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4 # Too wet for oaks? Inter-tree competition and recent persistent

5 wetness predispose oaks to rainfall-induced dieback in Atlantic

6 rainy forest

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Abstract

Forest dieback is usually triggered by climatic extremes, even if tree decline can be caused by diverse biotic and abiotic stressors acting synergistically on tree vitality. Many case studies worldwide illustrate the global importance of drought-induced forest dieback under a context of climate warming. However, forest decline is also occurring in regions that are not water-limited, but where increasing rainfall and exceptionally rainy events are observed. Here we assessed the influence of inter-tree competition, regional water availability, and large-scale climate variation on the decline and death of pedunculate oak (*Quercus robur*) in an Atlantic rainy forest in NW Spain. All healthy, declining, and dead trees in four replicated forest stands were mapped, and inter-tree competition was individually quantified with a distance-dependent competition index. Long-term variation of annual radial growth was analyzed on a selection of individuals per stand, and its dependence on climate variation was examined by correlation analysis with monthly climatic records. Trees under intense competition showed higher mortality risk. Increasing rainfall and the large-scale climatic pattern El Niño-Southern Oscillation (ENSO) have influenced tree growth during recent decades, acting as long-term stressors. A detrimental effect of water surplus during both the year preceding growth and spring of the current year has been noticed since 1980. Extremely rainy conditions in 2001 resulted in strong short-term stress that killed trees suffering from intense competition and wetness-induced stress. Our findings support that water excess is a relevant triggering factor for dieback of dominant forest trees in rainy temperate deciduous forest. This pattern is possible in regions where increasing precipitation and more frequent and intense rainfall extremes, associated with global climate warming, are happening. Since climate warming may lead to higher total annual rainfall, and to an increase in frequency and intensity of extreme precipitation events, forest dieback episodes associated with wetter conditions may become more common in the future.

Keywords: Climate dynamics, forest decline, increasing precipitation, *Quercus robur*, rainfall extremes, tree mortality.

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1. Introduction

Increasing drought frequency and duration are considered among the main causes of climatically-induced physiological stress and increased tree death under a context of global climate warming (van Mantgem and Stephenson, 2007). Numerous examples worldwide illustrate the role of water deficit as a triggering factor for forest decline, mainly in water-limited ecosystems where forests are increasingly responding to ongoing warming and drying (see review by Allen et al., 2010). Tree growth decline and dieback episodes in southern Europe are also commonly associated with long-term trends of falling water availability and/or short-term drought events, and this is contributing to forest decline under Mediterranean climate, where summer drought is the main factor limiting tree growth and survival (Di Filippo et al., 2010; Linares et al., 2010). Drought stress could be thought to be a primary cause for dieback of forest trees near the boundary between the Atlantic and Mediterranean biogeographical regions, as has been newly found in conifer forests of the northeastern Iberian Peninsula (Camarero et al., 2011; Hereş et al., 2012).

Recent studies from other not water-limited ecosystems, however, suggest that conditions related to increasing wetness would be also relevant triggering factors for tree decline. For instance, in a long-term assessment of forest dynamics in intact Amazon rainforests, tree mortality peaked and growth declined during atypically wet periods, while growth was fastest during dry periods, when reduced cloudiness might have increased available solar radiation (Laurance et al., 2009). Likewise, oak decline across deciduous forests of eastern North America began during a shift in climate regime, from nearly four centuries of oak dominance characterized by frequent, severe, multi-year droughts, to a period of increased moisture availability over the past century, during

which oak species have been declining, being replaced by mesophytic, drought-sensitive tree species (McEwan et al., 2011). An alternative hypothesis for tree dieback in deciduous forests under not water-limited climate would be that water excess is triggering forest dieback. However, little information is available on the climatic causes of increased tree mortality in deciduous European forests where conditions are not water-limited, such as at the southwest boundary of the Atlantic biogeographical region, towards its limit with the Mediterranean region in northwest Spain.

Pedunculate oak (*Quercus robur*) is a dominant tree species in temperate deciduous forests throughout Europe, which is at its south-western range boundary in northern Spain, and is among the tree species most frequently showing symptoms of decline (Gibbs and Greig, 1997; Führer, 1998; Thomas et al., 2002). The climatic stressors recurrently evidenced as related to *Q. robur* decline are winter-spring frosts and summer droughts (Amorini et al., 1996; Helama et al., 2009; Di Filippo et al., 2010; Doležal et al., 2010), which can respectively cause direct damage to the growing tissues, and limit photosynthetic rates during the active period. In addition, this species is known to be relatively intolerant to drought because of its vulnerability to air embolism (Bréda et al., 1993; Cochard et al., 1992; Thomas and Gausling, 2000), but it displays morphological and physiological adaptations that confer tolerance to waterlogging and root hypoxia, in comparison to other coexisting deciduous tree species (Dreyer, 1994; Schmull and Thomas, 2000; Parelle et al., 2006). In a recent work, we showed that El Niño-Southern Oscillation (ENSO) is controlling regional hydrological regime and *Q. robur* radial growth in northwest Spain (Rozas and García-González, 2012). We can therefore expect that growth decline and dieback of north-western Iberian populations of this species would be related to variability in regional water conditions, which are at least partially controlled by ENSO dynamics.

101   Although climatic stressors can be relevant triggering factors, other abiotic and biotic

102   factors can act synergistically with climate to speed up or increase the level of tree

103   decline and death. Inter-tree competition is a primary driving force that causes mortality

104   in temperate forests, inducing long-term stress and reducing tolerance of trees to further

105   stresses (Piutti and Cescatti, 1997; Olano et al., 2009). However, the diverse

106   environmental limitations and stresses usually drive the decline process synergistically,

107   and their individual impact on tree physiological status and mortality risk cannot easily

108   be assessed (Niinemets, 2010). Owing to heterogeneity in local tree densities, the actual

109   importance of long- and short-term climatic stress on dieback of natural forests can be

110   often hard to determine (Suarez et al., 2004; Linares et al., 2010). Due to the complexity

111   of causal factors involved in the oak decline syndrome, and the possible confounding

112   effects of local conditions, studies of forest decline integrating long- and short-term

113   potential stressors, including climatic variation as well as biotic interactions, are needed

114   but largely lacking (Führer, 1998; Marçais and Bréda, 2006).

115   Here we studied the association of tree health status and death with a potential biotic

116   stressor, namely inter-tree competition, and assessed whether tree growth was modulated

117   by the variation in regional water availability and the large-scale climatic pattern ENSO.

118   This was performed in a mature oak forest under rainy Atlantic conditions in northwest

119   Spain, where massive tree death has occurred over the past years. We checked the

120   following not mutually exclusive hypotheses: (1) competition intensity differs according

121   to the tree health status, and more specifically between living and dead trees; (2) water

122   availability controls tree growth and the probability of tree death; and (3) climate-driven

123   tree growth loss and death are related to the influence of the large-scale climatic pattern

124   ENSO on regional rainfall in the northwest Iberian Peninsula.

125

2. Materials and methods

2.1. Study area

Exceptionally high mortality rates of pedunculate oak have been noticed for the past years on the windward slopes of the Serra do Suido mountain range, Galicia, northwest Spain (Fig. 1A). The Serra do Suido is a north-to-south oriented range on granite bedrock, with a maximum elevation of 1,151 m, which directly receives wet fronts from the Atlantic Ocean, showing high incidence of fog and precipitation. This range is mainly deforested; the abundant rocky slopes on which heaths dominate are intermixed with some disperse oak woodlands on deeper soils. The dominant woodland is an Ibero-Atlantic acidophilous *Quercus* forest (G1.8/P-41.56, EUNIS habitat classification), with a main canopy almost exclusively composed of pedunculate oak, and a sparse understorey of *Ilex aquifolium*, *Pyrus cordata*, and *Crataegus monogyna*.

For this study, we selected the largest wooded sector in the Serra do Suido, with 385 ha of oak woodland covering the area between 42º22'40"–42º23'50" N and 08º21'10"–08º23'45" W, and ranging 580–800 m in elevation (Fig. 1B). This area comprises forest stands of varying tree density and clearings occupied by upland heath, pasture, bogs, and streams. Soils are nutrient-poor and narrow Lithic and Umbric Leptosols and Epileptic Umbrisols, generally less than 40 cm in depth, reaching exceptionally up to 80 cm in ravine bottoms (Calvo de Anta and Macías Vazquez, 2002). Soils are acidic (pH 3.2–4.3), with a high organic matter content (13.9–30.7%), and with relatively high aluminium content (151.1–396.6 mg kg^{-1}) and cation exchange capacities (77.9–197.4 mmol$_c$ kg^{-1}).

