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Drought and mistletoe reduce growth and water-use efficiency of Scots pine

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ABSTRACT

To what extent do mistletoes contribute to growth decline in drought-prone forests? Can the rising atmospheric CO_2 concentrations offset the negative impacts of drought and mistletoe infestation on tree growth? Long-term data on growth and intrinsic water use efficiency (iWUE) may allow answering both questions. We used dendrochronology to assess long-term changes in radial growth and iWUE in Scots pine (*Pinus sylvestris*) trees severely infested by mistletoe (*Viscum album*) as compared to non-infested trees. The relationships among tree variables and mistletoe infestation were quantified using structural equation models. Linear mixed-effects models of basal area increment as a function of climate were fitted to severely infested and non-infested trees. Infested trees showed higher stem and crown diameters because they grew faster than non-infested trees in the past. Mistletoe infestation enhanced defoliation and reduced radial growth for more than 10 years prior to sampling, while iWUE was significantly lower on severely infested trees only for the last 5 years. Severely infested trees had higher growth responsiveness to drought stress than non-infested trees. Although infested and non-infested trees displayed similar rising iWUE temporal trends, the combined effect of drought stress and mistletoe infestation caused a reduction in growth and reversed the CO_2-induced increase of iWUE in infested trees. We conclude that rising atmospheric CO_2 concentrations cannot compensate for the impacts of drought and mistletoe on tree growth and iWUE.

1. Introduction

Do mistletoes contribute to drought-induced forest decline (*sensu* Allen et al., 2010) by altering carbon and water use in trees? Mistletoes are usually regarded as biotic factors contributing to forest decline in areas with moderate to severe water deficit (Tsopelas et al., 2004; Dobbertin et al., 2005). However, mistletoes may also be predisposing factors (*sensu* Manion, 1991) by weakening host trees or inducing growth loss and enhanced defoliation in severely infested trees (Dobbertin and Rigling, 2006; Galiano et al., 2010). In this sense, Rigling et al. (2010) suggested that mistletoe infestation makes trees more vulnerable to drought stress when growing in a xeric site.

Global change components may have contrasting effects on mistletoe-tree interactions driving different trajectories of tree growth and vigour, and leading to divergent carbon balances at the stand level. First, rising air temperatures increase warming-induced drought stress which is sometimes exacerbated by mistletoe infestation on host trees due to the high transpiration rates of the hemiparasite (Dobbertin and Rigling, 2006). In addition, a warmer climate might also promote the expansion of some mistletoe species whose distribution area is mainly controlled by low temperatures (Dobbertin et al., 2005). Second, rising CO_2 concentrations in the atmosphere might benefit host trees through a fertilization effect increasing their photosynthetic rates and leading to higher growth rates in the tree and plausibly in the mistletoe (Bickford et al., 2005). If the elevated CO_2 leads to enhanced carbon uptake and growth stimulation through increasing intrinsic water-use efficiency (iWUE) such responses could alleviate the negative effects caused on host trees by the carbon and water removed from them by the mistletoe. However, this argument relies on the assumption that other factors (mesophyll conductance, evaporative demand) play a secondary role on iWUE changes which is not always the case (Seibt et al., 2008; Roden and Farquhar, 2012).

However, increasing iWUE with rising atmospheric CO_2 concentration is not leading to improved tree growth everywhere (Peñuelas et al., 2010) suggesting that tree growth does not seem to be limited by carbon supply (Körner, 2003). Indeed, tree growth has not been stimulated as expected in response to the CO_2 increase and it has remained stable or even declining in some areas, suggesting that other local factors override the expected CO_2

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fertilization effect (Martinez-Vilalta et al., 2008; Linares and Camarero, 2011). Hence, the extent that rising CO_2 may enhance tree growth and whether drought stress and mistletoe infestation could explain deviations from the projected CO_2-induced growth enhancement are still poorly understood in trees heavily affected by mistletoe living in drought-prone areas.

Several studies using $^{13}C/^{12}C$ isotopic ratios in annual tree rings show that trees respond to increasing atmospheric CO_2 concentrations in diverse ways, suggesting an interaction with other local environmental factors (Ferrio et al., 2003; Saurer et al., 2004). Climate warming-related drought and long-term acclimation to elevated CO_2 concentrations have been proposed as potential factors constraining the expected fertilization effect (Linares and Camarero, 2011). However, to the best of our knowledge no study has yet tackled the role of mistletoe infestation on driving changes in iWUE trends in response to rising CO_2 concentrations.

Mistletoes are aerial hemiparasitic plants which take water and carbohydrates from host trees (Glatzel and Geils, 2009). Mistletoes are also keystone species for maintaining biodiversity since their fruits feed several bird species during the winter (Mathiasen et al., 2008). Scots pine (*Pinus sylvestris* L.), the conifer with the widest geographical distribution area in the world, is the host of the European pine mistletoe (*Viscum album* ssp. *austriacum* L.; Zuber, 2004). Iberian Scots pine populations make up the southernmost distribution limit of the species and thus these stands are expected to be very vulnerable to drought-induced decline, particularly in xeric sites (Martinez-Vilalta and Piñol, 2002).

Here, we use dendrochronology to retrospectively assess long-term changes in growth and water-use efficiency in four Scots pine forests heavily affected by mistletoe and located near the southern margin of the species' distribution area in eastern Spain. Our specific objectives were: (i) to determine the relationships between different variables measured in host tress (diameter measured at 1.3 m, total height, crown height and diameter, crown cover, basal area increment, and sapwood area) and mistletoe infestation and to determine how this in turn affects tree defoliation and basal area increment, and (ii) to quantify how the combined stressing effects of drought and mistletoe infestation drive changes in basal area increment and iWUE.

2. Materials and methods

2.1. Study area and field sampling

The study area includes four Scots Pine (*Pinus sylvestris* L.) forests located in the Iberian System (Alcalá de la Selva, Teruel province, Aragón), eastern Spain, near the southern distribution limit of the species (Table 1; Supplementary material, Fig. S1). We selected four sites dominated by Scots pine and showing different topographical (altitude, slope) and structural (basal area, stem density) characteristics, and containing at least ten dominant trees heavily infested by mistletoe (Tables 1 and 2). The vegetation is dominated by *P. sylvestris*, junipers (*Juniperus sabina* L., *J. communis* L.) and shrubby species (*Berberis vulgaris* L., *Genista scorpius* L.). The soils are basic and calcareous. The climate in the study area is Mediterranean with continental influence according to local meteorological of the station "Alcalá de la Selva-Solano de la Vega" located at ca. 3 km from the study sites. The mean annual temperature is 9.4 °C and the annual precipitation is 670 mm (Supplementary material, Fig. S2). During the period 1987–2008 no seasonal climatic variable showed significant long-term trends while for the late 20th century temperature significantly rose only in fall (Supplementary material, Fig. S2).

