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Too wet for oaks? Inter-tree competition and recent persistent
wetness predispose oaks to rainfall-induced dieback in Atlantic
rainy forest

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22 **Abstract**

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

48

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

51

52 **1. Introduction**

53 Increasing drought frequency and duration are considered among the main causes of
54 climatically-induced physiological stress and increased tree death under a context of
55 global climate warming (van Mantgem and Stephenson, 2007). Numerous examples
56 worldwide illustrate the role of water deficit as a triggering factor for forest decline,
57 mainly in water-limited ecosystems where forests are increasingly responding to ongoing
58 warming and drying (see review by Allen et al., 2010). Tree growth decline and dieback
59 episodes in southern Europe are also commonly associated with long-term trends of
60 falling water availability and/or short-term drought events, and this is contributing to
61 forest decline under Mediterranean climate, where summer drought is the main factor
62 limiting tree growth and survival (Di Filippo et al., 2010; Linares et al., 2010). Drought
63 stress could be thought to be a primary cause for dieback of forest trees near the
64 boundary between the Atlantic and Mediterranean biogeographical regions, as has been
65 newly found in conifer forests of the northeastern Iberian Peninsula (Camarero et al.,
66 2011; Hereş et al., 2012).

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

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

83 Pedunculate oak (*Quercus robur*) is a dominant tree species in temperate deciduous
84 forests throughout Europe, which is at its south-western range boundary in northern
85 Spain, and is among the tree species most frequently showing symptoms of decline
86 (Gibbs and Greig, 1997; Führer, 1998; Thomas et al., 2002). The climatic stressors
87 recurrently evidenced as related to *Q. robur* decline are winter-spring frosts and summer
88 droughts (Amorini et al., 1996; Helama et al., 2009; Di Filippo et al., 2010; Doležal et
89 al., 2010), which can respectively cause direct damage to the growing tissues, and limit
90 photosynthetic rates during the active period. In addition, this species is known to be
91 relatively intolerant to drought because of its vulnerability to air embolism (Bréda et al.,
92 1993; Cochard et al., 1992; Thomas and Gausling, 2000), but it displays morphological
93 and physiological adaptations that confer tolerance to waterlogging and root hypoxia, in
94 comparison to other coexisting deciduous tree species (Dreyer, 1994; Schnull and
95 Thomas, 2000; Parelle et al., 2006). In a recent work, we showed that El Niño-Southern
96 Oscillation (ENSO) is controlling regional hydrological regime and *Q. robur* radial
97 growth in northwest Spain (Rozas and García-González, 2012). We can therefore expect
98 that growth decline and dieback of north-western Iberian populations of this species
99 would be related to variability in regional water conditions, which are at least partially
100 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

126

127 **2. Materials and methods**

128 *2.1. Study area*

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

139 For this study, we selected the largest wooded sector in the Serra do Suido, with 385
140 ha of oak woodland covering the area between 42°22'40"–42°23'50" N and 08°21'10"–
141 08°23'45" W, and ranging 580–800 m in elevation (Fig. 1B). This area comprises forest
142 stands of varying tree density and clearings occupied by upland heath, pasture, bogs, and
143 streams. Soils are nutrient-poor and narrow Lithic and Umbric Leptosols and Epileptic
144 Umbrisols, generally less than 40 cm in depth, reaching exceptionally up to 80 cm in
145 ravine bottoms (Calvo de Anta and Macías Vazquez, 2002). Soils are acidic (pH 3.2–
146 4.3), with a high organic matter content (13.9–30.7%), and with relatively high
147 aluminium content (151.1–396.6 mg kg⁻¹) and cation exchange capacities (77.9–197.4
148 mmol_c kg⁻¹).

149

150 *2.2. Climate data and climatic variation*

151 We used monthly gridded time series for total precipitation (Prec, CRU TS 3 data set,
152 $0.5^\circ \times 0.5^\circ$, period 1901–2006), and Palmer drought severity index (PDSI, CRU self-
153 calibrating PDSI data set, $0.5^\circ \times 0.5^\circ$, 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 0.5° latitude \times 0.5° 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 $0\text{--}10^\circ$ S, $90\text{--}80^\circ$ 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°C for 1901–2006, ranging between 6.0°C in January and 18.7°C 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; $y = 3.245x - 5030.31$; $n = 105$; $r^2 = 0.111$; $p < 0.001$), as did mean
175 annual PDSI (Fig. 2B; $y = 0.029x - 58.03$; $n = 101$; $r^2 = 0.232$; $p < 0.001$). An important

176 increase in water availability has been found since 1960; annual precipitation increased
177 from 1,194 mm in 1901–1959 to 1,458 mm in 1960–2006. Soil water availability also
178 changed from a net water deficit in 1901–1959 to a net excess of water in 1960–2002.
179 The period 1993–2002 was the longest one with sustained soil water excess, which was
180 particularly pronounced in 1998–2002, and particularly rainy conditions were recorded in
181 2001, with 2,163 mm in annual precipitation, and 4.14 in annual PDSI. This wet period
182 was coupled with the longest and most intense La Niña phase, which extended from July
183 1998 to February 2001, and can be recognized as a pronounced positive peak of mean
184 SST 1.2 anomalies (Fig. 2C).