2.2. Climate data and climatic variation

151   We used monthly gridded time series for total precipitation (Prec, CRU TS 3 data set,

152   0.5º × 0.5º, period 1901–2006), and Palmer drought severity index (PDSI, CRU self-

153   calibrating PDSI data set, 0.5º × 0.5º, period 1901–2002) as indicators of water

154   availability, taken from the online Climate Explorer of the Royal Netherlands

155   Meteorological Institute (http://climexp.knmi.nl/). The PDSI uses air temperature,

156   cumulated rainfall, and field water-holding capacity to compute a standardized measure

157   of soil moisture ranging from –6 to 6, which corresponds to extremely dry and wet soil

158   conditions, respectively (Dai et al., 2004). Regional climate series were obtained from

159   the 0.5º latitude × 0.5º longitude area in which the study site is included. Several indices

160   describing ENSO dynamics (Southern Oscillation Index, Sea Surface Temperature

161   indices from the regions Niño 1.2, 3, 4, and 3.4 in the tropical Pacific Ocean) were

162   obtained from the Web site of the National Oceanic and Atmospheric Administration,

163   USA (http://www.cdc.noaa.gov/). Among these, only the Sea Surface Temperature (SST)

164   index from the Niño 1.2 region (hereafter SST 1.2) showed significant relationships with

165   our tree-ring chronologies, and was used to monitor the effects of ENSO on tree growth

166   and regional climate. The SST 1.2 time series covers the period 1872–2007, and are SST

167   anomalies relative to the 1950–1979 base period in the area 0–10° S, 90–80° W (Stenseth

168   et al., 2003).

169   Climate in the study area is temperate and humid, with a mean annual temperature of

170   12.0 ºC for 1901–2006, ranging between 6.0 ºC in January and 18.7 ºC in August. Mean

171   annual precipitation is 1,315 mm, with a maximum during autumn-winter (911 mm in

172   October-March), and a summer minimum (125 mm in June-August). Annual

173   precipitation showed a significantly increasing linear trend in the study area during the

174   past century (Fig. 2A; $y = 3.245 \, x – 5030.31$; $n = 105$; $r^2 = 0.111$; $p < 0.001$), as did mean

175   annual PDSI (Fig. 2B; $y = 0.029 \, x – 58.03$; $n = 101$; $r^2 = 0.232$; $p < 0.001$). An important

increase in water availability has been found since 1960; annual precipitation increased

from 1,194 mm in 1901–1959 to 1,458 mm in 1960–2006. Soil water availability also

changed from a net water deficit in 1901–1959 to a net excess of water in 1960–2002.

The period 1993–2002 was the longest one with sustained soil water excess, which was

particularly pronounced in 1998–2002, and particularly rainy conditions were recorded in

2001, with 2,163 mm in annual precipitation, and 4.14 in annual PDSI. This wet period

was coupled with the longest and most intense La Niña phase, which extended from July

1998 to February 2001, and can be recognized as a pronounced positive peak of mean

SST 1.2 anomalies (Fig. 2C).

2.3. Sampling design

We performed a replicated sampling in four representative study stands located at

elevations ranging between 610 and 770 m, mainly facing north, and with mean slopes of

11.6–13.6º (Table 1; Fig. 1B). The first symptoms of individual tree decline (i.e., leaf

yellowing and partial crown lightning in several trees) in these stands were identified in

1998, but generalized evidence of tree dieback was observed in 2002–2003, and massive

tree death occurred since 2005. In 2007, a study plot of 60 m × 70 m was randomly

established within each stand, and all living and dead oaks found within the plots were

mapped with a laser total station (Pentax® R-325NX). All trees were tagged, their DBH

(stem diameter at 1.3 m above ground) measured, and their crown status registered

following a previously established rating for decline (Balci and Halmschlager, 2003),

which considers three classes: healthy, declining, and dead. Healthy trees were those

without symptoms of decline or only slightly damaged, with dieback of some tips of

branches, and slight crown transparency (< 25%). Declining trees were moderately to

severely damaged, with apparent dieback of twigs and branches, yellowing or wilting of

201 leaves, epicormic shoots, and conspicuous crown transparency (> 25%). Tree abundance,

202 basal area, and the proportion of trees in each decline class varied among the study

203 stands (Table 1). Stands showed an incidence of death ranging from 24.1–55.5% of the

204 total number of individuals, and 8.7–55.2% of the total basal area, with a higher

205 incidence of death in stands 2 and 3. Ten healthy, ten declining, and ten dead trees were

206 randomly selected within an inner rectangle of 40 m × 50 m, centered inside each study

207 plot, for dendrochronological sampling.

208

209 *2.4. Inter-tree competition assessment*

210 We analyzed the impact of inter-tree competition on oak death by quantifying

211 competitor interference with an index of competition intensity. We calculated basal area

212 (BA, cm^2) of each tree from its geometrical radius, and quantified competition intensity

213 on the thirty selected subject trees per stand with the distance-dependent competition

214 index (CI):

$$CI = \sum_{j=1}^{n(R)} \left(BA_j / BA_i \right) / D_{ij} \tag{1}$$

215 where BA_i is the basal area of subject tree i, BA_j is the basal area of competitor tree j

216 within the search radius R, and D_{ij} is the distance (m) between subject tree i and

217 competitor tree j. Competitors are defined as those living and dead oaks, with DBH > 5

218 cm, included inside a prescribed search radius R, equal to 8 m from the subject tree

219 (Piutti and Cescatti, 1997; Linares et al., 2010). The CI includes the relative size of

220 competitors in comparison to the subject tree, and their distance to the subject tree. Since

221 all dead trees keep its bark and its sapwood intact, and because of the very short time

222 since the trees were dead (1–3 years), and the slow radial growth rates of surviving trees

223 (0.88–1.32 mm yr^{-1} during 2003–2007), we assumed that CI provided a good estimation

224 of pre-mortality competition levels.

225   We were interested in specific differences among decline classes, but also among

226   stand replicates, since these would reflect local variation in tree traits and competition.

227   Two-way ANOVA was used to compare DBH, tree age, and CI among decline classes,

228   stands, and their interaction, considering decline class as a fixed factor and stand as a

229   random factor. Data were log-transformed when necessary to achieve the requirements of

230   normality and homoscedasticity. The differences among means were tested with Tukey's

231   HSD *post hoc* test. Logistic regressions were also calculated to estimate the risk of

232   mortality according to DBH, age, and competition intensity, considering stand as a

233   random factor. Statistical analyses were performed with the SPSS v.15.0 package (SPSS

234   Inc., Chicago IL, USA).

235

236   *2.5. Dendrochronological procedures*

237   We took two wood cores at opposite sides of the stem, perpendicularly to the

238   direction of the maximum slope to avoid reaction wood, from each of the thirty selected

239   trees per stand, using increment borers at breast height. As rapid sapwood decomposition

240   occurred after tree death, we used an electric drill to turn the increment borer, and we

241   successfully sampled most partially degraded sapwood in the majority of dead trees. The

242   cores were air dried, glued onto wooden mounts, and polished until the xylem cellular

243   structure was visible in the transverse plane. Tree-ring series were absolutely dated by

244   assigning calendar years to the rings, and tree age was estimated with a mean absolute

245   error of $\pm$ 4.3 yr based on a previously tested method for this species (Rozas, 2003). The

246   conspicuously larger vessels in the earlywood of deciduous oaks and their abrupt

247   transition to the latewood allowed an easy distinction between the two tree-ring

248   compartments. Series of earlywood widths (EW) and latewood widths (LW) were

249   measured on each core under magnification to the nearest 0.001 mm with a sliding-stage

250   micrometer (Velmex Inc., Bloomfield NY, USA) interfaced with a computer, and total

251   ring widths (TR) were obtained as the sum of EW and LW on a year-by-year basis. The

252   software COFECHA (Grissino-Mayer, 2001) was used to quantitatively check for

253   crossdating errors in the ring width series.

254   Each raw ring-width series was standardized with the ARSTAN computer program

255   (Cook and Holmes, 1996). Ontogenetic trends and the low-frequency variation of raw

256   ring-width series were minimized by means of a two-step standardization procedure. The

257   series were first fit to a negative exponential or straight line and then to a cubic

258   smoothing spline with a 50% frequency response of 50 years, which is flexible enough to

259   reduce considerably non-climatic variance, and maximize the high-frequency climatic

260   information (Helama et al., 2004). Autoregressive modelling of the residuals and

261   biweight robust estimation of the mean were used to calculate the chronology indices.

262   Since the resulting chronologies from this method represent the climatic signal, they

263   were used to evaluate the long-term relationships between radial growth and climate time

264   series for each decline class at every stand, and also at all four stands together. The

265   statistical quality of the chronologies was assessed in the optimum common period for

266   each decline class using basic statistics to measure the common signal (Briffa and Jones,

267   1990), i.e., mean sensitivity (MS), mean inter-series correlation (Rbar), signal-to-noise

268   ratio (SNR), and expressed populations signal (EPS).

269   In addition, we used the percentage of latewood (%LW) within a ring, calculated on

270   an annual basis for each raw tree-ring series,

$$\%LW = (LW/TR) \times 100 \qquad (2)$$

271   in order to assess the short-term effects of climate availability on tree growth and vitality.

272   In ring-porous oak species, %LW can be considered a good indicator of tree stress and

273   vitality, with low values being symptomatic of a strong physiological stress caused by,

274   for instance, massive defoliation, intense competition with neighbouring trees, or

275   climatic stresses such as a severe drought (Rubtsov, 1996; Gieger and Thomas, 2002;

276   Corcuera et al., 2006). Both %LW series per individual tree were averaged, and so were

277   individual %LW series per decline class and stand. Series of mean %LW chronologies

278   for every decline class, and the percentage of trees showing heavily suppressed growth

279   (%LW < 10%), were directly compared with climatic time series in order to assess the

280   short-term impact of extreme climatic events on tree growth.