The size (diameter at 1.3 m or at breast height –dbh–, total height, crown height and diameter – the later was based on the average of two horizontal crown diameters measured along N–S and E–W directions–) and the crown cover (in %) of all trees with dbh > 15 cm and located within a plot 30 m × 30 m were measured. To estimate crown defoliation (a proxy of crown transparency) we measured in the field crown cover (amount of crown stem, branches, twigs, shoots, buds, needles and reproductive structures that block light penetration through the crown), i.e. the opposite of crown defoliation. Crown cover was used as a proxy of tree vigor following Dobbertin (2005). Crown cover was measured in 5-percent classes following Schomaker et al. (2007). Since estimates of percent crown cover may vary among observers and places, we used as a reference a tree with the maximum amount of foliage at each site and this variable was always measured by the first author.

The mistletoe infestation degree (ID) was estimated using a modified 3-class rating system based on the original scale established by Hawksworth (1977). The tree crown was vertically divided in three similar sectors and each third was classified as 0 (absence of mistletoe) or 1 (presence of mistletoe) (see examples of severely infested trees in the Supplementary material, Fig. S3). Then, the total mistletoe abundance or infestation degree of each tree was obtained summing the rates of each crown third. Mistletoe abundance ranged from 0 to 3 and all analyses were done based on three classes of abundance or infestation degree (ID): trees without mistletoes (ID = 0, class ID1), moderately infested trees with mistletoe present in one or two thirds of the crown (ID = 1–2, class ID2) and severely infested trees with mistletoe present throughout the crown (ID = 3, class ID3). Tree variables were compared among trees of different infestation degrees in each of the study sites using ANOVAs. Variables expressed as percentages (e.g., crown cover) were previously arcsine-square-root transformed.

2.2. Climate data

To obtain a robust regional climatic series, local data from four meteorological stations located from 5 up to 30 km away from the study site were combined into a regional mean for the period 1954–2008 (Supplementary material, Table S1). To estimate the missing data for each station, and to combine them, we used the MET program from the Dendrochronology Program Library (Holmes, 1994). For each station, monthly variables (mean temperature, total precipitation) were transformed into normalized standard deviations to give each station the same weight in calculating the average monthly values for each year. The difference in the mean elevations of study sites and meteorological stations (on average 300 m) may imply slightly lower temperature values (on

Table 1
Geographical, topographical and structural features of the four study sites.

Site (code)	Latitude (N)	Longitude (W)	Altitude (m)	Aspect	Slope (°)	Basal area (m^2 ha^{-1})	Stem density (No. ha^{-1})
Solano de la Vega-zona Alta (SA)	40°23′15″	0°41′38″	1580	SE	19	16.5	556
Solano de la Vega-zona Baja (SB)	40°23′13″	0°42′17″	1520	SE	13	16.0	633
Puerto de Gúdar-zona Alta (PA)	40°21′46″	0°42′41″	1660	SW	0	19.4	711
Puerto de Gúdar-zona Baja (PB)	40°21′37″	0°42′26″	1500	SE	0	13.8	778

Table 2
Characteristics of the trees sampled in the four study sites (frequencies and mean ± SE values). Trees used in the fitting of Structural equation models (SEMs) are indicated in the third column. Age was estimated by counting rings on cores taken at 1.3 m.

Site	No. sampled and cored trees	No. trees used in SEM	Dead trees (%)	Age (years)	Dbh (cm)	Height (m)	Crown diameter (m)	Crown height (m)	Frequency of trees based on their mistletoe infestation degree (%)		
									ID1	ID2	ID3
SA	50	30	10	66.69 ± 2.23	25.55 ± 1.28	9.88 ± 0.36	5.36 ± 0.19	7.45 ± 0.34	60	20	20
SB	57	37	3	47.65 ± 1.58	20.26 ± 0.70	8.02 ± 0.28	4.70 ± 0.17	5.91 ± 1.91	70	10	20
PA	64	38	7	49.53 ± 1.05	21.04 ± 0.54	8.92 ± 0.19	4.59 ± 0.15	4.59 ± 0.15	44	36	20
PB	70	53	10	59.22 ± 3.35	23.45 ± 1.09	8.69 ± 0.49	4.62 ± 0.23	4.62 ± 0.23	47	23	30

average −1.0 °C) and higher annual precipitation amounts (ca. +55 mm) than in nearby stations.

We calculated a regional cumulative water budget using a modified Thornthwaite water-budget procedure based on monthly climatic data (mean temperature and total precipitation; see Willmott et al., 1985) and assuming a soil water holding capacity of 125 mm based on published data on soil types in the study area (Mapas Provinciales de Suelos, 1970). Soil water balance was modelled by estimating soil–water withdrawal, recharge, and surplus. Positive and negative values correspond to wet and dry conditions, respectively. We calculated the cumulative water deficit from January through June, when the study species performs most of its growth in the study area (JJ Camarero, *pers. observ.*). Then, severe drought events were defined as those years with the maximum cumulative water deficit values (1986, 1994 and 2005). The mean cumulative water deficit (±SE) for the period 1954–2008 was −21.7 ± 21.2 mm, whereas values for the selected years were: −117.8 mm for 1986, −165.4 mm for 1994 and −122.3 mm for 2005. Calculations were done by using the AET software available at http://geography.uoregon.edu/envchange/pbl/software.html.

2.3. Dendrochronological methods

Sampling was performed at each site using standard dendrochronological methods (Fritts, 1976). Two cores were taken at 1.3 m using a Pressler increment borer from each tree located within the 30 m × 30 m plot (see the total number of cored trees per site in Table 2). Sapwood depth was measured in the field for each core and averaged for each tree to obtain an estimate of sapwood area (%) which was calculated assuming a circular shape of the stem. The wood samples were air-dried and polished with a series of successively finer sand-paper grits until rings were clearly visible. The samples were visually cross-dated and a minimum of 50 cross-dated trees (100 radii) were measured for each site. Tree rings were measured to the nearest 0.01 mm using a binocular scope and a LINTAB measuring device (Rinntech, Heidelberg, Germany). Cross-dating of the tree rings was checked using the program COFECHA (Holmes, 1983). Tree age at 1.3 m was estimated by counting rings in the oldest core of living trees and by fitting a geometric pith locator to the innermost rings to estimate the distance missing up to the theoretical pith. The estimated distance to the theoretical pith was also used to correct the calculation of basal area increment which was calculated assuming a circular shape of stems. The trend due to the geometrical constraint of adding a volume of wood to a stem of increasing radius was corrected by converting tree ring widths into basal area increments, which is a more biologically meaningful descriptor of growth trends than ring widths (Biondi and Qaedan, 2008). Basal area increment, hereafter abbreviated as BAI, was calculated from tree-ring widths as the difference between consecutive cross-sectional basal areas (BA) estimated for years $t + 1$ and t as:

$$\mathrm{BAI}_{t+1} = \mathrm{BA}_{t+1} - \mathrm{BA}_t = \pi((\mathrm{CL}_t + \mathrm{TRW}_{t+1})^2 - (\mathrm{CL}_t)^2) \tag{1}$$

where CL is the core length measured for dated tree-rings formed in years $t + 1$ and t and TRW is the tree-ring width.