185

186 *2.3. Sampling design*

187 We performed a replicated sampling in four representative study stands located at
188 elevations ranging between 610 and 770 m, mainly facing north, and with mean slopes of
189 11.6–13.6° (Table 1; Fig. 1B). The first symptoms of individual tree decline (i.e., leaf
190 yellowing and partial crown lightning in several trees) in these stands were identified in
191 1998, but generalized evidence of tree dieback was observed in 2002–2003, and massive
192 tree death occurred since 2005. In 2007, a study plot of 60 m × 70 m was randomly
193 established within each stand, and all living and dead oaks found within the plots were
194 mapped with a laser total station (Pentax® R-325NX). All trees were tagged, their DBH
195 (stem diameter at 1.3 m above ground) measured, and their crown status registered
196 following a previously established rating for decline (Balci and Halmschlager, 2003),
197 which considers three classes: healthy, declining, and dead. Healthy trees were those
198 without symptoms of decline or only slightly damaged, with dieback of some tips of
199 branches, and slight crown transparency (< 25%). Declining trees were moderately to
200 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, cm²) 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):

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

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 ± 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,

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

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 35°N–45°N, longitude 10°W–4°E) 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/>).

294

295

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.

323 An assessment of the correlations of monthly climatic time series with tree-ring
324 indexed chronologies showed that the influence of climate (SST 1.2, Prec, and PDSI) on
325 tree growth has been conspicuously varying through time, and the significant correlations
326 were always negative (Fig. 3). Significant correlations with SST 1.2 were found for all
327 decline classes between February to August in the period 1955–1980, and only for
328 healthy trees from March to May in 1981–2006 (Fig. 3A). In 1955–1980, significant
329 correlations with precipitation were found for all decline classes in September, while
330 significant correlations with April-May precipitation were found in 1981–2006, also for
331 all decline classes (Fig. 3B). Correlations with PDSI were significant only for 1981–
332 2002, spanning from August to November of the previous year mostly for dead trees, and
333 from current May to July for all decline classes (Fig. 3C).

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

340 Moving correlations revealed that April-May precipitation in the study area was
341 negatively related to April-May SST 1.2 during the late 1960s, and positively since 1982,
342 but the association was nearly absent before 1964 and in 1970–1981 (Fig. 4A). In fact,
343 April-May precipitation in northwestern Iberian Peninsula, and particularly in the study
344 area, was strongly positively correlated with April-May SST 1.2 ($r = 0.725$, $p < 0.001$)
345 only for 1981–2006, but not before 1981 (Fig. S3). Moreover, tree-ring chronologies
346 were negatively related to April-May SST 1.2 since the 1950s–1960s and up to the
347 1980s, even if the effect on growth of healthy trees remained significant up to the 1990s

348 (Fig. 4A). The negative association between mean tree-ring indexed chronologies and
349 April-May precipitation was significant during 1943–1951, mainly for healthy trees, and
350 since 1981 for all decline classes (Fig. 4B). For the period 1981–2006, April-May
351 precipitation in the study area showed negative correlations with tree-ring growth indices
352 for healthy ($r = -0.654$), declining ($r = -0.647$), and dead trees ($r = -0.636$), all of them
353 highly significant ($p < 0.001$). A negative association between tree-ring growth and
354 previous August-November PDSI has also been found during the last years only (Fig.
355 4C), which was not significant for healthy trees ($p > 0.05$), but significant for declining (r
356 $= -0.426$, $p = 0.042$), and dead trees ($r = -0.551$, $p = 0.006$), in the period 1981–2003.

357

358 *3.4. Tree-ring growth patterns and impact of water excess on oak growth*

359 The relative long-term variation of oak growth for healthy, declining, and dead trees
360 slightly differed among the study stands, at least for the period 1921–2001. At stands 1,
361 2, and 3, all decline classes showed very similar mean tree-ring growth and %LW
362 patterns, except since 2001, in which the growth rates of dead trees become considerably
363 reduced in comparison of those of healthy and declining trees (Figs. S4A, B, and C). At
364 stand 4, however, healthy and declining trees showed very similar mean tree-ring growth
365 and %LW variation, while the correspondence with trees that died were low in the
366 complete period since 1930 (Fig. S4D).

367 Coupled with the wettest year recorded in the study area, a harsh reduction of tree
368 growth occurred in 2001, mainly for dead trees in comparison to healthy and declining
369 trees (Fig. 5). This reduction of growth was revealed by mean tree-ring widths for the
370 different decline classes (Fig. 5A), coinciding with a conspicuous reduction of mean
371 %LW for dead trees (Fig. 5B), and a maximum proportion of trees with heavily
372 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 rhizosphere of waterlogged oaks is over three times lower than in O₂
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.