281

282   *2.6. Climate sensitivity assessment*

283   Correlations between tree-ring indexed chronologies and the climatic time series (i.e.,

284   monthly time series of Prec, PDSI, and SST 1.2) were calculated in three consecutive 25-

285   yr intervals (1929–1954, 1955–1980, and 1981–2006) to assess the role of climate on

286   tree growth in each decline class during the past decades. We also calculated moving

287   correlations, in 75 intervals of 25-yr width shifted year-by-year, to assess the temporal

288   consistency of both tree growth-climate and ENSO-regional climate relationships for the

289   period 1920–2006. The geographical variation of ENSO-regional climate relationships

290   for the Iberian Peninsula (latitude 35ºN–45ºN, longitude 10ºW–4ºE) was assessed by

291   means of spatial field correlations between SST 1.2 and the most limiting climatic

292   variable   for   tree-ring   growth,   using   the   on-line   Climate   Explorer

293   (http://climexp.knmi.nl/).

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296   **3. Results**

297   *3.1. Dependence of tree decline on inter-tree competition*

298   DBH, tree age, and CI significantly differed among stands, but only DBH and CI

299   differed among decline classes (Table 2). However, no significant effect of the

300   interaction "decline × stand" was noticed, suggesting a similar variation of tree size and

301   inter-tree competition among decline classes at all stands. Dead trees were smaller than

302   healthy trees, and experienced higher competition intensities than living trees (Table 2),

303   with healthy and declining trees showing quite similar CI values. Trees at stand 1 were

304   larger and older than trees at the other stands, and showed lower CI values than trees at

305   stands 3 and 4. In stands 1 and 2, trees from all decline classes showed similar DBH ($p >$

306   0.05), while, at stands 3 and 4, healthy trees were larger than declining and dead trees

307   (Fig. S1A; $F_{2,29} = 5.238$, $p = 0.012$ at stand 3; $F_{2,29} = 8.704$, $p = 0.001$ at stand 4).

308   Competition intensity did not significantly differ among decline classes at stand 1 ($p >$

309   0.05), while dead trees showed the highest CI values at stands 2, 3 and 4 (Fig. S1B; $F_{2,29}$

310     $= 4.305$, $p = 0.024$ at stand 2; $F_{2,29} = 7.759$, $p = 0.002$ at stand 3; $F_{2,29} = 6.688$, $p = 0.004$

311   at stand 4). Logistic regression revealed that only competition intensity, but not tree DBH

312   and age, was a significant predictor of the probability of oak mortality (logistic model χ^2

313     $= 15.13$, $p < 0.001$).

314

315   *3.2. Climate-driven modulation of oak growth*

316   Chronologies of tree-ring growth indices were very similar among decline classes

317   within each of the study stands, and also for all stands considered together (Fig. S2). The

318   descriptive statistics of tree-ring indexed chronologies, calculated separately for every

319   decline class considering all stands together, showed low radial growth rates, especially

320   for dead trees, relatively high values of MS and Rbar, and high values of SNR and EPS.

321   EPS values were greater than 0.90 for all decline classes (Table S1), suggesting a

322   satisfactory replication and an optimum common signal for the three groups of trees.

An assessment of the correlations of monthly climatic time series with tree-ring indexed chronologies showed that the influence of climate (SST 1.2, Prec, and PDSI) on tree growth has been conspicuously varying through time, and the significant correlations were always negative (Fig. 3). Significant correlations with SST 1.2 were found for all decline classes between February to August in the period 1955–1980, and only for healthy trees from March to May in 1981–2006 (Fig. 3A). In 1955–1980, significant correlations with precipitation were found for all decline classes in September, while significant correlations with April-May precipitation were found in 1981–2006, also for all decline classes (Fig. 3B). Correlations with PDSI were significant only for 1981–2002, spanning from August to November of the previous year mostly for dead trees, and from current May to July for all decline classes (Fig. 3C).

Since 1981, correlations between tree-ring growth indices and water availability were relatively homogeneous among decline classes, but variable among stands. Negative effects of April-May precipitation on tree-ring growth were found for all decline classes (Table 3). Soil water excess in previous August-November and current May-July affected radial growth of all decline classes in the majority of stands, as evidence to the negative relation to PDSI.

Moving correlations revealed that April-May precipitation in the study area was negatively related to April-May SST 1.2 during the late 1960s, and positively since 1982, but the association was nearly absent before 1964 and in 1970–1981 (Fig. 4A). In fact, April-May precipitation in northwestern Iberian Peninsula, and particularly in the study area, was strongly positively correlated with April-May SST 1.2 ($r = 0.725$, $p < 0.001$) only for 1981–2006, but not before 1981 (Fig. S3). Moreover, tree-ring chronologies were negatively related to April-May SST 1.2 since the 1950s–1960s and up to the 1980s, even if the effect on growth of healthy trees remained significant up to the 1990s

(Fig. 4A). The negative association between mean tree-ring indexed chronologies and April-May precipitation was significant during 1943–1951, mainly for healthy trees, and since 1981 for all decline classes (Fig. 4B). For the period 1981–2006, April-May precipitation in the study area showed negative correlations with tree-ring growth indices for healthy ($r = -0.654$), declining ($r = -0.647$), and dead trees ($r = -0.636$), all of them highly significant ($p < 0.001$). A negative association between tree-ring growth and previous August-November PDSI has also been found during the last years only (Fig. 4C), which was not significant for healthy trees ($p > 0.05$), but significant for declining ($r = -0.426$, $p = 0.042$), and dead trees ($r = -0.551$, $p = 0.006$), in the period 1981–2003.

3.4. Tree-ring growth patterns and impact of water excess on oak growth

The relative long-term variation of oak growth for healthy, declining, and dead trees slightly differed among the study stands, at least for the period 1921–2001. At stands 1, 2, and 3, all decline classes showed very similar mean tree-ring growth and %LW patterns, except since 2001, in which the growth rates of dead trees become considerably reduced in comparison of those of healthy and declining trees (Figs. S4A, B, and C). At stand 4, however, healthy and declining trees showed very similar mean tree-ring growth and %LW variation, while the correspondence with trees that died were low in the complete period since 1930 (Fig. S4D).

Coupled with the wettest year recorded in the study area, a harsh reduction of tree growth occurred in 2001, mainly for dead trees in comparison to healthy and declining trees (Fig. 5). This reduction of growth was revealed by mean tree-ring widths for the different decline classes (Fig. 5A), coinciding with a conspicuous reduction of mean %LW for dead trees (Fig. 5B), and a maximum proportion of trees with heavily suppressed growth (%LW < 10%) for all decline classes (Fig. 5C). While for healthy and

373 declining classes the amount of trees with heavily suppressed growth suddenly decreased

374 after 2001, growth of trees that died became increasingly reduced.

375

376

377 **4. Discussion**

378 *4.1. Long- and short-term stresses causing the forest decline*

379   Our results fit well to the established conceptual scheme of tree decline process

380 (Pedersen, 1998; Dobbertin, 2005), and support that predisposing factors can affect the

381 vitality of trees during long periods of time, and can increase their sensitivity to further

382 stresses, being every individual able to recover or die, depending on the tree's condition

383 and the severity of the stress. In our study case, oaks predisposed to die by sustained

384 inter-tree competition and recent persistent wetness were more prone to be severely

385 affected by an additional stress, such as a rainfall extreme. Water excess caused long-

386 term stress since the 1980s, which has negatively affected growth of trees from all

387 decline classes, but has had little direct effect on mortality. Extremely wet conditions in

388 2001, the wettest year within the studied period, also resulted in a short-term stress for all

389 decline classes, but mortality was restricted to trees that were predisposed to die, i.e.,

390 those suffering from the most intense inter-tree competition, and more detrimental effects

391 of water excess during previous late summer-autumn.

392   It is likely that the persistent wetness observed in our study area during recent

393 decades induced a permanent latent stress in oaks, which together with the synergistic

394 effects of local competition intensity, predisposed trees to become extremely sensitive to

395 the impact of an additional stress. The individual response of oaks and the manifestation

396 of disease have been variable, depending on local site conditions, and also probably on

397 differences in the tolerance of the affected trees to the underlying stress and their

398   capacity for recovery (Niinemets, 2010). As our results indicated, trees at stand 1 were

399   less susceptible to competition intensity but more to water excess. At stands 2 and 3,

400   however, trees experienced the combined impact of both competition and wetness. By

401   contrast, trees at stand 4 were mainly subjected to the detrimental effects of competition

402   since about 1930, while the impact of the rainfall extreme in 2001 was just limited to

403   trees that died. Symptoms of decline caused by similar mechanisms may have occurred

404   earlier in the study area, probably around 1940, but negative short-term effects of the

405   climatic extreme on tree health are probably more significant now than in the past

406   because the oaks are more predisposed to stress.