2.4. Structural equation models

Structural equation models (SEM; Grace, 2006) were used to statistically evaluate postulated relationships between tree variables (dbh, crown cover, sapwood area), basal area increment (mean value for the common period 1970–2008) and mistletoe infestation degree (see Supplementary material, Appendix 1). First, we specified several theoretical models based on *a priori* assumed relationships among variables considering the available literature (Zuber, 2004; Dobbertin and Rigling, 2006; Rigling et al., 2010; Galiano et al., 2010, 2011). Second, we tested if the variance–covariance matrix obtained from observational data significantly differed from the matrix imposed by the hypothetical models. To perform SEM analyses we selected a subset of all cored trees ($n = 158$ trees) in which all the aforementioned variables have been measured and located at more than 5 m from the closest plot margin in order to avoid edge effects (Table 2). To estimate SEMs we used the maximum likelihood method. The use of several indices to evaluate the model fitness provides a robust assessment of the fitted SEM (Jöreskog 1993). Hence, we evaluated the fitted models using the chi-square (χ^2) test and its related probability level (P), as well as complementary goodness-of-fit indices (AGFI, Adjusted Goodness-of-Fit Index; RMSEA, Root Mean Square Error of Approximation; AIC, the Akaike Information Criterion). Values close to zero for the χ^2 and RMSEA statistics and values close to one of the AGFI index would indicate that the evaluated models are consistent with the theoretical ones. Lower AIC values correspond to more parsimonious models. In relative terms, models with low AIC and high P values associated with χ^2 correspond to better fits than models with the reverse characteristics. Since mistletoe infestation is an ordinal variable we also performed a Bayesian estimation using a Markov Chain Monte Carlo algorithm because this is the method suggested when ordinal variables are modeled as ordered-categorical data (Arbuckle, 1995–2009). Nevertheless, maximum likelihood estimates are usually robust when ordinal variables contain few categories as is the case of mistletoe infestation (Lee, 2007).

2.5. Linear mixed-effects models of basal area increment

We tested the following linear mixed-effects model of BAI (standardized data for the period 1954–2008):

$$Y_i = X_i\beta + Z_i b_i + \varepsilon_i \tag{2}$$

where Y_i represents BAI, and β is the vector of fixed effects (i.e. climate variables), b_i is the vector ofrandom effects (i.e. tree dbh, tree identity and tree age at coring height), X_i and Z_i are, respectively, fixed and random effects regressor matrices, ε_i is the within group error vector. Linear mixed-effects models of BAI were built separately for non-infested (class ID1, trees without mistletoe) and infested trees (class ID2, moderately infested trees, and class ID3, severely infested trees) considering the four study sites (SA, SB, PA, PB) to test if infested and non-infested trees show contrasting growth responses to climate. BAI of the previous year was introduced into the model as an additional fixed effect to account for the first-order temporal autocorrelation of this variable, while tree dbh was introduced as a random factor into the model to account for potential tree-size effects, and tree age was also introduced to account for potential tree-age effects. Residuals of the models were checked for normality, homoscedasticity and autocorrelation. The effects of climate on BAI were tested and compared with a null model considering BAI of the previous year as a constant (see Biondi and Qaedan, 2008). The random effects and the covariance parameters were estimated using the restricted maximum likelihood method (Zuur et al., 2009). We used an information-theoretic approach for multi-model selection (see Burnham and Anderson, 2002), based on the AIC corrected for small sample sizes (AICc). The AIC combines the measure of goodness of fit with a penalty term based on the number of parameters (k) used in the model, i.e. it selects the most parsimonious models. We also calculated Δi (difference in AICc with respect to the best model) and W_i (relative probability that the model i was the best model for the observed data). We considered models with substantial support to be those in which the ΔAIC, i.e. the difference of AICc between models, was less than 2 (Zuur et al., 2009). We fitted linear mixed-effects models using the *nlme* library of the R statistical suite version 2.14 (R Development Core Team 2013)

2.6. Changes in intrinsic water-use efficiency

To compare the changes in intrinsic water-use efficiency (iWUE) of co-occurring non-infested and infested Scots pine trees we measured $^{13}C/^{12}C$ isotope ratios in wood from cross-dated annual tree rings during the late 20th century. For this purpose we sampled ten additional trees located near the plot located in site PA. We randomly selected trees of similar size and sampled them taking two additional cores at 1.3 m from five trees without mistletoe (ID1) and five trees severely infested by mistletoe (ID3). The sampled trees were dominant and of similar size and age (mean ± SE values: dbh = 22.1 ± 0.6 cm, mean height = 8.9 ± 0.2 m, mean age = 50.0 ± 4.3 years). Cores were cross-dated, sapwood length was measured, and tree-ring width and basal area increment were measured as explained before (see *Dendrochronological methods*).

Wood segments containing five contiguous annual tree-rings were carefully separated with a razor blade with the help of a binocular microscope. Samples were grouped in 5-year segments starting in 1970 (1970–1974, 1975–1979, 1980–1984, 1985–1989, 1990–1994, 1995–1999, 2000–2004) and ending with a 4-year segment (2005–2008). We analyzed five-ring instead of one-ring wood segments in this study to account for a large enough number of tree individuals while maintaining mid to low frequency temporal variability. Wood samples were carefully homogenized and milled using an ultra centrifugation mill (Retsch ZM1, mesh size of 0.5 mm). An aliquot of 0.5–0.7 mg of each wood sample was weighed on a balance (Mettler Toledo AX205) and placed into a tin capsule for isotopic analyses. Cellulose was not extracted as both whole wood and cellulose isotope time-series show similar long-term trends related to atmospheric CO_2 concentration and climate (Saurer et al., 2004). Furthermore, a carryover effect from year to year would be negligible because we analyzed 4- or 5-year segments. The isotopic ratio $^{13}C/^{12}C$ ($\delta^{13}C$) was determined on an isotope ratio mass spectrometer (Thermo Finnigan MAT 251) at the Stable Isotope Facility (University of California, Davis, USA). The results were expressed as relative differences in $^{13}C/^{12}C$ ratio of tree material with respect to the Vienna Pee-Dee Belemnite (V-PDB) standard. Two analytical standards were included for analysis after every ten wood samples: cellulose ($\delta^{13}C = -24.72‰$) and phthalic acid ($\delta^{13}C = -30.63‰$). The repeated analysis of these two internal standards yielded a standard deviation lower than 0.1‰ and the accuracy of analyses was 0.07‰. The estimated precision of the measurements was ±0.1‰.