530

531

532

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

731 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 (°)	0 (N)	45 (NE)	35 (N-NE)	325 (N-NW)
Mean slope \pm SD (°)	11.6 \pm 1.2	12.1 \pm 0.5	13.6 \pm 0.4	12.5 \pm 1.6
Mean DBH \pm SD (cm)	37.8 \pm 7.5	28.4 \pm 9.1	31.5 \pm 7.9	27.3 \pm 6.7
Mean tree age ^a \pm SD (yr)	162 \pm 18	106 \pm 42	100 \pm 28	120 \pm 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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736 **Table 2.** Summary of F values from two-way ANOVA for the differences in tree
 737 diameter (DBH), tree age, and competition intensity (CI), among decline classes and
 738 stands (error term $df = 108$). Mean (\pm SE) values for DBH, tree age, and CI, for healthy,
 739 declining, and dead trees, and for the four study stands. Different superscript letters
 740 indicate significant differences ($p < 0.05$) among decline classes and stands using
 741 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 \times 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 * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

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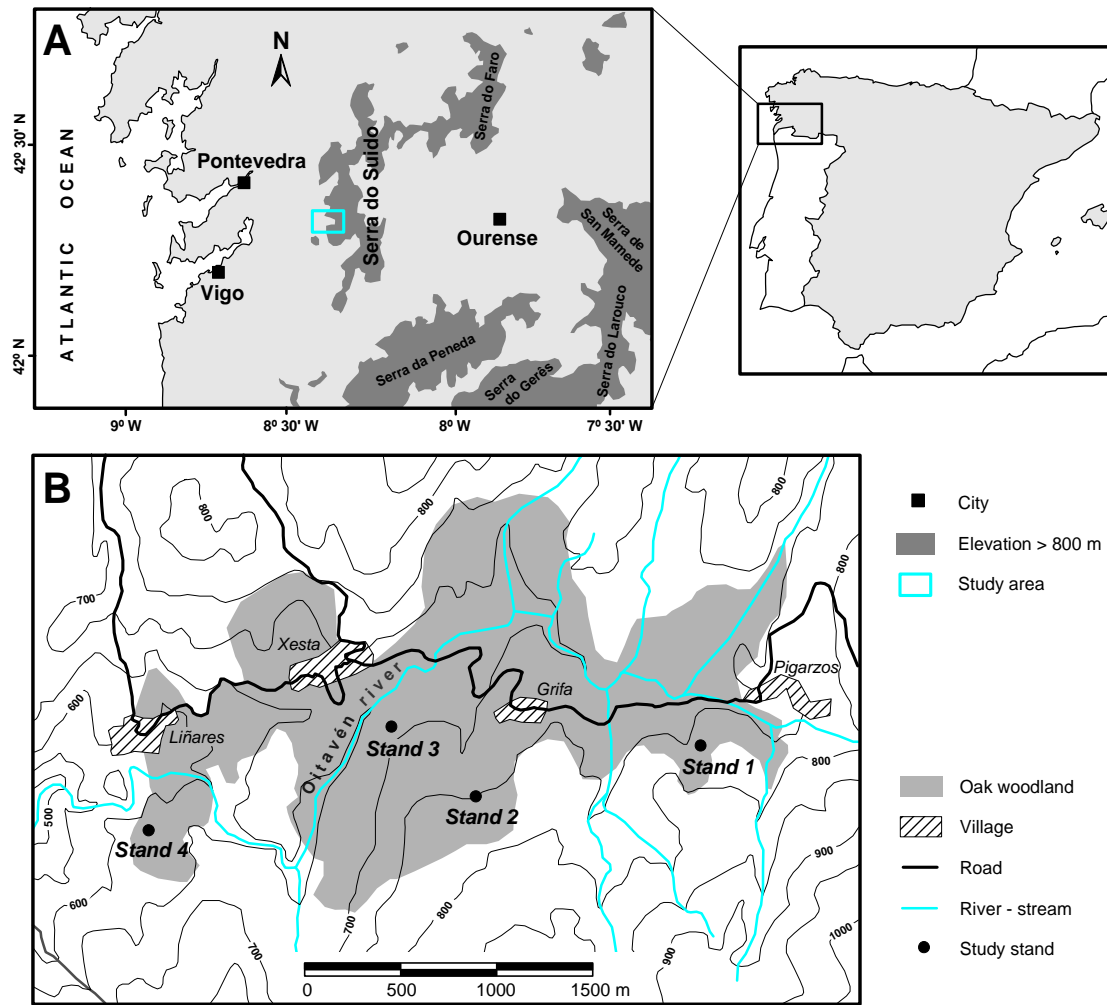


Fig. 1. (A) Study area location on the Serra do Suido, NW Iberian Peninsula, and (B) location of the four study stands within the declining oak woodland. Contour lines indicate 50 m elevation intervals.