407   Such findings contradict the majority of literature on forest dieback, which usually

408   considers forest decline and massive tree mortality episodes to be the result of increasing

409   water deficit (van Mantgem and Stephenson, 2007; Allen et al., 2010; Linares et al.,

410   2010). The occurrence of severe droughts during the active period has been also shown

411   to be a relevant triggering factor for oak decline and death throughout Europe (Amorini

412   et al., 1996; Di Filippo et al., 2010; Doležal et al., 2010). Accordingly, the positive

413   impact of spring-summer rainfall on oak growth is a general feature in Northern, Central,

414   and Southern Europe, with characteristic beneficial effects on radial growth of wet

415   March-May to June-August (García-González and Eckstein, 2003; Rozas, 2005;

416   Friedrichs et al., 2009; Helama et al., 2009). In addition to drought-driven growth decline

417   and forest dieback, our results support that conditions related to water excess and

418   extreme rainfall events can also be limiting for growth and trigger dieback in non water-

419   limited ecosystems, such as rainy deciduous forests

420   In some areas where forest dieback is occurring, trends of increasing moisture and

421   precipitation extremes are evident. For instance, in a previous study of *Q. robur* mortality

422   in northeastern France, a severe reduction in radial growth in the years 1995–1996

423   coincided with an excess of water in the studied forest stand, due to an especially rainy

424   spring in 1995 (Marçais and Bréda, 2006). Likewise, exceptionally rainy conditions in a

425   boreal Siberian forest of *Larix cajanderi* greatly increased the water saturation of the

426   soils, and critically reduced their relative gas diffusivity in declining stands in

427   comparison to non-declining ones (Iwasaki et al., 2010). Even in a semiarid ecosystem, a

428   trend of increasing rainfall during past decades has driven woodland dieback, causing

429   growth decline and massive mortality of the drought-tolerant species *Prosopis caldenia*

430   due to sustained groundwater level rise in the sedimentary plains of the Argentinean

431   Pampas (Bogino and Jobbágy, 2011). Our findings, together with such examples, suggest

432   that climate-driven forest decline, induced by persistent wetness and rainfall extremes,

433   may be more abundant than expected.

434

435   *4.2. Possible causes of water excess restraining oak vitality and survival*

436   Soil water excess, and more frequently strongly fluctuating groundwater levels,

437   contributes to root death and oak decline on alluvial hydromorphic soils in Europe

438   (Oosterbaan and Nabuurs, 1991; Thomas and Hartmann, 1998). Changes in site

439   hydrology that cause a rise of groundwater level or the increased likelihood of flooding

440   significantly contribute to the gradual manifestation of the oak decline syndrome by

441   increasing the predisposition of trees to other biotic or climatically induced stresses

442   (Führer, 1998). In our case, however, the observed change in water regime was entirely

443   of climatic origin, since soils are not hydromorphic but located on gentle slopes,

444   suffering from soil water excess since 1960, and particularly in 1998–2002. Given the

445   seasonal distribution of rainfall in our study area, with a maximum in autumn-winter, a

446   rainy spring may dilate the period with soil water saturation, and the associated stress.

447   Hypoxia is known to be a severe stress for aerobic organisms such as trees, because

448   essential physiological functions like mitochondrial respiration, oxidation, and

449   oxygenation cannot take place. The diffusion resistance of oxygen is over 10,000 times

450   higher in water than in air (Vartapetian and Jackson, 1997), and the concentration of

451   oxygen near the rhizospere of waterlogged oaks is over three times lower than in O_2

452   saturated water (Parelle et al., 2006). Even if severe oxygen deprivation may be expected

453   in temporally flooded soils, *Q. robur* is considered to be tolerant to soil oxygen

454   deficiency, showing adaptations that reduce damage derived from root anaerobic stress.

455   Its main morphological adaptations include the development of structures that enhance

456   oxygen diffusion towards the roots, such as hypertrophied lenticels and adventitious

457   roots (Schmull and Thomas, 2000; Parelle et al., 2006). Additional metabolic

458   adaptations, such as adjustment of root internal carbon metabolism (switch from

459   respiration to alcoholic fermentation), may help to maintain the energetic status of cells

460   during hypoxia (Dreyer, 1994; Gérard et al., 2009). However, these adaptations seem not

461   to be enough to overcome the anaerobic stress experienced by trees in the studied stands.

462   This was probably due to a long-lasting deprivation of oxygen in the rhizosphere that

463   inevitably reduced photosynthetic rates and induced carbon starvation. According to

464   Vartapetian and Jackson (1997), carbohydrate requirements under conditions of anoxia

465   can be as high as 19-fold in order to maintain the cellular energy status normally

466   achieved through the oxidative respiration pathway. A decrease of shoot water potential

467   is expected in *Q. robur* after 15 days of flooding (Alaoui-Sossé et al., 2005), with

468   associated reduction in root hydraulic conductivity, leaf water potential, stomatal

469   conductance, carbon assimilation, and carbon allocation to the roots (Kreuzwieser et al.,

470   2004).

471   When considering additional predisposing factors to tree dieback, a limited

472   nutritional availability to trees in the poor and acidic soils of our study stands would have

473   been aggravated during recent decades by soil water excess. The normal function of the

474   root-mycorrhizal system can be disrupted by the direct impact of abiotic stressors such as

475   anaerobic conditions caused by flooding and waterlogging (Führer, 1998). Transient

476   saturation of soil by water may result in a massive impact on nutrient uptake and

477   consequently on whole tree metabolism, since hypoxia inhibit both the release of mineral

478   nutrients and their uptake by the roots (Kreuzwieser et al., 2004; Rennenberg et al.,

479   2009). The uptake of nitrate and ammonium is strongly reduced after prolonged flooding,

480   and the internal pools of nitrogen compounds dramatically decrease as a consequence of

481   diminished nitrogen uptake rates, suggesting that the compensation capacity for hypoxia

482   is limited too (Kreuzwieser et al., 2002; Alaoui-Sossé et al., 2005). Our retrospective

483   assessment of tree-growth patterns suggests that oaks preconditioned by high

484   competition levels and persistent wetness seem to have a low plasticity, and the damaged

485   oaks fail to compensate for the prolonged hypoxia in the rhizosphere.

486   The coincidence of stressful anoxic conditions with other biotic stressors such as root

487   pathogens or defoliators, whose effects on tree health and survival were not evaluated,

488   would also aggravate the carbon starvation of trees, thus reducing their vitality and

489   increasing death risk. High soil moisture levels may have increased the production and

490   dispersion of *Phytophthora* spp. zoospores in the past, thereby increasing the probability

491   of root infection and damage (Jönsson et al., 2005). However, soil chemical traits in our

492   study stands, i.e., low pH and relatively high aluminium content, are particularly

493   unfavourable for *Phytophthora* infection (Jung et al., 2000; Jönsson et al., 2005). Oak

494   powdery mildew (*Erysiphe alphitoides*) also critically impacts net carbon assimilation of

495   host oaks, mainly by reducing the life-span of heavily infected leaves (Hajji et al., 2009).

496   Powdery mildew is frequent in our study area, and mild overcast conditions are optimal

497   for development of this disease (Gibbs and Greig, 1997). Even if the participation of

498   opportunistic pathogens as additional contributing factors to oak decline is unknown in

499   our case study, an increased impact under a scenario of warmer and wetter climate may

500   be expected in the future (Sturrock et al., 2011).

501

502   *4.3. Influence of large-scale climate variation on regional water availability*

503   The detrimental impact of water excess on oak growth and survival was associated

504   with ENSO influence on regional hydrological regime and water availability. Previous

505   evidence suggested that the strength of ENSO teleconnection to extratropical areas, and

506   particularly to southern Europe, has been changing through time in recent decades

507   (Knippertz et al., 2003; Pozo-Vázquez et al., 2005; Sterl et al., 2007). Our findings agree

508   with such previous studies; oak growth has been sensitive to ENSO since the late 1950s,

509   and linked to water surplus conditions since the mid 1980s. Spring precipitation that

510   apparently increased sensitivity of oaks to water excess during the past decades was

511   strongly associated with SST 1.2 anomalies since 1981. The particularly wet conditions

512   in 1998–2002, which triggered massive oak mortality in the study area, were coupled

513   with the intense 1998–2000 La Niña episode. In addition, a significant positive trend of

514   mean annual temperature was recorded in the study area over the past century (del Río et

515   al., 2011; Rozas and García-González, 2012), and the increasing rainfall trend in the

516   study area may well be linked with climate warming. In most middle and high latitudes

517   of both hemispheres, land precipitation has systematically increased over the 20th

518   century as a direct consequence of global climate warming, since rising temperatures

519   increase evapotranspiration rates, the total content of water vapour in the atmosphere,

520   and the intensity of rainfall (Dai, 2006; Wentz et al., 2007). Extreme precipitation events

521 will become also more common under a warmer climate, with heavy rain events typically

522 increasing during warm periods, and decreasing during cold periods (Allan and Soden,

523 2008). Since water availability may increase, and precipitation extremes may become

524 more frequent and intense under a context of climate warming, forest dieback episodes

525 associated to wetter conditions may become more common in the future. Further

526 assessment of the relative importance of rainfall excess acting as predisposing/triggering

527 factor for oak decline should be performed to elucidate if this climatically-induced

528 dieback is restricted to windward slopes on Atlantic ranges in northwestern Iberian

529 Peninsula, or if it occurs over a wider spectrum of site conditions throughout Europe.

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546 **References**

547

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Table 1. Description of the study stands and sampled trees in the Serra do Suido, NW

Spain. DBH: tree bole diameter at 1.30 m above ground.