Isotopic discrimination between the carbon of atmospheric CO_2 and plant carbon (Δ; see Farquhar and Richards, 1984) was defined as:

$$\Delta = (\delta^{13}C_{atm} - \delta^{13}C_{plant})/(1 + \delta^{13}C_{plant}/1000), \tag{3}$$

where $\delta^{13}C_{atm}$ and $\delta^{13}C_{plant}$ are the isotope ratios of carbon ($^{13}C/^{12}C$) in atmospheric CO_2 and plant material (tree rings and needles) respectively, expressed in parts per thousand (‰) relative to the standard V-PDB; Δ is linearly related to the ratio of intercellular (c_i) to atmospheric (c_a) CO_2 mole fractions, by (see Farquhar et al., 1982):

$$\Delta = a + (b - a)c_i/c_a, \tag{4}$$

where a is the fractionation during CO_2 diffusion through the stomata (4.4‰), and b is the fractionation associated with reactions by Rubisco and PEP carboxylase (27‰; Farquhar and Richards, 1984). The values for variables c_a and $\delta^{13}C_{atm}$ were obtained from published data (see Table 2 in McCarroll and Loader, 2004). Since all sampled trees were located at similar elevation, a correction for differences in ambient CO_2 partial pressure was not needed.

The c_i/c_a ratio reflects the balance between net assimilation (A) and stomatal conductance for CO_2 (g_c) according to Fick's law: $A = g_c(c_a - c_i)$. Stomatal conductances for CO_2 and water vapour (g_w) are related by a constant factor ($g_w = 1.6g_c$), and hence these last two variables allow linking the leaf-gas exchange of carbon and water. The linear relationship between c_i/c_a and Δ may be used to calculate the intrinsic water-use efficiency (iWUE), defined as the ratio of net assimilation to stomatal conductance to water vapour (A/g_w), which is calculated as follows:

$$\text{iWUE} = (c_a/1.6)[(b - \Delta)/(b - a)] \tag{5}$$

The iWUE (μmol mol^{-1}) inferred from $\delta^{13}C$ has been widely related to long-term trends in the internal regulation of carbon uptake and water loss in plants (see McCarroll and Loader, 2004; Robertson et al., 2008) assuming that Δ relates linearly to c_i/c_a, despite the iWUE is not equivalent to actual water use efficiency, which is the ratio of assimilation (gained carbon) to transpiration (lost water) (see Seibt et al., 2008).

3. Results

3.1. Relationships between mistletoe infestation, tree variables and growth

On average, 20% of sampled trees were severely infested by mistletoe (Table 2). Severely infested trees contained a mean number of 820 mistletoe individuals per tree and the oldest living mistletoes reached a maximum age of 30 years (results not presented). In all studied sites, severely infested trees had thicker diameter (dbh) and wider crown but lower crown cover than non-infested trees, whereas in three out of four sites infested trees had less BAI and sapwood area than non-infested trees (Table 3). No significant differences in age were observed among trees of contrasting infestation degree.

The variable most strongly and positively related to infestation degree was the tree diameter (Fig. 1). The mistletoe infestation

Table 3
Comparison of structural and growth (basal area increment, BAI) variables among Scots pine according to their infestation degree (ID1, trees without mistletoe; ID2, moderately infested trees; ID3, severely infested trees) for trees sampled within plots in the four study sites (SA, SB, PA, PB). Mean ± SE values are displayed and related statistics (*F* ratio). Different letters indicate significant ($P < 0.05$) differences among infestation classes. The BAI was calculated for the period 1995–2008. Age was estimated by counting rings on cores taken at 1.3 m.

Variable	Infestation degree	SA	*F*	SB	*F*	PA	*F*	PB	*F*
Dbh (cm)	ID1	22.3 ± 0.8a	15.3^{***}	19.9 ± 0.6a	13.2^{***}	20.0 ± 0.6a	9.8^{***}	22.5 ± 1.1a	10.0^{***}
	ID2	29.0 ± 1.2b		22.1 ± 1.7a		21.5 ± 0.7b		25.8 ± 1.1b	
	ID3	29.5 ± 1.2b		27.2 ± 1.6b		24.6 ± 0.9b		28.0 ± 1.0b	
Age (years)	ID1	67.5 ± 2.8	0.3	48.2 ± 1.2	0.8	51.2 ± 4.6	0.8	58.5 ± 5.9	0.9
	ID2	70.6 ± 5.3		47.1 ± 2.7		48.0 ± 4.0		58.6 ± 9.1	
	ID3	67.6 ± 3.9		47.5 ± 1.3		49.8 ± 4.1		60.3 ± 3.6	
Tree height (m)	ID1	9.1 ± 0.3	0.8	8.4 ± 0.3	1.9	8.5 ± 0.3	0.1	8.3 ± 0.5	0.2
	ID2	9.5 ± 0.6		8.4 ± 0.6		8.6 ± 0.2		8.4 ± 0.8	
	ID3	9.8 ± 2.0		9.4 ± 0.3		8.8 ± 1.7		8.9 ± 0.5	
Crown height (m)	ID1	7.0 ± 0.3	0.6	6.3 ± 0.3	0.1	6.1 ± 0.3	0.5	6.0 ± 0.4	0.28
	ID2	7.1 ± 0.5		6.0 ± 0.8		6.0 ± 0.3		6.6 ± 0.8	
	ID3	7.2 ± 0.5		6.4 ± 0.4		5.7 ± 0.3		6.1 ± 0.4	
Crown diameter (m)	ID1	4.9 ± 0.2a	3.5^{*}	4.7 ± 0.1a	7.0^{*}	4.5 ± 0.3a	4.5^{*}	4.6 ± 0.2a	5.5^{**}
	ID2	5.3 ± 0.3b		5.1 ± 0.5ab		5.0 ± 0.2ab		5.2 ± 0.4ab	
	ID3	5.7 ± 0.2b		5.5 ± 0.5b		5.6 ± 0.4b		5.9 ± 0.3b	
Crown cover (%)	ID1	82.9 ± 4.4a	39.6^{***}	84.8 ± 2.5a	33.4^{***}	79.6 ± 5.4a	30.5^{***}	87.0 ± 3.2a	25.4^{***}
	ID2	39.4 ± 5.4b		60.6 ± 6.5b		61.7 ± 4.6b		72.0 ± 7.1a	
	ID3	29.2 ± 4.5b		41.7 ± 6.3b		30.8 ± 5.5c		39.0 ± 6.6b	
BAI (cm^2 $year^{-1}$)	ID1	3.0 ± 0.3a	3.9^{*}	3.7 ± 0.3	0.3	2.7 ± 0.5a	11.0^{*}	6.1 ± 0.7ab	3.4^{*}
	ID2	2.4 ± 0.5ab		3.6 ± 0.8		1.6 ± 0.3b		7.8 ± 1.5a	
	ID3	1.6 ± 0.3b		3.5 ± 0.9		1.5 ± 0.3b		4.3 ± 0.7b	
Sapwood area (%)	ID1	67.0 ± 1.9a	16.4^{***}	72.7 ± 1.5	0.8	80.2 ± 3.1a	4.9^{*}	79.5 ± 2.0a	6.7^{*}
	ID2	52.1 ± 4.3b		71.6 ± 5.3		72.4 ± 4.1ab		72.7 ± 5.2ab	
	ID3	51.5 ± 2.9b		68.3 ± 3.9		66.2 ± 3.3b		68.3 ± 2.7b	