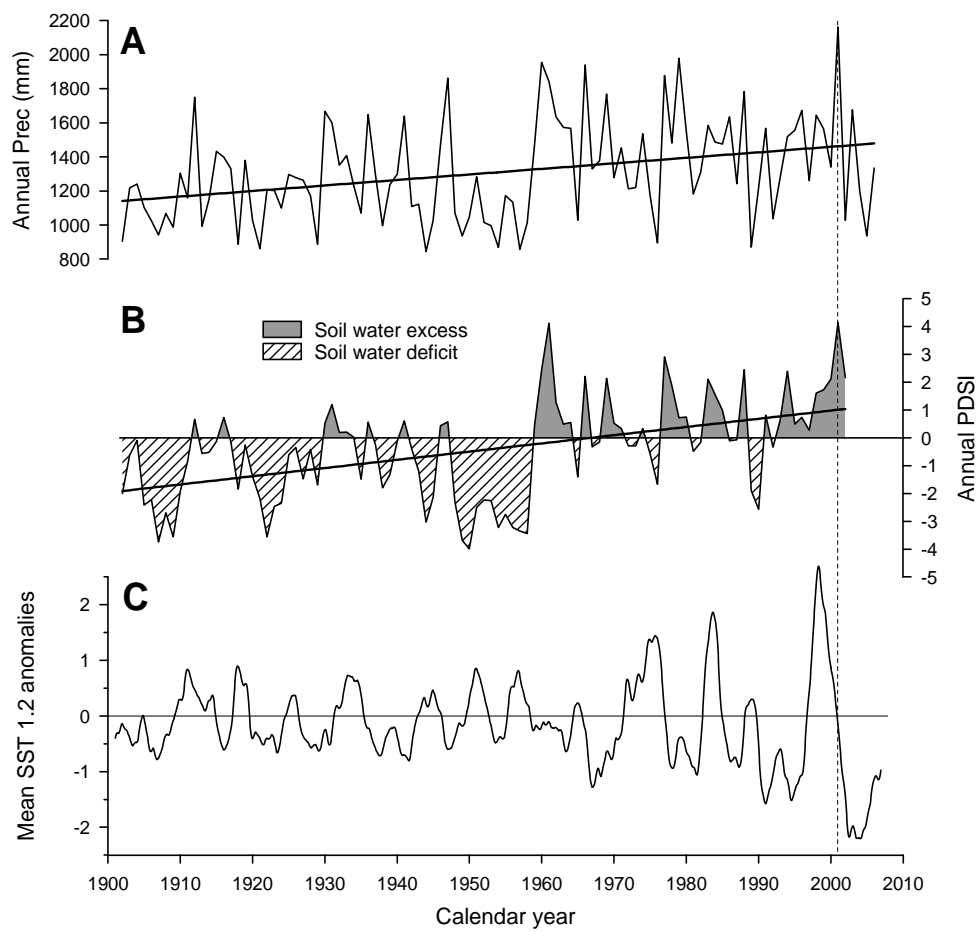


Fig. 2. Temporal variation of (A) annual precipitation (Prec), (B) annual Palmer drought severity index (PDSI) in the study area, and (C) 21-month running means of SST 1.2 anomalies. The linear trends for Prec and PDSI are shown. Periods of soil water deficit and excess, according to annual PDSI, are highlighted. Vertical dashed line highlights the wettest year 2001.