	Stand 1	Stand 2	Stand 3	Stand 4
Elevation (m)	770	750	690	610
Aspect (º)	0 (N)	45 (NE)	35 (N-NE)	325 (N-NW)
Mean slope ± SD (º)	11.6 ± 1.2	12.1 ± 0.5	13.6 ± 0.4	12.5 ± 1.6
Mean DBH ± SD (cm)	37.8 ± 7.5	28.4 ± 9.1	31.5 ± 7.9	27.3 ± 6.7
Mean tree age[a] ± SD (yr)	162 ± 18	106 ± 42	100 ± 28	120 ± 22
Total tree abundance (ha^{-1})	305	360	430	455
Total basal area (m^2 ha^{-1})	58.5	47.5	53.4	47.4
Abundance per decline class (%)				
Healthy	21.3	27.8	18.6	46.2
Declining	41.0	16.7	27.9	29.7
Dead	37.7	55.5	53.5	24.1
Basal area per decline class (%)				
Healthy	23.7	28.8	26.2	61.8
Declining	39.9	16.0	27.7	29.5
Dead	36.4	55.2	46.1	8.7

732   [a] Based on 30 cored trees per stand

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Table 2. Summary of *F* values from two-way ANOVA for the differences in tree diameter (DBH), tree age, and competition intensity (CI), among decline classes and stands (error term *df* = 108). Mean (± SE) values for DBH, tree age, and CI, for healthy, declining, and dead trees, and for the four study stands. Different superscript letters indicate significant differences ($p < 0.05$) among decline classes and stands using Tukey's HSD test.

	df	DBH (cm)	Tree age (yr)	CI
Factor				
Decline class	2	13.58***	2.28	11.77***
Stand	3	12.23***	21.24***	4.98**
Decline × stand	6	1.28	0.34	0.86
Model	11	6.59***	6.35***	4.03***
Decline class				
Healthy		34.5 ± 1.1 [A]	129.5 ± 5.4 [A]	1.65 ± 0.17 [A]
Declining		32.2 ± 1.4 [AB]	116.0 ± 5.8 [A]	1.94 ± 0.23 [A]
Dead		26.8 ± 1.3 [B]	120.4 ± 6.3 [A]	3.12 ± 0.29 [B]
Stand				
1		37.8 ± 1.4 [A]	161.8 ± 3.3 [A]	1.48 ± 0.18 [A]
2		28.4 ± 1.6 [B]	106.2 ± 7.7 [BC]	2.16 ± 0.32 [AB]
3		31.5 ± 1.4 [B]	100.1 ± 5.2 [C]	2.47 ± 0.29 [B]
4		27.3 ± 1.2 [B]	119.8 ± 4.0 [B]	2.77 ± 0.30 [B]

742   * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

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747 **Table 3**. Pearson's correlations for the relationships between tree-ring growth indices

748 from healthy, declining, and dead oaks at the four study stands; and climate predictors

749 for water availability. Climate predictors are total precipitation (Prec, period 1981-2006),

750 and mean Palmer drought severity index (PDSI, period 1981-2002). N: number of years.

Decline class	Climatic predictor	N	Stand 1	Stand 2	Stand 3	Stand 4
Healthy	Apr-May Prec	26	–0.684***	–0.598***	–0.668***	–0.459*
	Aug-Nov(–1) PDSI	23	–0.274	–0.479*	–0.418*	–0.024
	May-Jul PDSI	22	–0.470*	–0.491*	–0.526**	–0.351
Declining	Apr-May Prec	26	–0.686***	–0.582**	–0.644***	–0.529**
	Aug-Nov(–1) PDSI	23	–0.495*	–0.435*	–0.386	–0.248
	May-Jul PDSI	22	–0.602**	–0.499*	–0.499*	–0.465*
Dead	Apr-May Prec	26	–0.647***	–0.569**	–0.537**	–0.636***
	Aug-Nov(–1) PDSI	23	–0.505*	–0.556**	–0.574**	–0.359
	May-Jul PDSI	22	–0.488*	–0.485*	–0.401	–0.566**