Significance levels.
[*] $P < 0.05$.
[**] $P < 0.01$.
[***] $P < 0.001$.

degree drove BAI decline, both directly by reducing radial growth and indirectly by decreasing crown cover. The sapwood area was positively related to crown cover and BAI, while the tree diameter was also positively related to cover but negatively to BAI. Lastly, the two methods of SEM estimation (maximum likelihood *vs.* bayesian estimations) yielded similar results (Supplementary material, Table S2).

3.2. Effects of drought and mistletoe on basal area increment

Currently infested trees showed in the past higher BAI values than non-infested trees. We found noticeable BAI decreases during severe droughts for both non-infested and infested trees (Fig. 2). Growth of infested trees has steadily declined since the 1994 severe drought in those sites where these trees showed the lowest BAI levels (e.g., sites SA and PA; Table 3).

On average, the previous-year BAI explained about 15% of total BAI variance (Table 4; see also all fitted linear-mixed effects models used to predict tree BAI in the Supplementary material, Table S3). The selected linear-mixed effects models showed that the most significant climate driver of BAI was the negative effect of spring-to-summer temperatures (about 38% of the explained variance), whereas BAI was also positively affected by previous autumn rainfall (3%) and spring-to-summer rainfall (4%). Previous autumn temperature was negatively related to BAI and this effect was more intense in trees infested by mistletoe (8%) than in non-infested trees (3%; see Table 4). Previous December temperature showed a positive effect on BAI, being also slightly higher in infested (5%) than in non-infested trees (2%). On average, the total variance explained by climate was slightly higher for trees infested by mistletoe (56%) than in non-infested trees (50%). Finally,

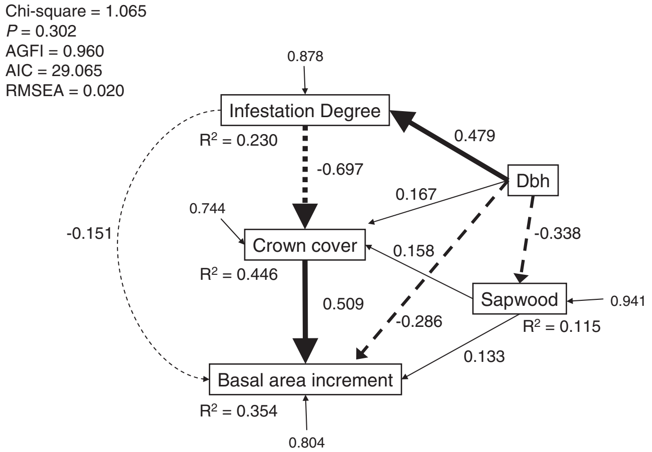

Fig. 1. Selected structural equation model describing the effects of mistletoe infestation degree on crown cover and basal area increment in Scots pine. Goodness of fit statistics appear in the upper left part. Positive and negative effects are indicated by solid and dashed lines, respectively. Arrow widths are proportional to the absolute value of standardized path coefficients (numbers located near arrows). Only significant ($P < 0.05$) coefficients are displayed. The observed variances of dependent variables (R^2) explained by the model are also presented. Unexplained variance, i.e. error terms, of each observed variable is indicated by arrows located near response variables. In the upper left corner several goodness-of-fit indices are indicated: the chi-square (χ^2) and its associated probability (P); the Adjusted Goodness-of-Fit Index (AGFI); the Akaike Information Criterion (AIC), and the Root Mean Square Error of Approximation (RMSEA). In relative terms, models with low AIC and RMSEA statistics, and also showing values close to one of the AGFI index and high P values associated with low χ^2 values correspond to better fits than models with the reverse characteristics.