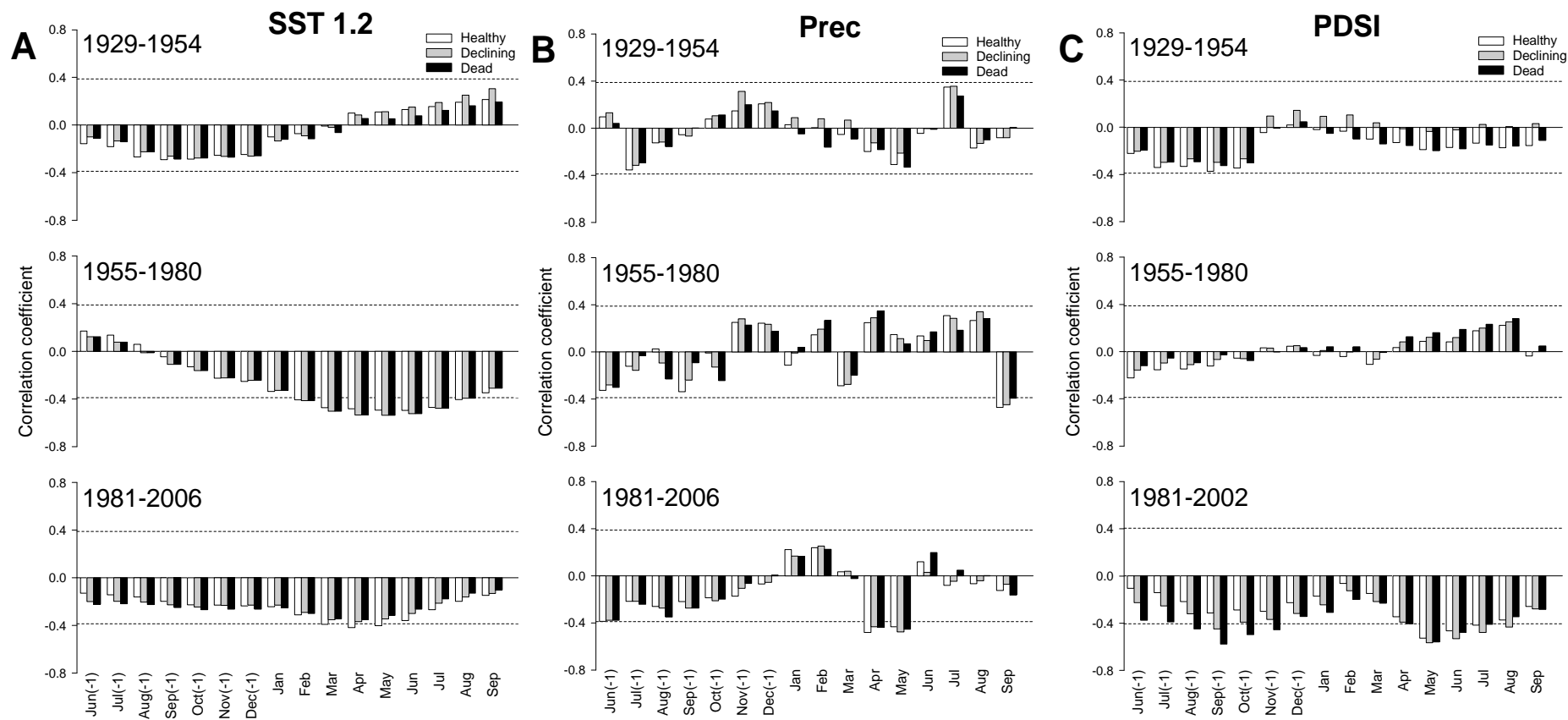


Fig. 3. Correlations between tree-ring indexed chronologies for healthy, declining, and dead trees; and monthly (A) SST 1.2, (B) Prec, and (C) PDSI in three consecutive periods. Horizontal dashed lines indicate the significance level ($p < 0.05$) for correlations.

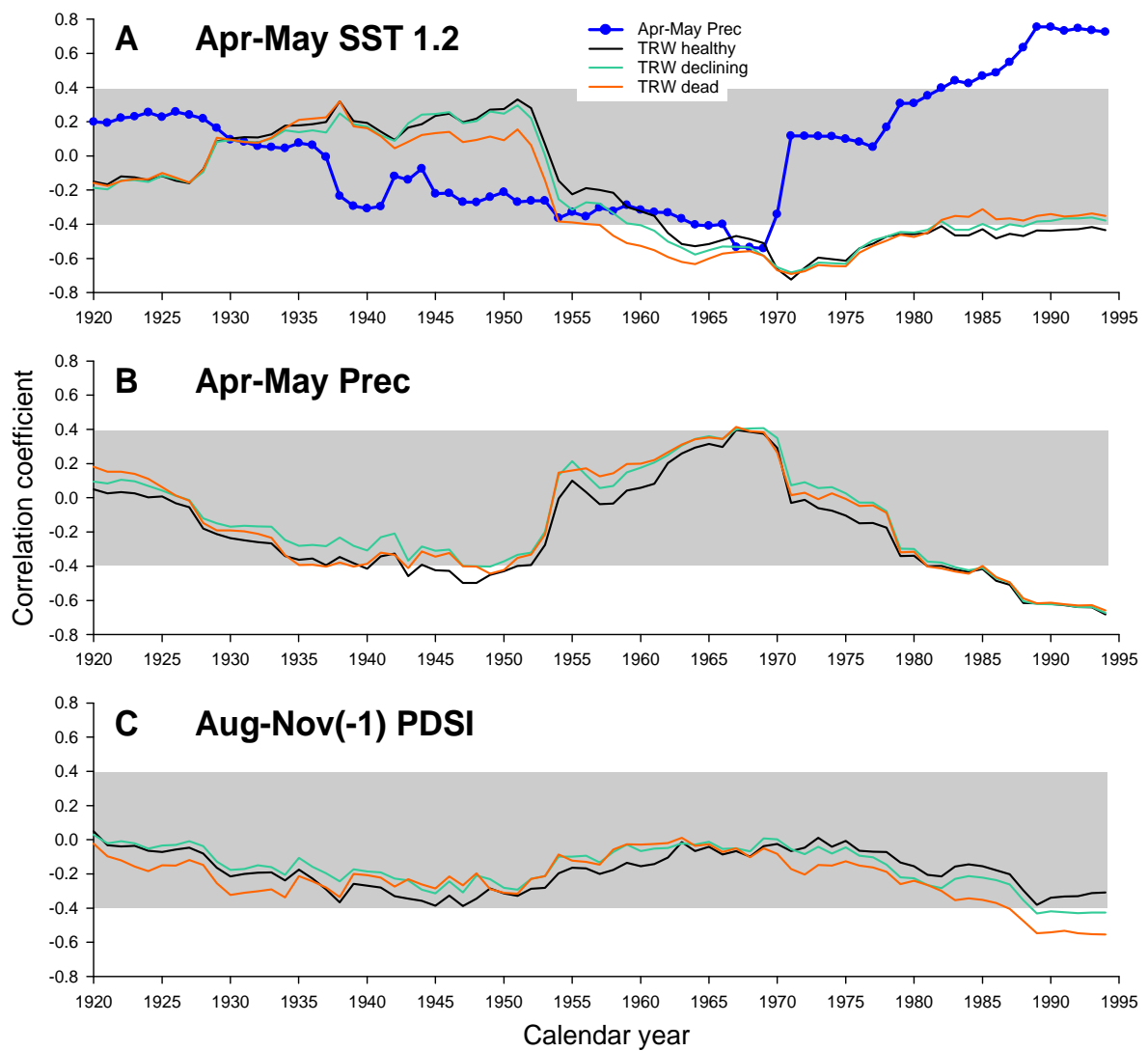


Fig. 4. 25-yr moving correlations between April-May precipitation in the study area and tree-ring width (TRW) chronologies for healthy, declining and dead trees, with (A) April-May SST 1.2 anomalies, (B) April-May precipitation, and (C) previous August-September PDSI. Each correlation represents the central year of the interval. Correlations within the shaded area are not significant at the $p = 0.05$ level.

