and because the same growth pattern was observed in young chestnut plantations throughout the region using hybrid clones and *C. sativa* (Álvarez-Álvarez et al., 2010).

ANOVA was applied to the data from the “Esperante” and “O Corgo” plots (which include both attacked and unaffected

trees) to test the influence of the gall wasp attack on annual BAI and periodic height increment. We considered the factors attack and plot, and their interaction, as explanatory variables. In order to take into account the size of the tree, we also included the value of the basal area of each tree (BA) at the beginning of the current growth season (for the annual BAI model) and the value of tree height at the time of the first measurement (h_{2017} , for periodic height increment model) as covariates.

Annual BAI data from the 14 plots where *C. sativa* was present (which include trees with different levels of infestation) were analyzed using a linear mixed model. We included SPEI_{JJA}, individual-tree basal area (BA), site index (SI), relative spacing (RS) and the infestation level (given by GpB or AB) as fixed factors. The plot was included in the model as a random effect to account for the correlated BAI data from the same plot. A random effect for individual trees could not be included because of the short length of the growth series. The “lme” function of the R package “nlme” (Pinheiro et al., 2022) was used to fit the linear mixed model using the restricted maximum likelihood (REML) method.

The variable indicating the infestation level (GpB or AB) was selected by comparing the value of the Akaike information criterion (AIC) of the fitted models using each variable independently. The configuration of the random effect (random intercept or random intercept and slope) was determined following the procedure described by Zuur et al. (2009). Model validity was assessed by plotting the residuals against fitted values and the predictive variables and the quantile-quantile distribution of the residuals. Both marginal and conditional R^2 were used as goodness-of-fit metrics, representing the proportion of the variance explained by the fixed effects, and by the combined fixed and random effects (i.e., the entire model), respectively (Nakagawa and Schielzeth, 2013). The relative importance of each fixed-effect predictor was calculated using the “relaimpo” package (Grömping, 2006). All analyses were carried out with R statistical software (R Core Team, 2022).

3. Results

The *D. kuriphilus* infestation generally increased between 2017 and 2018, peaked in 2020 and then decreased in 2021 (Figure 2 for GpB and AB; Supplementary Figure 3 for LoA). In 2017, susceptible hybrid clones in the “Esperante” and “O Corgo” plots already displayed high levels of infestation, possibly due to earlier arrival of the wasp. The epidemic peak corresponding to the 2020 growing season was common for all plots except those mentioned above and the “Castroverde” and “Masoucos” plots.

In the two plots in which intensive monitoring of diameter growth was conducted (“Esperante” and “O Corgo”), the growth peak corresponds to the months of June, July and August, both for the attacked and unaffected trees (Supplementary Figure 4).

For these plots, there was no significant difference in the mean of individual-tree basal area at plot establishment [ANOVA, $F_{(1,18)} = 0.20$, $p = 0.65$ and $F_{(1,18)} = 0.37$, $p = 0.55$]; nevertheless, in the “Esperante” plot, mean tree height was significantly higher for attacked trees [ANOVA, $F_{(1,18)} = 20.3$, $p = 0.0003$] (Supplementary Figure 5).