751 * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

752
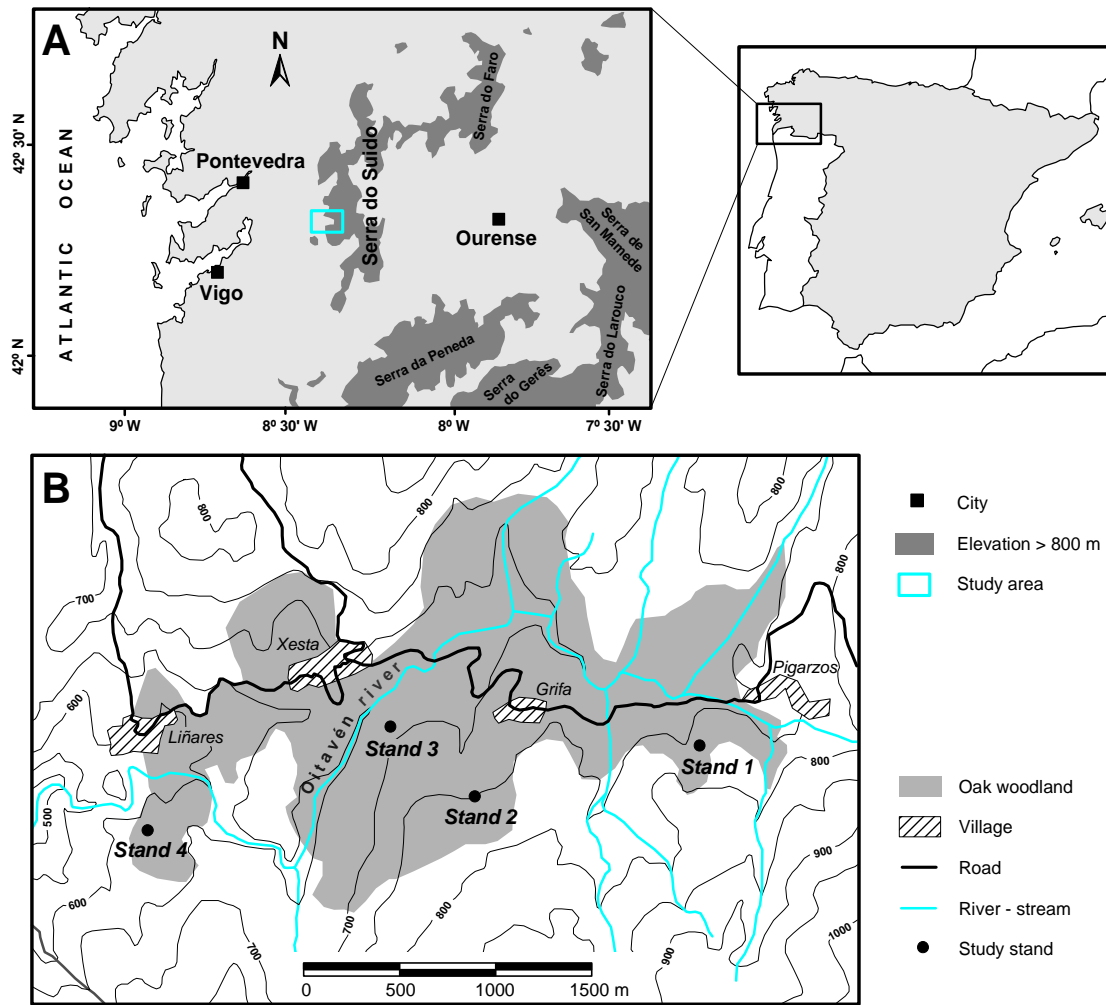
Fig. 1. (**A**) Study area location on the Serra do Suido, NW Iberian Peninsula, and (**B**) location of the four study stands within the declining oak woodland. Contour lines indicate 50 m elevation intervals.
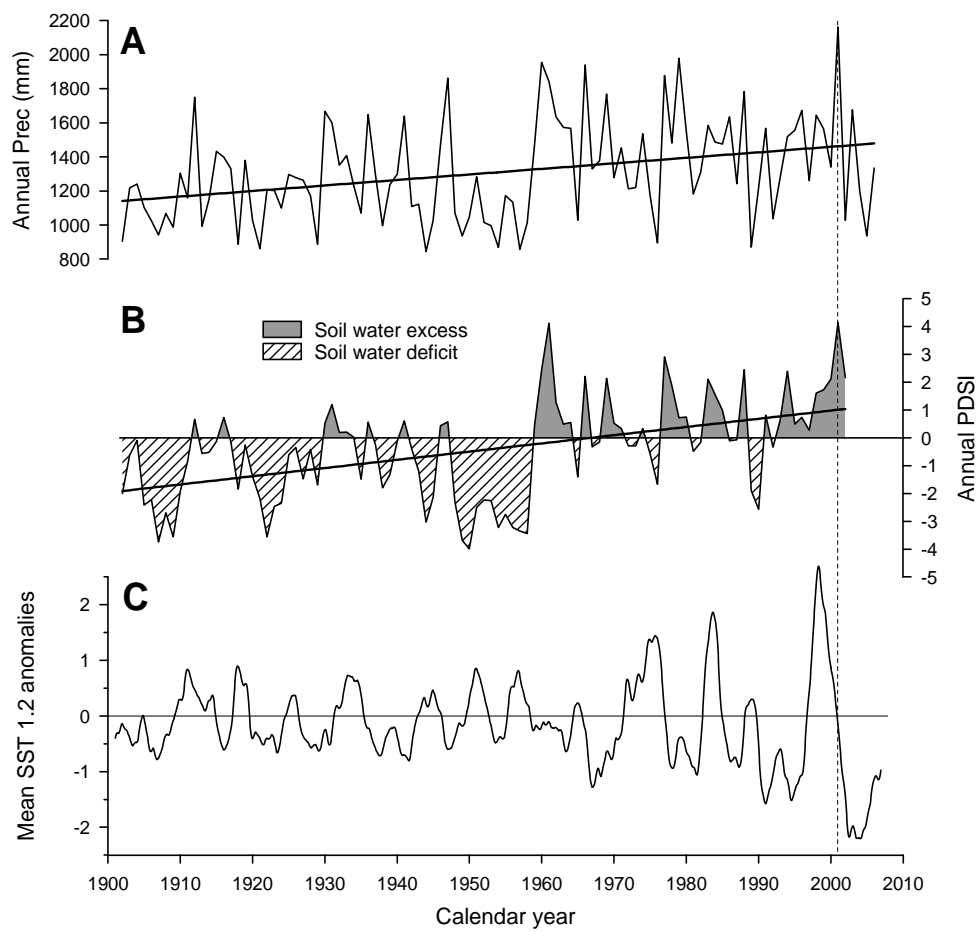
Fig. 2. Temporal variation of (**A**) annual precipitation (Prec), (**B**) annual Palmer drought severity index (PDSI) in the study area, and (**C**) 21-month running means of SST 1.2 anomalies. The linear trends for Prec and PDSI are shown. Periods of soil water deficit and excess, according to annual PDSI, are highlighted. Vertical dashed line highlights the wettest year 2001.
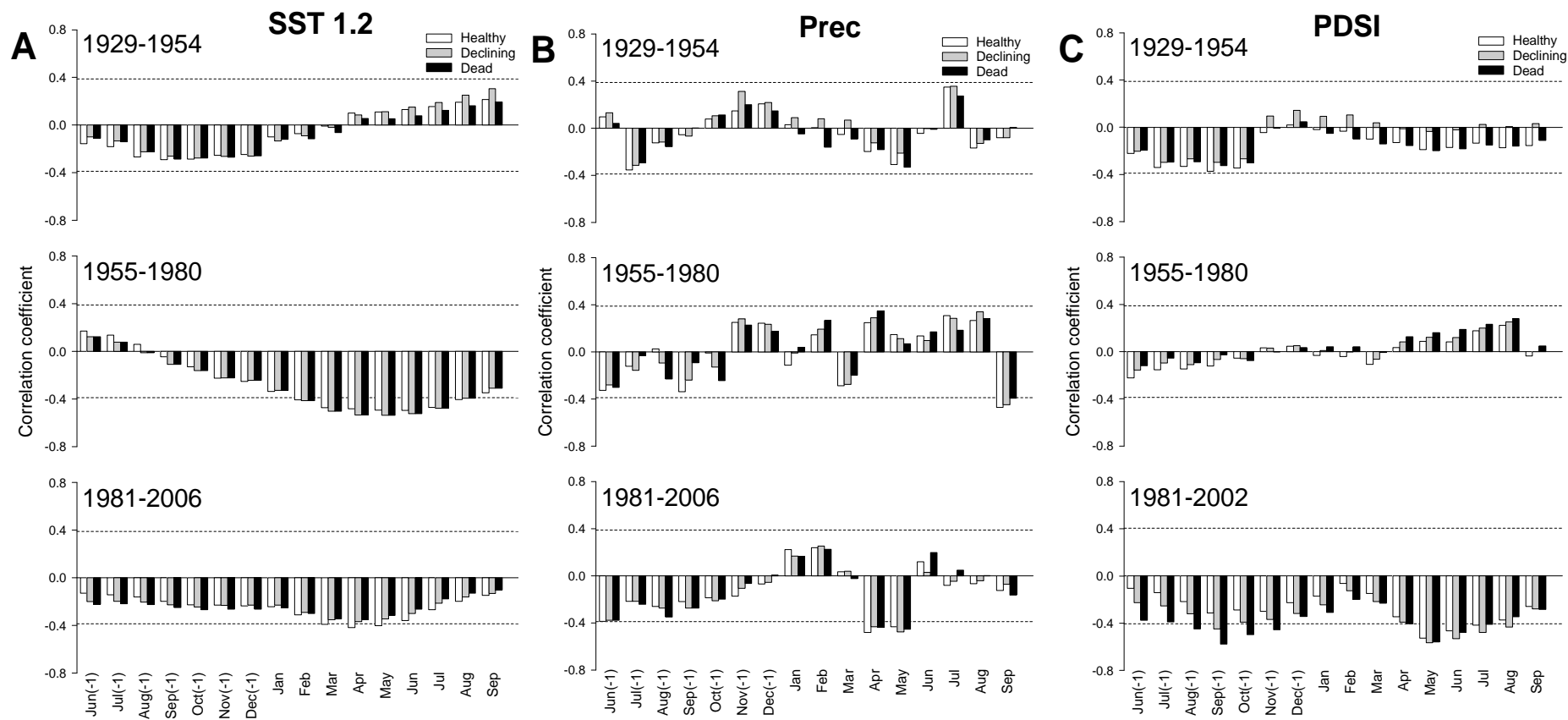
Fig. 3. Correlations between tree-ring indexed chronologies for healthy, declining, and dead trees; and monthly (**A**) SST 1.2, (**B**) Prec, and (**C**) PDSI in three consecutive periods. Horizontal dashed lines indicate the significance level ($p < 0.05$) for correlations.