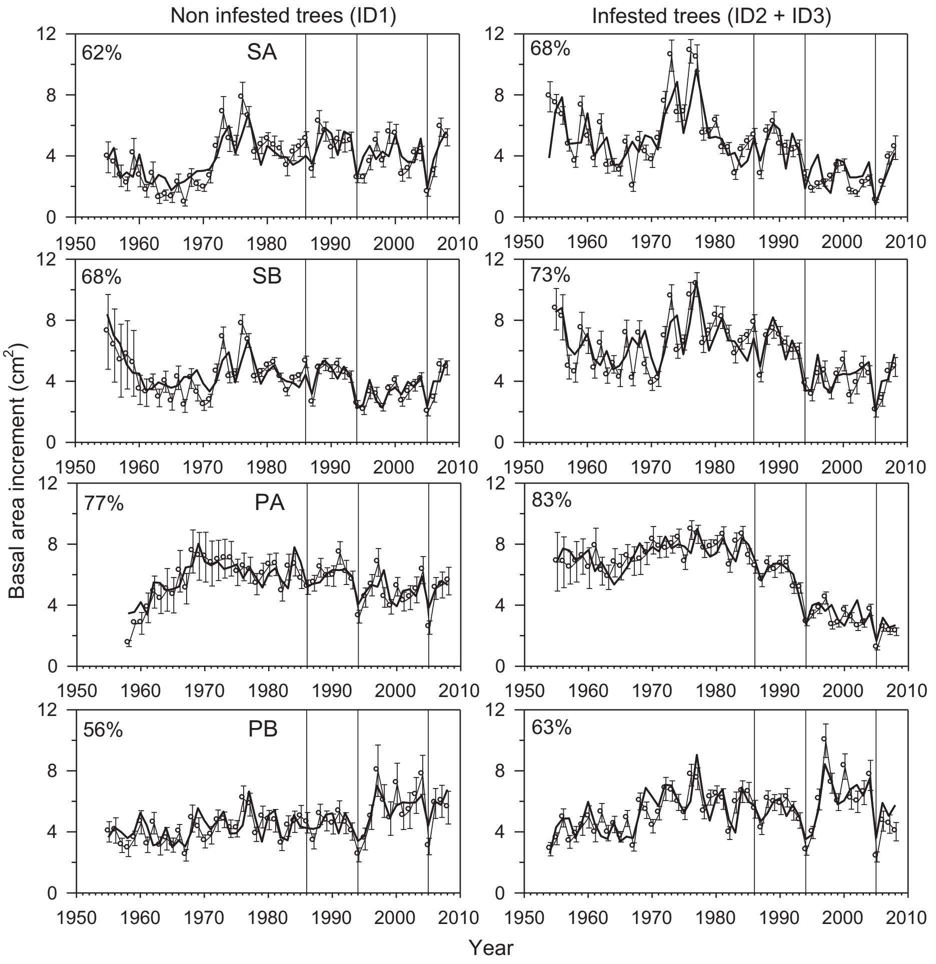

Fig. 2. Observed (thin lines) and predicted (thick lines) trends in basal area increment (BAI) based on linear mixed-effects models for non-infested (class ID1, trees without mistletoe) and infested trees (moderately – class ID2 – and severely infested trees – class ID3) considering the four study sites (SA, SB, PA, PB). BAI values are annual means ± SE. The three vertical lines indicate the severe droughts in 1986, 1994 and 2005. The percentages in the upper left corner of each graph indicate the amount of variability in BAI explained by the models.

Table 4

Basal area increment (BAI) variance (%) of Scots pines explained by climate variables and by previous-year BAI (BAI_{t-1}) according to linear mixed-effects models. The models were fitted considering the four study sites (SA, SB, PA, PB) and comparing non-infested (class ID1, trees without mistletoe) vs. infested trees (moderately – class ID2 – and severely infested trees – class ID3). The last two lines summarize the percentage of variance explained by: temperature (Var. Temp.) and precipitation (Var. Prec.) variables. Positive (+) and negative (−) effects on BAI are indicated for the following climatic variables: TSEp, previous September temperature; TNOp, previous November temperature; TDEp, previous December temperature; TMR, March temperature; TMY, May temperature; TJL, July temperature; PSEp, previous September precipitation; PNOp, previous November precipitation; PFE, February precipitation; PMY, May precipitation; PJN, June precipitation; PJL, July precipitation; PAU, August precipitation.

Fixed factors (effect)	SA		SB		PA		PB	
	ID1	ID2 + ID3	ID1	ID2 + ID3	ID1	ID2 + ID3	ID1	ID2 + ID3
BAI_{t-1} (+)	12.18	10.34	11.51	13.04	36.39	37.26	16.40	17.04
TSEp (−)							15.09	15.09
TNOp (−)		5.19	6.04	7.43		8.36		
TDEp (+)	3.14	7.62	3.40	6.70		3.48		
TMR (−)	14.36	18.35	16.79	16.96	11.41	11.54		
TMY (−)					24.50	14.16		6.34
TJL (−)	27.41	21.47	25.44	24.12			28.94	31.06
PSEp (+)	2.70	1.39						
PNOp (+)					4.60	2.49	3.71	2.48
PFE (+)			1.49	1.29				
PMY (+)							5.00	4.23
PJN (+)							3.61	2.05
PJL (+)		1.08				1.89		1.80
PAU (+)	2.11	2.49	2.97	3.63		3.40		
Var. Temp (%)	44.91	52.63	51.67	55.21	35.91	37.54	44.03	52.49
Var. Prec. (%)	4.81	4.96	4.46	4.92	4.60	7.78	12.32	10.56

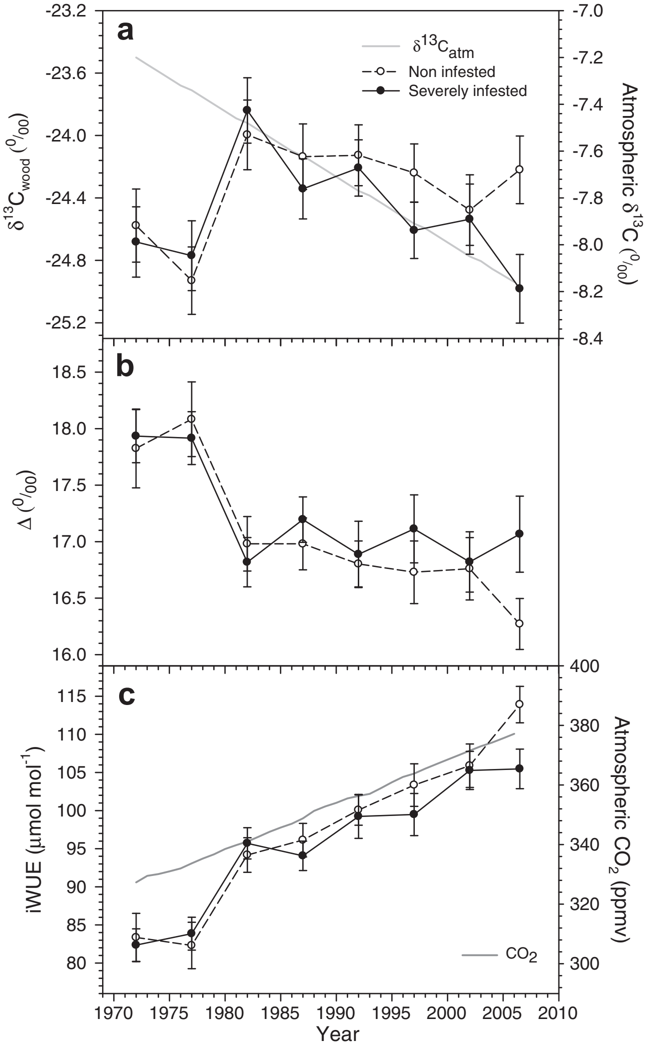

Fig. 3. Trends in the carbon isotopic ratio $^{13}C/^{12}C$ ($\delta^{13}C$) (a), isotopic discrimination between the carbon of atmospheric CO_2 and plant carbon (b), and inferred intrinsic water use efficiency (iWUE) (c) in non-infested trees (class ID1, empty symbols) and trees severely infested by mistletoe (class ID3, filled symbols). The values (means ± SE) are for five trees for each infestation class and considering 5-year intervals excepting the last segment (2005–2008). The carbon isotopic ratio in atmospheric CO_2 ($\delta^{13}C_{atm}$) and the rising atmospheric CO_2 concentrations are also presented.

infested and non-infested trees showed similar patterns in their BAI residuals (see Supplementary material, Fig. S4).