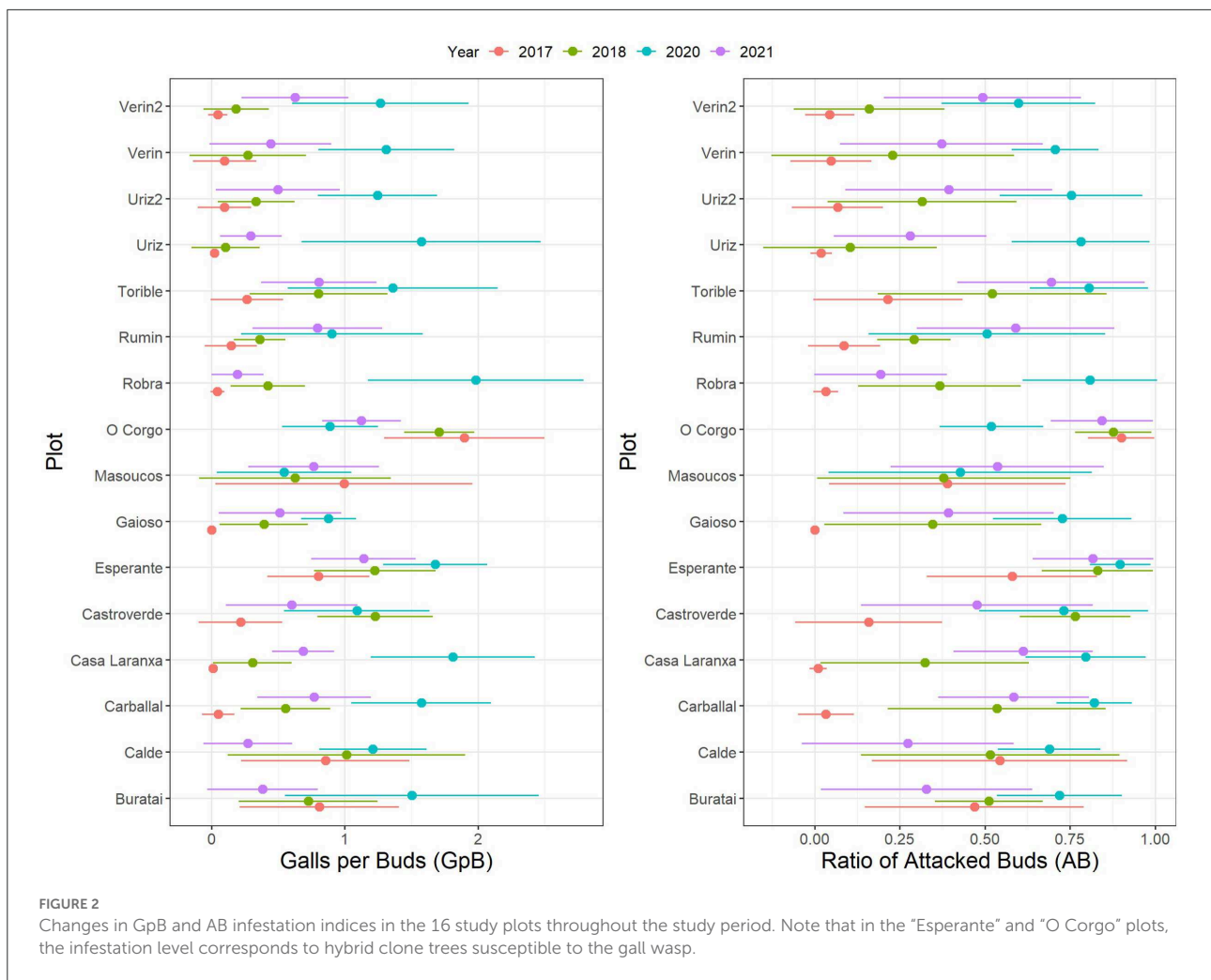
The mean annual BAI was around 60 and 40 cm^2 in “Esperante” and “O Corgo,” respectively, for the 4 years evaluated, with a generally lower mean value for the attacked trees (Figure 3A). The ANOVA revealed that the individual-tree basal area at the beginning of the growth period (BA), the plot and SPEI_{JJA} were highly statistically significant variables ($p < 0.01$) for explaining the annual BAI. The effect of the attack was not statistically significant ($p = 0.07$), and the effect of the interaction between the plot and the attack was modest ($p = 0.04$) (Table 2).

The trend in periodic height increment varied between plots: a higher mean height growth of attacked trees was observed in the “O Corgo” plot, whereas the opposite was observed in the “Esperante” plot (Figure 3B). The ANOVA results confirmed that the plot was statistically significant, but not the initial height (h_{2017}) nor the attack factor in isolation or the plot \times attack interaction (Table 2).

For the fourteen plots where *C. sativa* was present, mean annual BAI was lowest in 2020 and highest in 2021, although with a high level of variability (Figure 4A). There appeared to be slight decrease in annual BAI when the infestation level increased (as indicated by the ratio of attacked buds -AB), although the relationship was weak (Figure 4B).

The ratio of attacked buds (AB) yielded a lower AIC value than the number of galls per bud (GpB) in the linear mixed effect model explaining the annual BAI and was therefore used in subsequent modeling. According to the results of the mixed model, only the Standardized Precipitation Evapotranspiration Index averaged over the three summer months (SPEI_{JJA}), the individual tree basal area at the beginning of the growing period (BA) and the relative spacing (RS) highly statistically significantly explained the annual BAI. The effect of the infestation level (AB) was modest ($p = 0.030$), and the negative sign of the parameter estimates for this variable is logical (Table 3). These results are consistent with the relative importance of the variables: BA was by far the relatively most important variable, followed by the RS and SPEI_{JJA}. The relative importance of the infestation level, given by AB, was modest, only 5.83% (Table 3). According to the results of the mixed model, the average reduction in BAI for all the plots was -9.86% [95% CI $(-9.10, -10.63\%)$], with mean losses of the single plot spanning from -6.06% in “Uriz” [$-3.45, -8.68\%$] to -13.42% [$-11.91\%, -14.93\%$] in “Castroverde.”