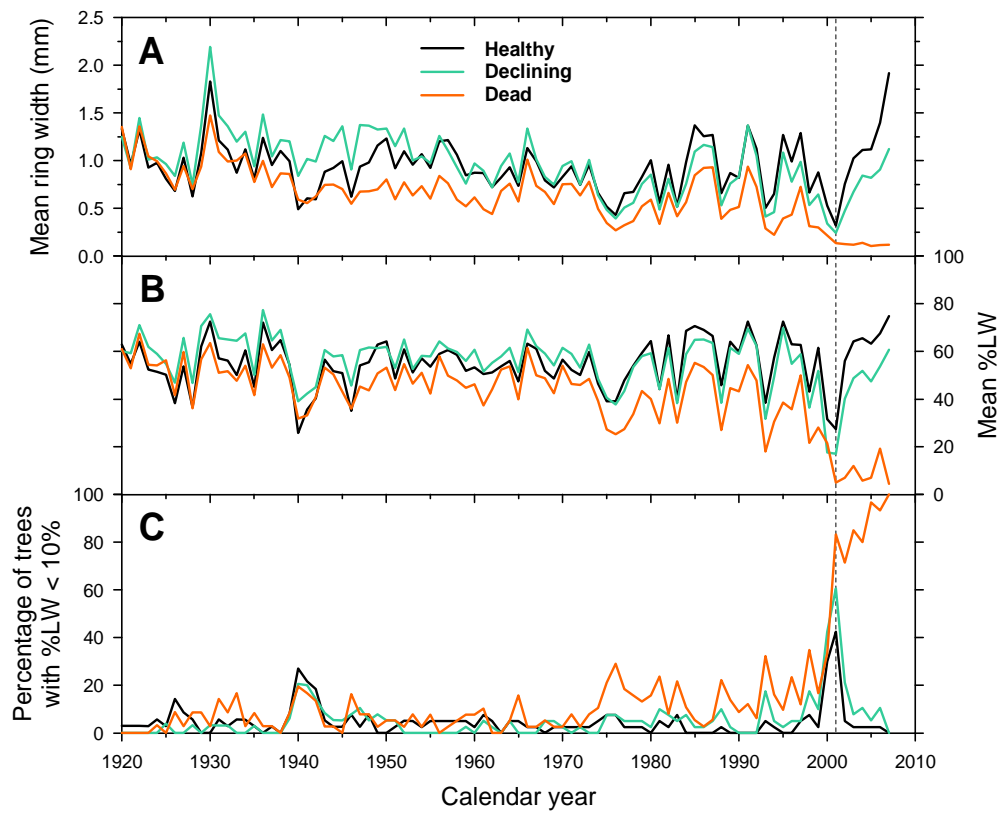


Fig. 5. Mean tree-ring width chronologies (A), tree-ring indexed chronologies (B), mean %LW chronologies (C), and percentage distributions of trees showing heavily suppressed growth (i.e. %LW < 10%; D), for healthy, declining, and dead trees. Vertical dashed line highlights the wettest year 2001.

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.

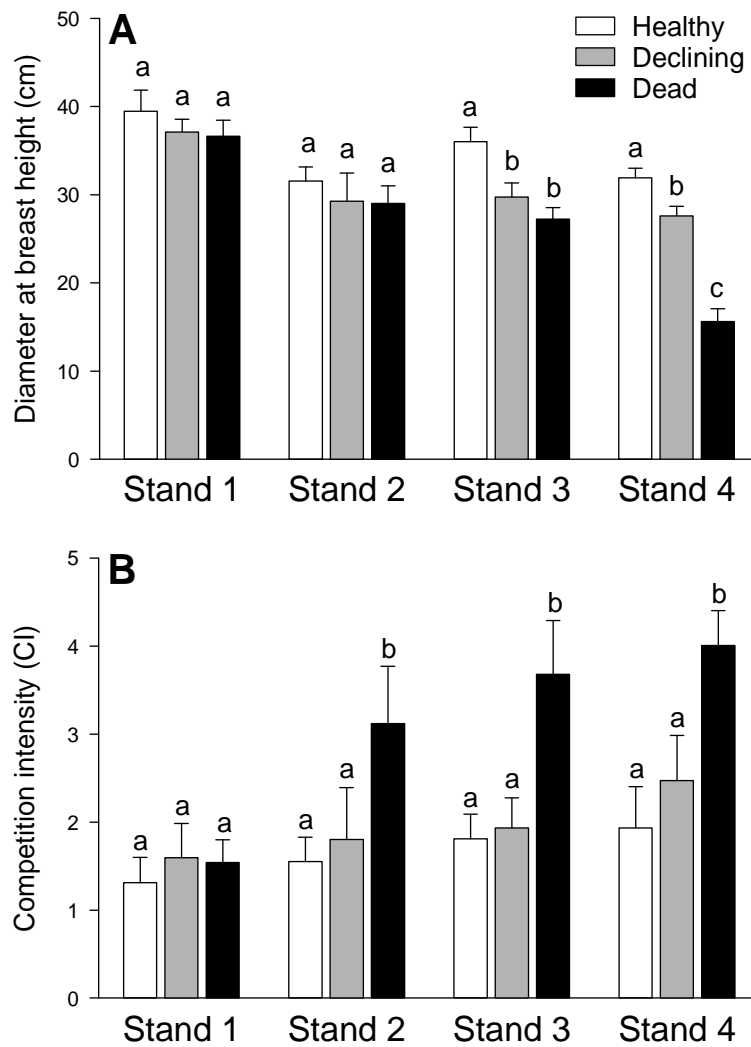


Fig. S1. Differences in mean (+ SE) bole diameter at breast height (A) and competition intensity (B) among decline classes at the four study stands. Different letters within each stand indicate significant differences ($p < 0.05$) among healthy, declining, and dead trees, according to Tukey's HSD *post hoc* test.