3.3. Effects of drought and mistletoe on iWUE

Non-infested and severely infested trees showed similar long-term trends in $\delta^{13}C$, Δ and iWUE until 2005 (Fig. 3). Severely infested trees usually had lower iWUE values than non-infested trees. In the interval 2005-2008 severely infested trees had a significantly lower iWUE than non-infested trees ($F = 5.64$, $P = 0.044$). Such difference appeared because in severely infested trees the iWUE stabilized at 105 μmol mol^{-1}, i.e. they stopped rising their iWUE, whereas the non-infested trees decreased in discrimination and consequently their iWUE increased up to 114 μmol mol^{-1}.

4. Discussion

Our findings indicate that warming-induced drought stress and mistletoe infestation were the main stressors explaining the growth decline of the studied Scots pine populations in xeric sites. Our results suggest that if climate becomes drier, *P. sylvestris* will undergo significant growth reductions while those individuals infested by mistletoe may be not able to overcome this additional stress factor, likely inducing stand-level dieback. These results support taking into account biotic factors (mistletoes, fungi, and insects) in drought-prone forests as contributing drivers of warming-induced growth declines.

4.1. Effects of mistletoe infestation on intrinsic water use efficiency

In this study, severely infested trees grew less and recently they showed smaller increase in iWUE (+0.05 μmol mol^{-1} yr^{-1}) as compared with non-infested trees (+1.78 μmol mol^{-1} yr^{-1}), based on carbon isotopic data. This implies that the rate of iWUE rise as atmospheric CO_2 concentrations increase was almost nil in infested trees. Carbon discrimination supports that, on average, non-infested trees have higher iWUE than infested trees (about 8.4 μmol mol^{-1} yr^{-1} higher for the 2005–2008 period) whereas the BAI difference between non-infested and infested trees was about 2.5 cm^2 year^{-1}. However, these recent divergences were only evident after a pronounced drought occurred in 2005. The studied Scots pine populations showed a fairly stable discrimination rate since the 1980s and thus a constant c_i/c_a scenario may be assumed for these trees. These findings concur with other studies indicating that gains in iWUE were the result of rising CO_2 concentrations (c_a) rather than any functional responses by trees (Körner et al., 2007 and references therein). In the last analysed interval (2005–2008), the non-infested trees did decrease c_i/c_a as compared to the previous time period and such decrease was linked to the aforementioned deceleration of the iWUE increase of infested trees. The lack of growth and iWUE responses to the increase in carbon availability observed in infested trees agrees with other research confirming that rising CO_2 levels are not stimulating tree growth in drought-prone areas (Peñuelas et al., 2010). On the other hand, increasing water-use efficiency from a variety of tree species, exposed to variable environmental conditions over time, seem to show species-specific ecophysiological mechanisms (Battipaglia et al., 2013). For instance, some tree species displayed downward adjustment of photosynthesis under elevated air CO_2 concentration (i.e. higher discrimination under elevated CO_2) in dry and nutrient-poor environments (Saurer et al., 2003).

Severely infested and non-infested trees showed similar values of carbon isotopic discrimination (between −24‰ and −25‰) along the ca. one half century studied here, although they were slightly lower in the infested trees for the last 20 years and significantly lower for the last 5 years. As a consequence, excluding the most recent period, long-term iWUE increases in a similar way for both infested and non-infested trees, while contrasting growth trends in response to drought and mistletoe abundance were significantly present as long as a decade prior to sampling. It has been hypothesized that rising atmospheric CO_2 concentrations could compensate for drought effects since increasing CO_2 partial pressure should allow to maintain tree carbon gain at a lower cost of water loss. If physiological or morphological tree adjustments allow photosynthesis rates (A; i.e. the carbon gain-related term in the iWUE) to be maintained, while stomatal conductance (g; the tree water status-related term in the iWUE) is reduced, then the iWUE should increase (Körner 2003). However, if drought-induced stomatal closure surpasses the CO_2-induced rising photosynthetic rate, carbon gain will decrease and therefore growth would decline. Our findings suggest that rising atmospheric CO_2 concentrations do not stimulate growth of infested trees under water-limited conditions, since the drought-induced reduction in photosynthesis rates and the warming-enhanced respiration costs override any positive effect caused by the increasing availability of atmospheric CO_2. In addition, we also illustrate how mistletoe infestation might be increasing the likelihood of warming- or drought-induced mortality on host trees, as the hemiparasite is constraining both the growth dynamics and the inferred water use of infested trees.

4.2. Effects of mistletoe infestation on tree growth and sensitivity to climate

Severely infested Scots pine trees showed a reduced basal area increment, as compared with the non-infested trees, after the 1994 and 2005 droughts. Such irreversible growth loss was not fully explained by drought stress alone, since non-infested trees did not present an equivalent growth decline. In *Pinus nigra* mistletoe seems to reach maximum infestation levels about 10–15 years after the colonization of the host tree started (Vallauri, 1998). This suggests that severely infested trees would show a decline in growth once a threshold of mistletoe abundance is surpassed. Indeed, in *Abies alba* Noetzli et al. (2004) detected that growth continuously declined in infested host trees once the mistletoe population invaded the whole crown and occupied the main stem and branches. In the study area winter temperatures steadily and significantly ($P = 0.04$) rose by ca. $+0.01\ yr^{-1}$ during the 20th century. Such winter warming and the observed expansion of thrushes (Vorisek et al., 2008) may have boosted mistletoe abundance in some Spanish pine stands (López-Sáez, 1993) perhaps surpassing the mentioned threshold of mistletoe infestation.