The model provided a good fit to the data, as indicated by the fact that the residuals did not depart significantly



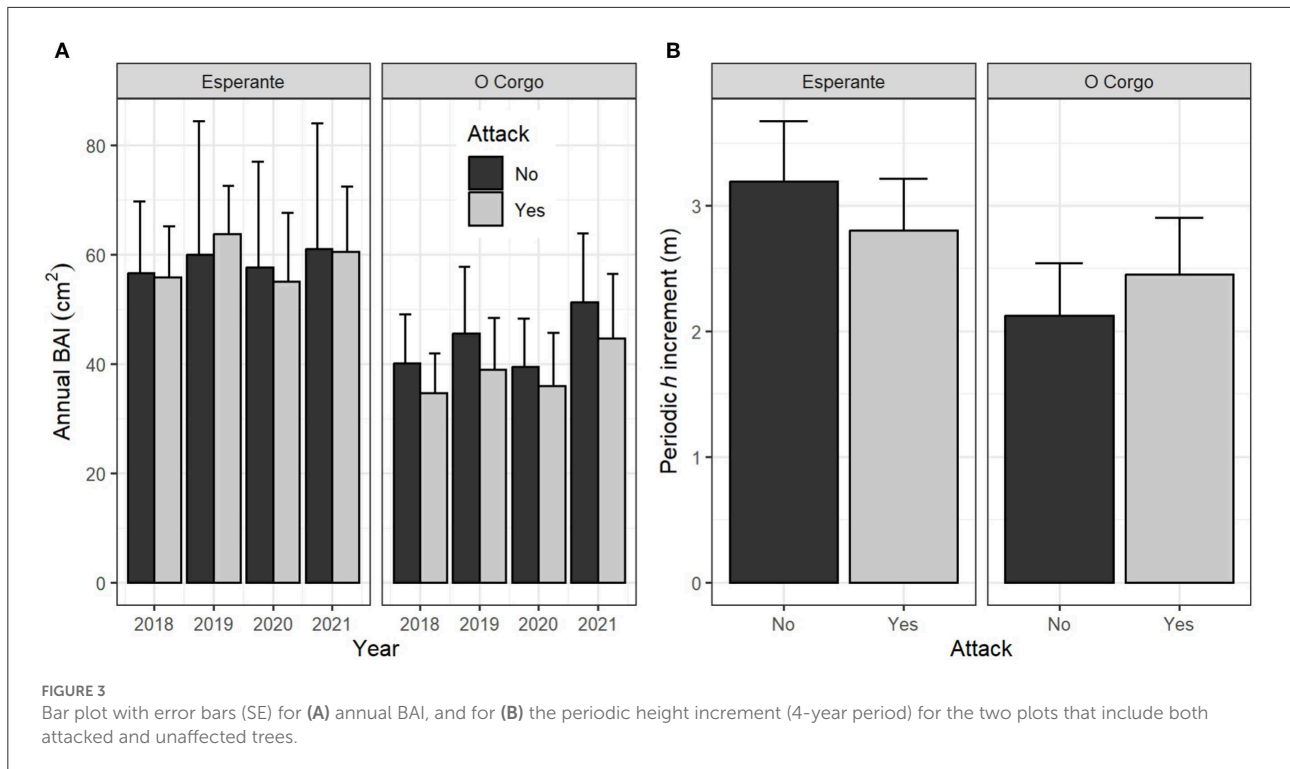
from normality and the relatively high proportion of variance explained (marginal $R^2 = 0.468$; conditional $R^2 = 0.670$).