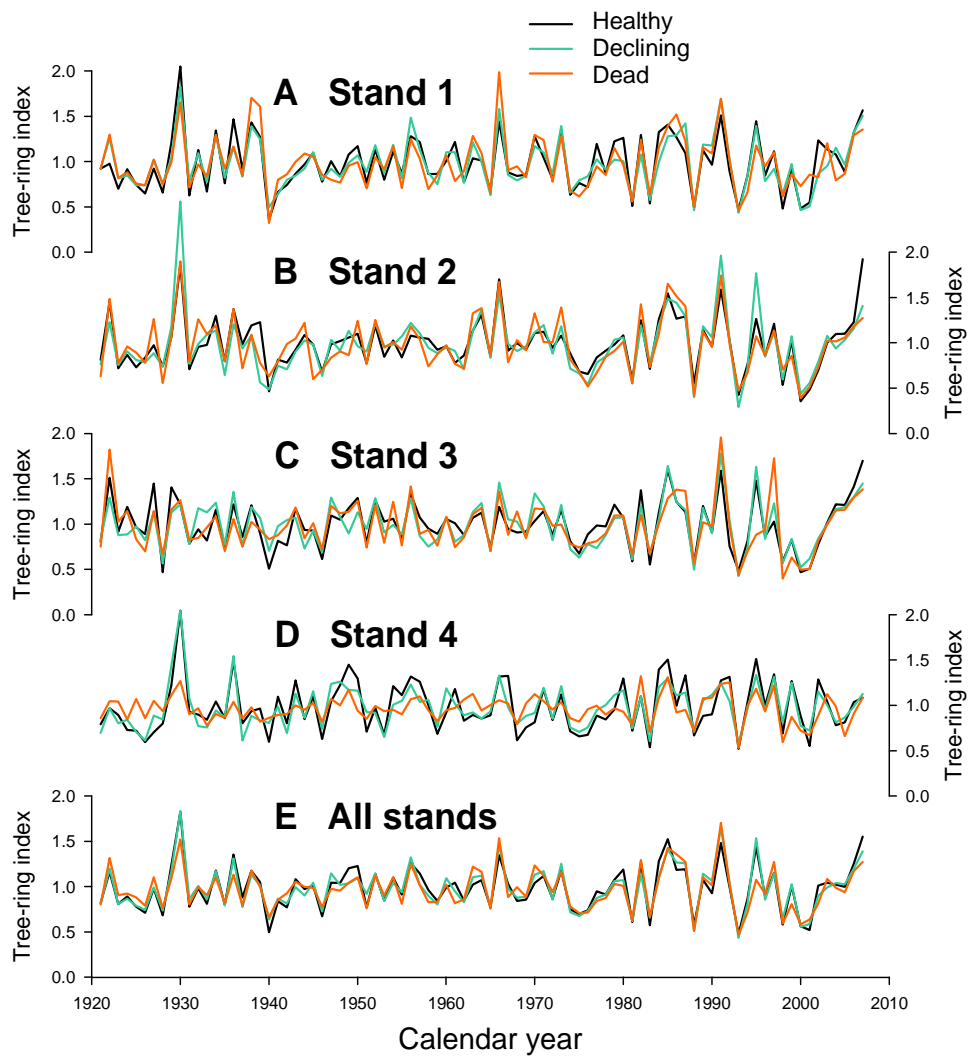


Fig. S2. Mean tree-ring indexed chronologies for healthy, declining, and dead trees at stands 1 (A), 2 (B), 3 (C), and 4 (D), and at all stands together (E).