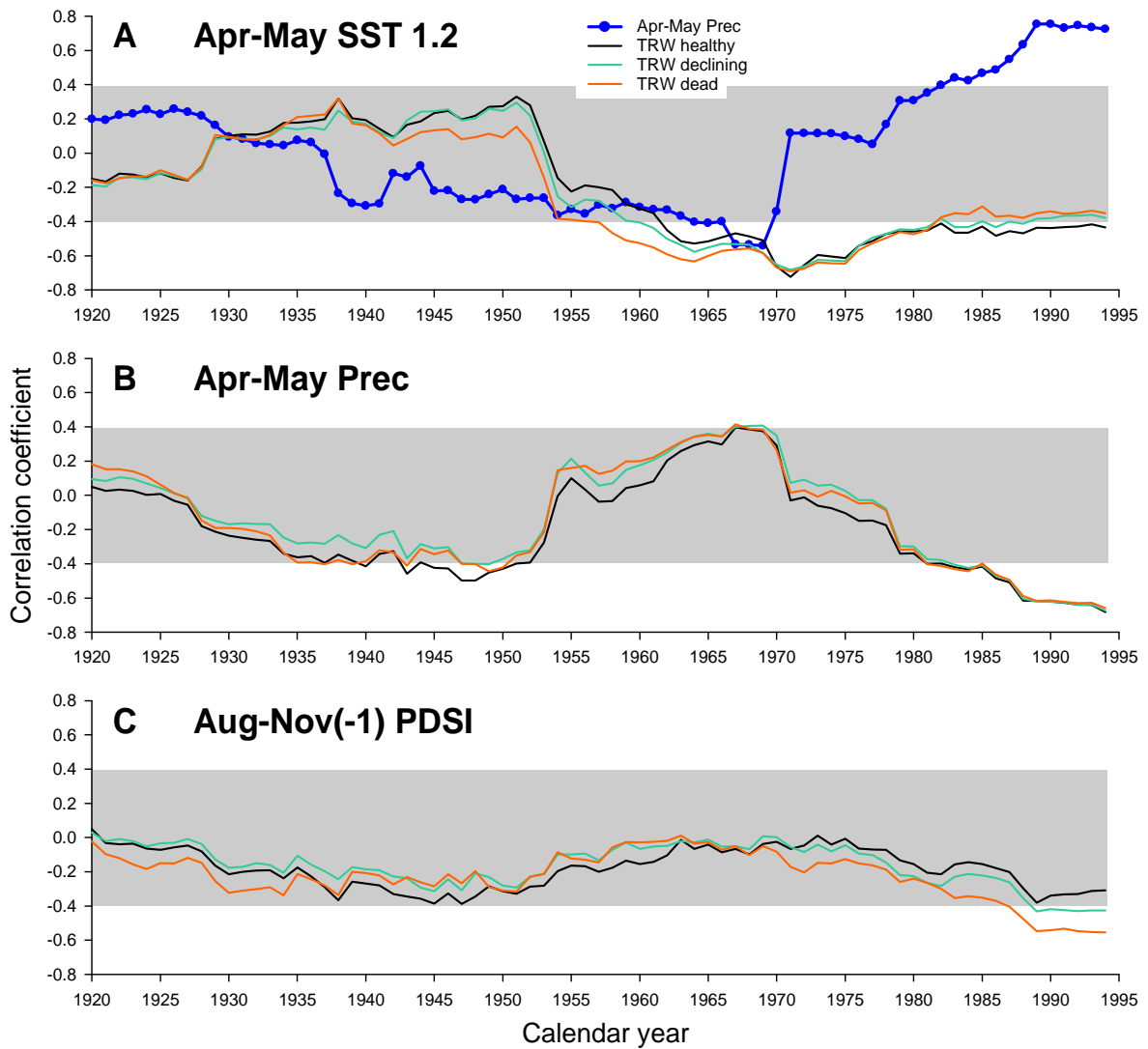
Fig. 4. 25-yr moving correlations between April-May precipitation in the study area and tree-ring width (TRW) chronologies for healthy, declining and dead trees, with (**A**) April-May SST 1.2 anomalies, (**B**) April-May precipitation, and (**C**) previous August-November PDSI. Each correlation represents the central year of the interval. Correlations within the shaded area are not significant at the $p = 0.05$ level.
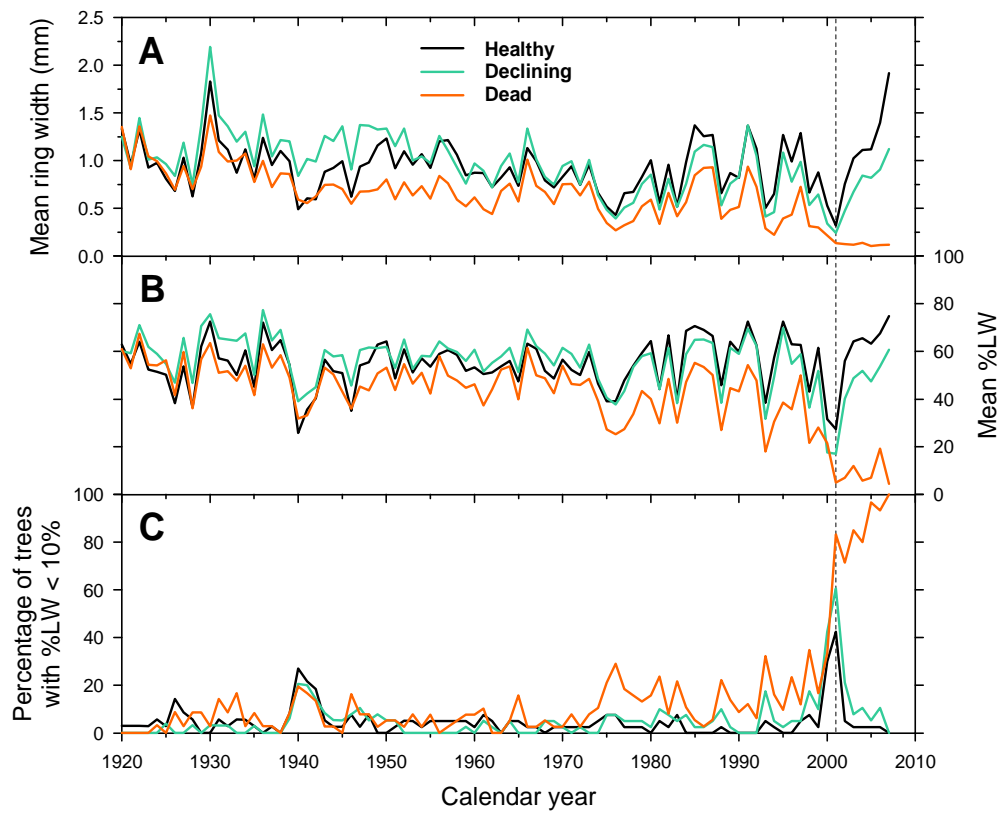
Fig. 5. Mean tree-ring width chronologies (**A**), tree-ring indexed chronologies (**B**), mean %LW chronologies (**C**), and percentage distributions of trees showing heavily suppressed growth (i.e. %LW < 10%; **D**), for healthy, declining, and dead trees. Vertical dashed line highlights the wettest year 2001.