4. Discussion

We assessed the impact of *D. kuriphilus* on the growth of chestnut trees in two types of plots managed as high forest. Two of the plots corresponded to hybrid clone trees that were either attacked or unaffected by the gall wasp, while in the other 14 plots trees were affected by variable levels of infestation. For both type of plots, Standardized Precipitation Evapotranspiration Index averaged over June, July and August, and individual tree basal area at the beginning of the growth period were statistically significant variables influencing the annual BAI. The importance of temperature extremes and total precipitation in summer months on secondary growth confirms previous findings in sweet chestnut studies (Rubio et al., 1997; Fonti and García-González, 2004; Álvarez-Álvarez et al., 2010; Camarero et al., 2018; Marcolin et al., 2021). On the other

hand, the importance of the tree size (i.e., BA) in explaining BAI has long been established (e.g., Monserud and Sterba, 1996; Hasenauer, 2006; Burkhart and Tomé, 2012; Vospernik, 2021).

In assessing tree responses to stressors such as herbivores, trees that are assumed to have no damage or trees with assumed optimal growth can be used for reference purposes (Dobbertin, 2005). At a local level, the scarcity of healthy *C. sativa* trees that are not affected by gall wasp attack makes it difficult to find specimens that can be used as reference trees. In the present study, two plots included trees of a hybrid clone that have not been attacked, which are potentially suitable for use as reference trees to assess the effect of the pest on growth. We did not find any evidence of the effect of the attack and only a modest effect of the attack \times plot interaction (Table 2). The weak significance of this interaction suggests that the attack had slightly different effects on growth in the two plots. We acknowledge that these results could be partly mediated by the genotype, although the average basal areas of trees from each pair of clones within



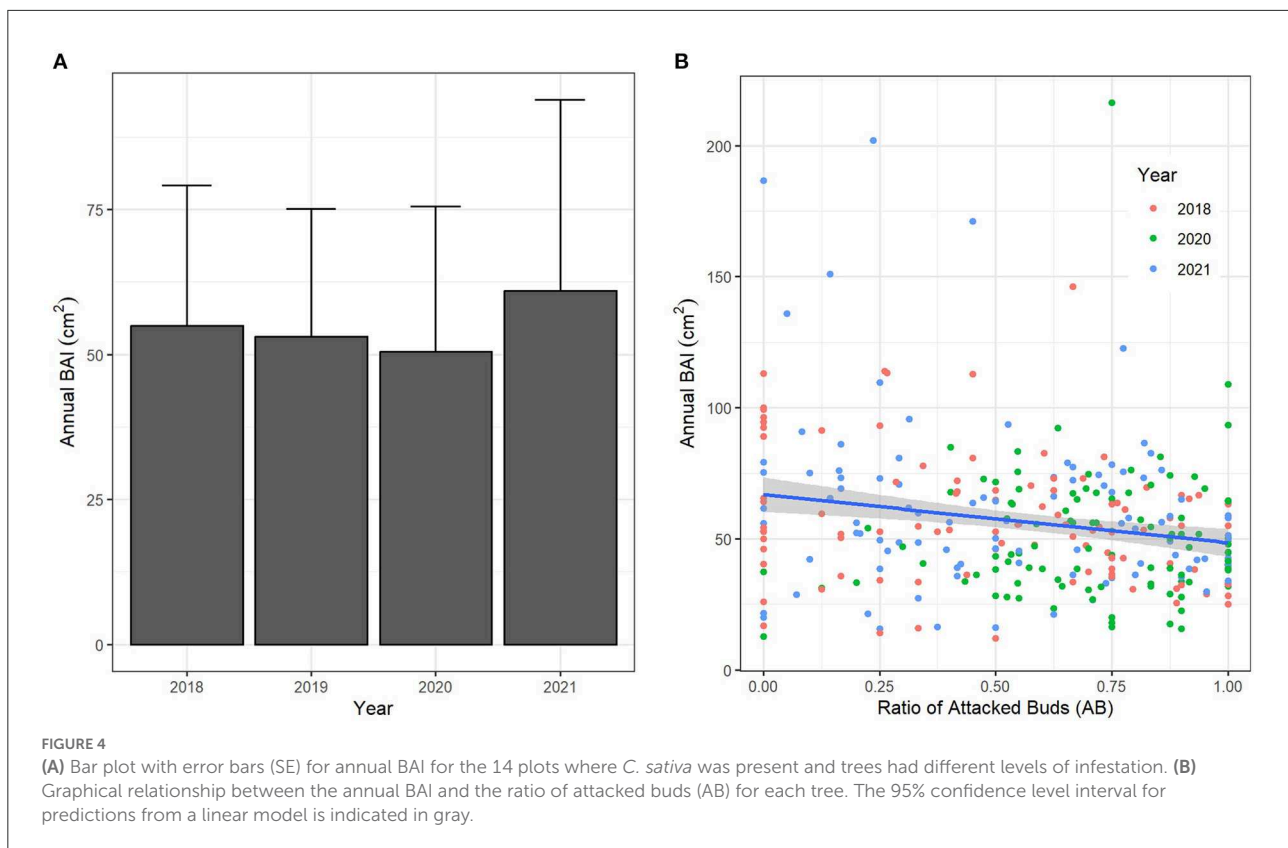
each plot at the beginning of our study were not significantly different (Supplementary Figure 5). The same rationale applies to periodic height increment, where the attack × plot interaction was weakly significant. It has been reported that genotype can influence the vigor and apical dominance of the hybrid clones under study (Fernández-López et al., 2009), thus potentially leading to a different growth pattern of the clones during the study period.