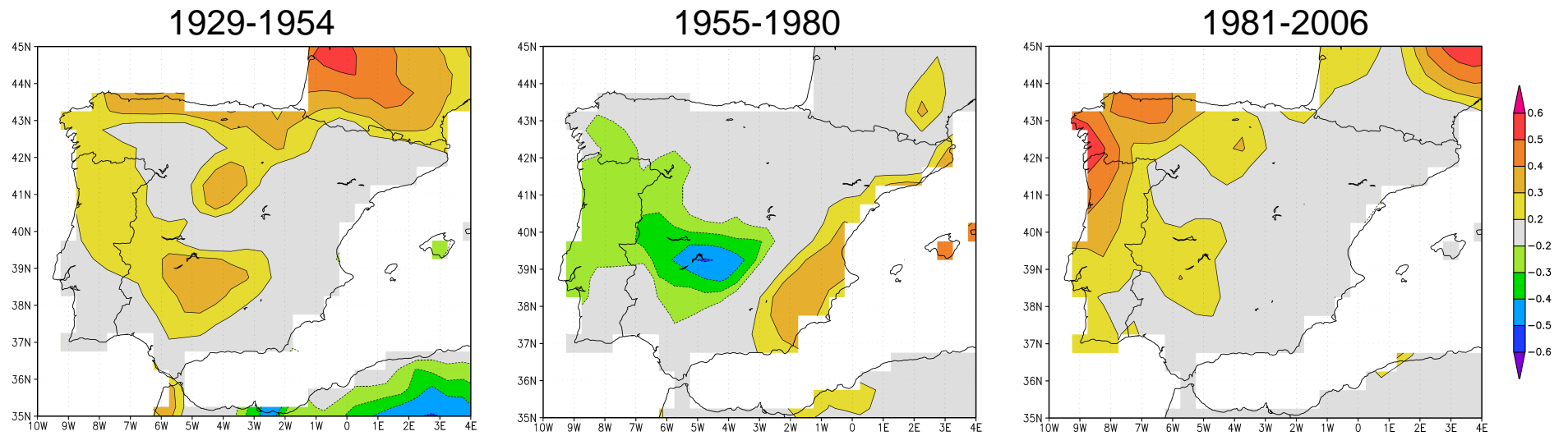


Fig. S3. Spatial field correlations between April-May precipitation in the Iberian Peninsula, and the April-May SST 1.2 anomalies in 1929–1954, 1955–1980, and 1981–2006. Values above 0.4, and below -0.4 , are statistically significant ($p < 0.05$).

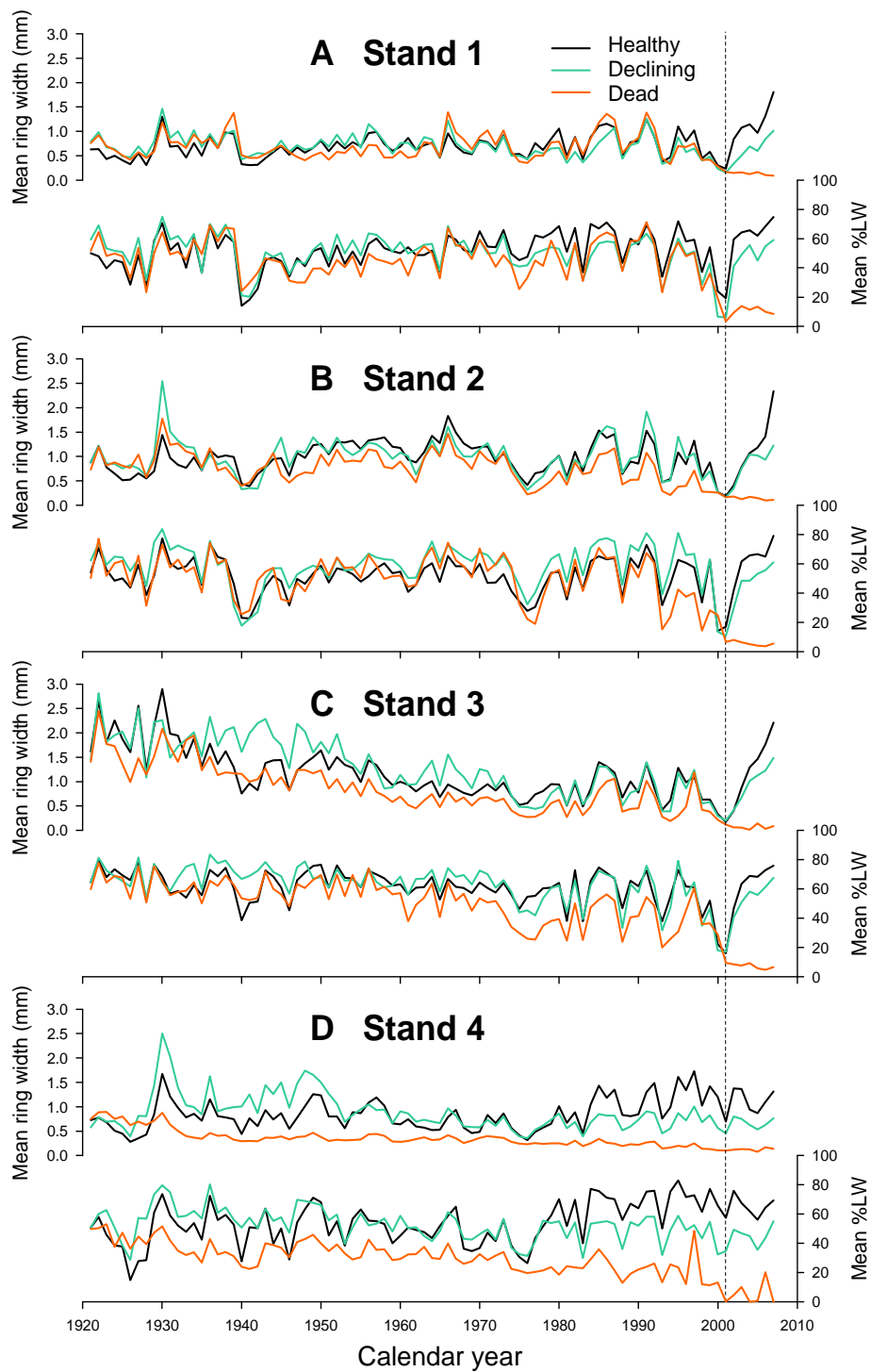


Fig. S4. Mean tree-ring width chronologies, and mean %LW chronologies for healthy, declining, and dead trees in stands 1 (**A**), 2 (**B**), 3 (**C**), and 4 (**D**). Vertical dashed line highlights the wettest year 2001.