The recent reduction in basal area increment caused by mistletoe was noticeable in all sites (Fig. 2). This growth loss was also contingent on local conditions, since precipitation variables were more relevant drivers of growth in the drier and less productive sites (e.g., site PB). Mistletoes derive substantial amounts of water and carbon from their host trees and show higher transpirations rates than the host trees (Marshall et al., 1994). Trees reduce its transpiration rates through stomatal closure in response to drought but mistletoe continues transpiring, thus increasing the water loss and drought stress experienced by host trees (Fischer, 1983; Zweifel et al., 2012). It is therefore plausible that mistletoe infestation shifts the biomass allocation pattern of host trees, changing for instance their leaf to sapwood ratio (Sala et al., 2001), and increasing warming-induced drought stress in infested trees (Rigling et al., 2010). On the other hand, infested trees might allocate more carbon to fine root production to meet the extra water demand but this has not been tested to our knowledge.

Basal area increment in the infested trees responded more strongly to climate than in non-infested trees during the analysed period (1954–2008). Such findings agree with those found by Stanton (2007) in ponderosa pines infested by western dwarf mistletoe. Probably, infested trees displayed a higher growth rate and hydraulic conductivity than non-infested trees under wet conditions such as the early 1970s in our study case. Further, mistletoe infestation induces a decline in apical growth (Zuber, 2004) which could lead to altered biomass allocation favouring radial growth. Nevertheless, testing this last idea would require a long-term monitoring of mistletoe infestation and defoliation in selected trees and comparing dry *vs*. wet years to disentangle the mistletoe effects on growth and water use from those due to ontogenetic changes in tree size.

4.3. Characteristics and responses of infested trees to the combined effects of drought and mistletoe

We found that infested trees tend to have thicker diameters and more recent crown defoliation and to show higher radial-growth rates in the past compared to non-infested trees. The greater diameters of infested trees suggest that they are able to form more stem wood, and probably display higher conductivity rates than non-infested trees. However, the bigger size and growth rates of infested trees are not explained by differences in age or competition degree as compared to non-infested trees. Therefore, in our case the oldest trees did not present the highest infestation levels which might be the case if they have had more time to accumulate mistletoes. Finally, tree height did not differ among infestation classes indicating that infested trees were not necessarily those preferred by birds for perching and dispersing mistletoe seeds.

Consistent with the negative impacts of drought and mistletoe on growth and iWUE of Scots pine, Sala et al. (2001) and Meinzer et al. (2004) observed a decline in foliar $\delta^{13}C$ values of infested trees suggesting either a poor stomatal adjustment or a diminished photosynthetic capacity in the host tree. Meinzer et al. (2004) found that photosynthesis rates and needle nitrogen contents declined in infested trees. In Scots pine mistletoe-induced stomatal closure allows avoiding hydraulic failure under short-term dry conditions but severely reduces carbon uptake in the long term (Zweifel et al., 2012). These ecophysiological findings suggest that trees show transient responses to different mistletoe infestation stages. According to Galiano et al. (2011) mistletoe infestation would reduce growth by limiting carbon assimilation, mediated by foliage loss and sapwood reduction. In summary, altered growth patterns in severely infested trees are related to increased needle loss and decreasing basal area increment. Overall, this indicates that severe mistletoe infestation alters the long-term carbon source-sink balance.

Our findings suggest that the size and growth rates of host trees modulate how mistletoe infestation affects tree performance. In agreement with this suggestion, dominant trees were the most severely infested by mistletoe in Pyrenean silver fir forests (Oliva and Colinas, 2007). Such results and the fact that this hemiparasite further decreases growth and water-use efficiency in trees already stressed by drought indicate that we need a better understanding of the interactions between host trees, mistletoes and climate warming to forecast the future of pine stands affected by mistletoes in xeric sites (Dobbertin, 2005). Our findings confirm that mistletoe infestation contributes to drought-induced forest decline in xeric sites and mainly affects those trees showing the highest growth rates before infestation proceeds. It may be worthy to evaluate if this pattern is general in other forests and considering decline episodes induced synergistically by drought and other organisms (fungi, insects).

In conclusion, mistletoe infestation and drought caused short-term growth and water-use efficiency declines, leading to a reduced growth and sapwood production and enhancing defoliation in Scots pine stands located near the southernmost limit of the species distribution. Currently infested trees showed in the past higher growth rates than non-infested trees. Infested trees had a higher growth responsiveness to water availability as compared to non-infested trees, but in the last years the former did not improve their intrinsic water-use efficiency as much as the later did. The cumulative effects of mistletoe and drought reduced the intrinsic water-use efficiency in severely infested Scots pine trees by 9%, but this was observed when host trees were severely infested. Mistletoe infestation and drought stress reduced much more secondary growth than water-use efficiency.

4.4. Management implications

Mistletoes are keystone species for maintaining biodiversity since their fruits constitute one of the main food resources for birds during the winter (Mathiasen et al., 2008). Birds feed on mistletoe fruits and promote the long-distance dispersal and germination of the sticky and sugar-rich mistletoe berries. Consequently, to reduce mistletoe dispersal it may be helpful to plant and promote other shrub and tree species producing berries in winter, which can feed birds, reducing mistletoe fruit consumption and seed dispersal. This could help to reduce the incidence of mistletoe on the biggest trees, which usually show the highest growth rates before infestation started. These dominant individuals are usually considered the most valuable trees for wood extraction but they can also be selected perching sites for some bird species, acting as initial infestation foci (Dobbertin and Rigling, 2006; Mathiasen et al., 2008).

It would be also advisable to remove the biggest and most vigorous mistletoe female individuals, usually colonizing the upper third of the tree crown (Sangüesa-Barreda et al., 2012), before they start producing seeds. In drought-prone areas mistletoe removal should be more effective before or while severe droughts occur, in order to reduce the combined negative effects of both stressores on needle retention, tree growth, and water use efficiency. In addition, removing and pruning out big mistletoe female individuals or heavily infested branches would further decrease the overall production of mistletoe fruits and seeds and their dispersal within the host tree (mistletoe seeds tightly stick to any branch or shoot that they fall on) thus reducing the number of new infestations at the lower levels of the canopy.

In the last term, heavily infested trees could be selectively thinned to keep them in a low density and widely separated to limit dispersal among neighboring trees and to alleviate drought stress by decreasing tree density and competition for soil water (Dobbertin, 2005). Mistletoes are hemiparasites. Therefore, their negative effects on tree water use may be more noticeable under conditions of severe water deficit and mostly affect already stressed trees in drought-prone habitats. Consequently, an effective and long-term control program of mistletoe infestation should select the potentially most sensitive trees and stands to mistletoe infestation, and it would require the combined efforts of researchers, managers, owners, and public agencies.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2013.01.028.

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