Regarding the results from the 14 *C. sativa* plots, the goodness of fit of the fitted linear mixed model is considered appropriate, taking into account that the fixed factors explained almost 50% of the existing variability, which reached almost 70% when random effects were considered. The model highlights the importance of the relative spacing index (RS) and the low significance of the site index (SI) in explaining annual BAI. The positive sign of the parameter estimate for RS reveals that a higher annual BAI is expected at lower stand densities (i.e., higher RS value, less tree competition). These results are consistent with the findings indicating that secondary growth is enhanced in trees in low density stands (e.g., Burkhart and Tomé, 2012). The absence of significance of SI in our study could be masked by the narrow range of site indices among the plots analyzed. Site indices in the study plots varied in a relatively narrow range (22–28 m) (Table 1), within the range of 14 to 26 m for which the site index curves have been developed for high forests in the NW Iberian Peninsula (Patrício and Nunes, 2017).

TABLE 2 ANOVA results testing for patterns in annual BAI and periodic height increment for the two plots that include both attacked and unaffected trees.

Variable	Source	df	F	p
Annual BAI	Attack	1	3.253	0.0737
	Plot	1	87.077	<0.0001
	BA	1	33.361	<0.0001
	SPEI ₁₇ A	1	0.521	0.0219
	Attack × plot	1	4.262	0.0407
	Error	148		
Periodic h increment	Attack	1	0.794	0.3796
	Plot	1	20.853	<0.0001
	h ₂₀₁₇	1	0.174	0.6796
	Attack × plot	1	4.801	0.0358
	Error	32		

Previous studies have shown that repeated attack by the chestnut gall wasp affects the secondary growth of chestnut coppice trees (Mariotti et al., 2013; Marcolin et al., 2021), with an average annual BAI reduction of 60% during the epidemic (Marcolin et al., 2021). By contrast, the results of the present study indicate that the secondary growth of chestnut trees under the conditions of the study plots was scarcely affected by the pest



(only an average 9.9% decrease of annual BAI was observed). Other authors have highlighted the resilience of chestnut trees in response to isolated events of damage by herbivores (e.g., Camarero et al., 2018). Our findings seem to confirm the resilience of chestnut trees even beyond 5–6 years of attacks and when the infestation level corresponding to the theoretical damage threshold is surpassed. This threshold was established by Gyoutoku and Uemura (1985) as 30% of AB and by 0.3 GpB by Gehring et al. (2018c) and was clearly surpassed in most plots during the study period.

The present findings are consistent with the continuum of responses hypothesis (Maschinski and Whitham, 1989), which assumes that the probability of compensation for herbivory decreases as competition with neighbors (mainly for light and water) increases and nutrient availability decreases (e.g., Björkman et al., 2000; Guillet and Bergström, 2006; Helbig et al., 2021). As chestnut is considered poorly competitive and light-demanding (Covone and Gratani, 2006; Conedera et al., 2021), the different conditions of competition for light resources may mainly explain the apparently contradictory findings of the present study and of the studies by Mariotti et al. (2013) and Marcolin et al. (2021).