Supplementary material

Table S1

Summary statistics for the tree-ring indexed chronologies for healthy, declining, and dead trees. All chronologies were calculated from 80 cores sampled from 40 trees.

	Healthy	Declining	Dead
Chronology period	1864–2007	1867–2007	1856–2006
Optimum common period	1920–2005	1942–2006	1900–1989
MRW (mm)	1.053	1.035	0.855
SD (mm)	0.720	0.781	0.669
AC	0.652	0.705	0.716
MS	0.287	0.248	0.272
Rbar	0.327	0.345	0.274
SNR	16.046	17.409	9.056
EPS	0.941	0.946	0.901

MRW: mean ring width; SD: standard deviation; AC: first order autocorrelation; MS: mean sensitivity;

Rbar: mean between trees correlation; SNR: signal to noise ratio; EPS: expressed population signal.
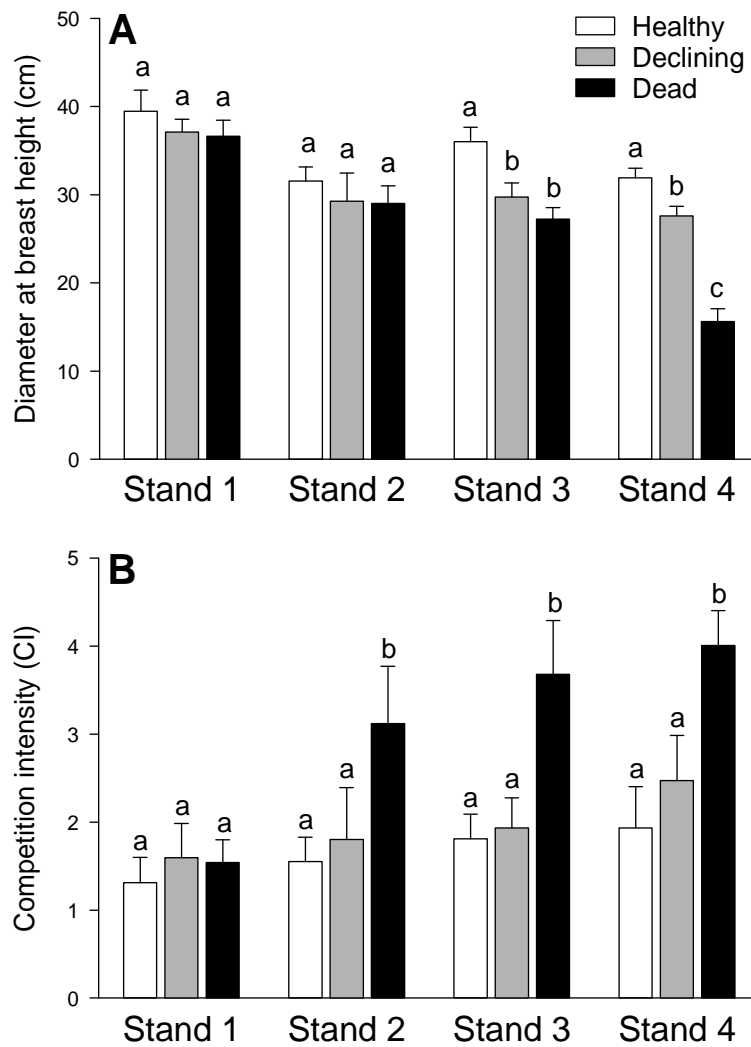
Fig. S1. Differences in mean (+ SE) bole diameter at breast height (A) and competition intensity (B) among decline classes at the four study stands. Different letters within each stand indicate significant differences ($p < 0.05$) among healthy, declining, and dead trees, according to Tukey's HSD *post hoc* test.
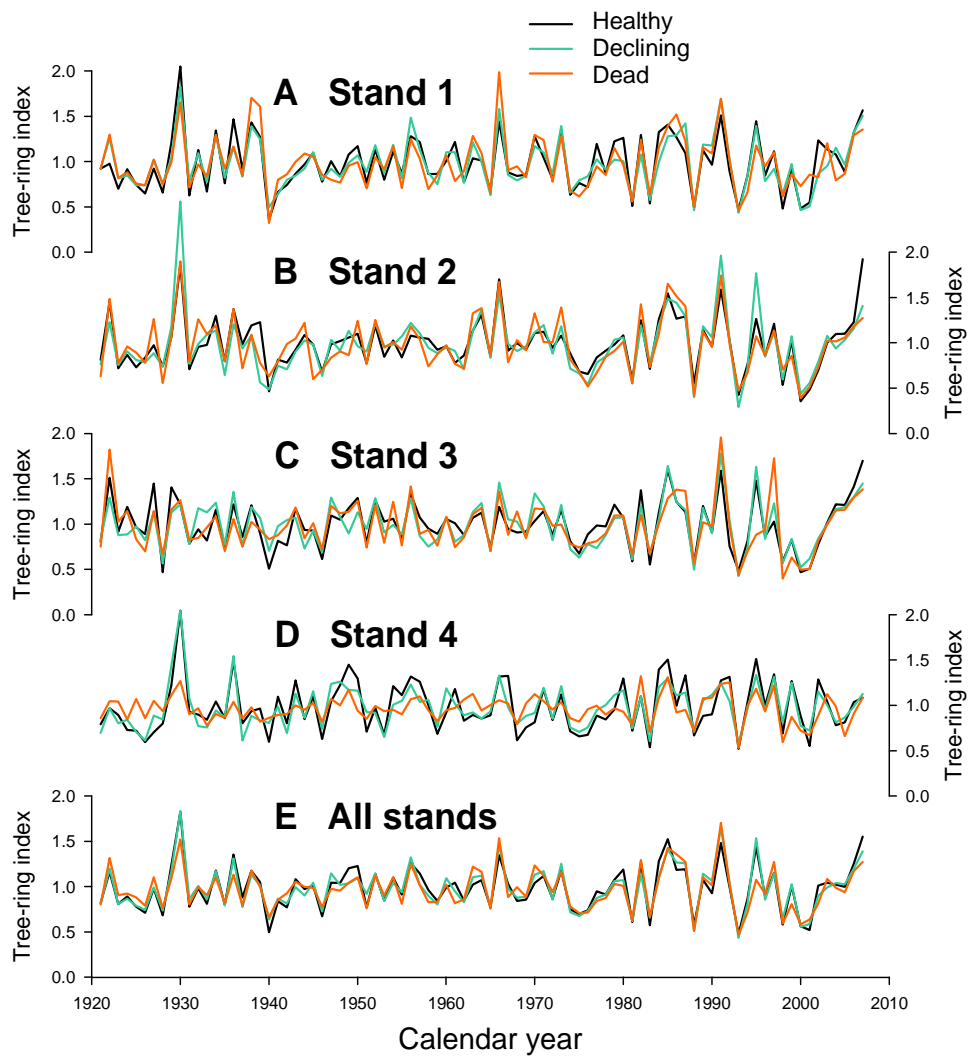
Fig. S2. Mean tree-ring indexed chronologies for healthy, declining, and dead trees at stands 1 (**A**), 2 (**B**), 3 (**C**), and 4 (**D**), and at all stands together (**E**).
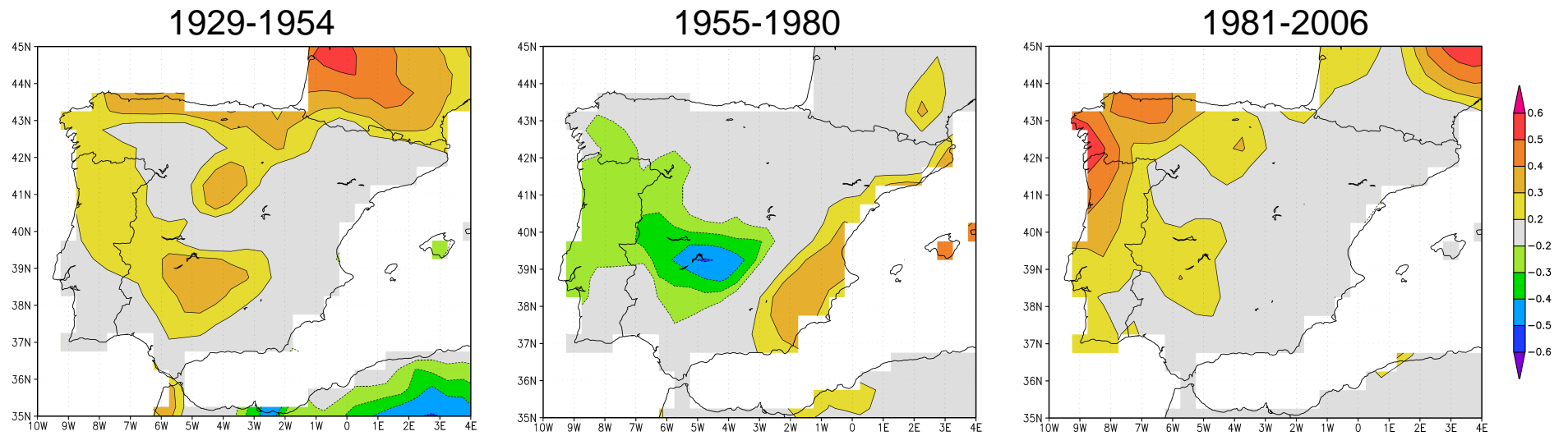
Fig. S3. Spatial field correlations between April-May precipitation in the Iberian Peninsula, and the April-May SST 1.2 anomalies in 1929–1954, 1955–1980, and 1981–2006. Values above 0.4, and below –0.4, are statistically significant ($p < 0.05$).
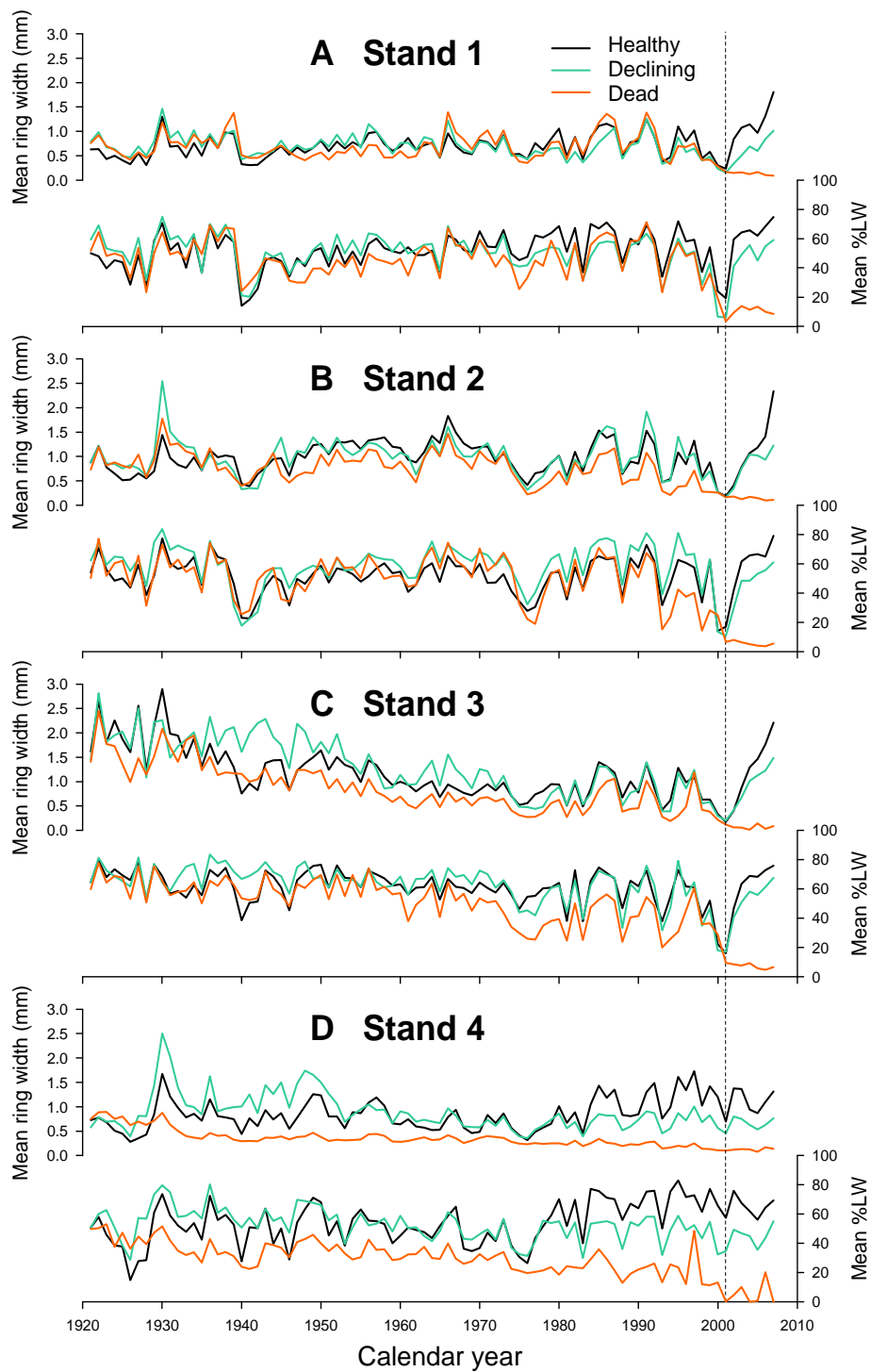
Fig. S4. Mean tree-ring width chronologies, and mean %LW chronologies for healthy, declining, and dead trees in stands 1 (**A**), 2 (**B**), 3 (**C**), and 4 (**D**). Vertical dashed line highlights the wettest year 2001.