Wood formation in chestnut trees has not been widely studied (but see Cufar et al., 2011; Marini et al., 2019). Nevertheless, it has been established that the development

of earlywood vessels begins some 2–3 weeks before the development of leaves, as in other ring-porous species (Sass-Klaassen et al., 2011; González-González et al., 2014). This is consistent with the monthly diameter measurements in our two experimental plots, in which we recorded diameter growth even in March and April (see Supplementary Figure 4), although bud break does not occur in the study area until the beginning of May. Earlywood represents around a quarter of xylem ring width (Cufar et al., 2011) and its development draws on reserves accumulated in the previous growing season (Ermich, 1959). Formation of latewood, which represents a large part of chestnut tree xylem rings, starts in June and continues in the summer months, and is associated with summer precipitation (Cufar et al., 2011). Therefore, chestnut trees may compensate for growth by increasing the photosynthesis rate in these months. As photosynthesis is enhanced in sunlit parts of the crown (sunlit leaves) (Proietti et al., 2000), in widely spaced trees less of the crown will be shaded and photosynthetic activity will therefore be higher, increasing the plant's capacity to grow by increasing carbohydrate production (e.g., Thomson et al., 2003), and subsequently masking the effect of pest attack. The present results could also partly explain the findings reported by Marcolin et al. (2021), who found that the gall wasp attack had higher relative importance in reducing BAI in young coppices (denser) than in old coppices (less dense).

TABLE 3 Parameter estimates and the corresponding *p*-values of the linear mixed-effects models fitted to annual BAI.

Variable	Estimate	SE	<i>p</i> -value	Relative importance (%)
Intercept	-10.620	5.362	0.0727	-
SPEI _{JJA}	0.3521	0.158	0.0265	8.59
BA	0.00506	0.000466	<0.001	69.73
SI	0.4413	0.202	0.0570	3.70
RS	0.1121	0.0346	0.00155	12.13
AB	-0.695	0.312	0.03021	5.83

Relative importance (%) represents the importance of each fixed-effect predictor.

Regarding other limiting resources (e.g., nutrients, water), all of our plots were established on former agricultural land, in which soil and nutrients do not usually restrict growing chestnut (Álvarez-Álvarez et al., 2010). This is reflected in the high site indices in our study plots, relative to those in the NW Iberian Peninsula (Patrício and Nunes, 2017). Finally, competition can reduce water availability through increased stand transpiration and rainfall interception (Bréda et al., 2006; Inagaki et al., 2008; Słodičák et al., 2011), worsening plant water status and therefore tending to restrain compensatory growth (McNaughton et al., 1983).

In addition to the availability of resources, we recognize that other factors related to the differences in the infestation level and the combined effect of the attack of the gall wasp with other phytosanitary problems may also help to explain the differences between our results and those obtained in the above-mentioned studies. Although Marcolin et al. (2021) did not provide information on gall wasp infestation level in each plot, it seemed to be higher than in the present study. Thus, at the peak of the outbreak these authors reported a systematic, gradual activation of dormant buds in an attempt to restore the lost crown biomass and, accordingly, large number of suckers. Taking into account that these stress-induced reactions were not apparent in our trees, it is therefore reasonable to argue that our study plots suffered a comparatively lower level of infestation (Gehring et al., 2018a). On the other hand, although chestnut blight disease [*Cryphonectria parasitica* (Murrill) Barr] was present in these plots, we avoided selecting trees with blight symptoms in order to separate the effects of the two stressors. *D. kuriphilus* infestation occurring in conjunction with other stressors such as chestnut blight can result in additive negative effects on tree growth (Meyer et al., 2015; Schuldt et al., 2017; Rigling and Prospero, 2018). Alternatively, after intense wasp attack, if the vitality of chestnut trees decreases, the trees may become more vulnerable to pathogens, which in turn weaken their competitive fitness (Ugolini et al., 2014).

In summary, in widely spaced high forest chestnut stands located in good quality sites, annual reductions in BAI induced

by the gall wasp were modest, reaching only 9.9% on average. This apparently contradicts previous findings in much denser chestnut coppices stands, in which a marked reduction in radial growth was observed. Due to the differences in density between these two types of stands, we suggest that inter-tree competition, mainly for light resources, may mediate the impact of attack by the Asian chestnut gall wasp on chestnut tree growth. Additionally, nutrient availability may also have helped chestnut trees to compensate for the pest-induced damage. The study findings suggest that maintaining a lower stand density and promoting plantations in high quality sites may mitigate the impact of gall wasp attack on secondary growth.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Author contributions

FC-D: conceptualization, data acquisition, data curation, formal analysis, investigation, methodology, and writing—original draft. PÁ-Á: data acquisition, data curation, resources, formal analysis, and writing—review and editing. ML: conceptualization, data acquisition, funding acquisition, methodology, project administration, resources, and writing—review and editing. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/ffgc.2022.1095185/full#supplementary-material>

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