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Soil fertilization transiently increases radial growth in sessile oaks but does not change their resilience to severe soil water deficit

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1 Title

2 Soil fertilization transiently increases radial growth of sessile oaks but
3 does not change their resilience to severe soil water deficit

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11 **Abstract (400 words max)**

12 The future climate is projected increasingly rougher for the European forest ecosystems, likely leading
13 to decline episodes for many tree species. Forest management has to be adapted to cope with the
14 negative effect of these changes. Despite the close interactions between nutrients and water in plant
15 physiology, very few studies have investigated the link between soil fertility and tree response to soil
16 water availability and vapour pressure deficit. This study's goal was to test whether fertilization might
17 modify the forest trees resilience to soil water deficit.

18 The potential impact of fertilization on trees during soil water deficit was assessed from a fertilization
19 experiment carried on sessile oaks. Three fertilization treatments (NCa, NPKCaMg and control) were
20 applied on 40-year-old oaks that were cored almost 50 years later. The drought response of fertilized
21 and control trees were compared by analysing the radial growth chronologies according to two
22 complementary approaches. Firstly, the relationships between radial growth and climate interannual
23 variations were investigated through dendroclimatic modelling including water deficit indices

24 computed with the daily soil water balance model Biljou©. Secondly, resistance, recovery and
25 resilience to drought-induced crises were evaluated from tree-ring width and compared between
26 treatments. In addition, the carbon isotope composition ($\delta^{13}\text{C}$) of tree rings was measured to evaluate
27 potential differential gas-exchange processes between fertilized and control trees.

28 Fertilization had an immediate and strong positive effect on oak growth that rapidly faded. NCa and
29 NPKCaMg fertilizations had similar effects suggesting that adding P, K and Mg had no more impact on
30 radial growth. Whatever the treatment, ring width variations appeared to be identically constrained
31 by climate, especially by summer water deficit of the current and previous years. The tree resistance
32 to soil water deficit was negatively affected by the severity of the drought event but did not
33 significantly differ between control and fertilized trees. The tree resilience was not affected by
34 fertilization and remained stable and close to 1 across crises. The tree-ring $\delta^{13}\text{C}$ was clearly increased
35 by the severe 1976 water deficit but did not vary between treatments. The possible mechanisms
36 involved in growth change and the lack of significant effect on resilience to drought events observed
37 after fertilization are discussed.

38

39 **Keywords**

40 Fertilization, tree ring, *Quercus petraea*, resilience, drought, $\delta^{13}\text{C}$.

41

42 **1. Introduction**

43

44 Most scenarios for future climate project that the increase in global mean surface temperature due to
45 anthropogenic emissions will be accompanied in Europe by an augmentation in intensity and
46 frequency of severe climate events like drought episodes (IPCC 2013). Intense or recurrent drought
47 events have long been identified as a major contributing factor of tree decline and mortality (Bréda *et*

48 *al.* 2006, Carnicer *et al.* 2011, Sergent *et al.* 2014). To avoid widespread forest declines, and their
49 catastrophic ecological and economic consequences, forest management practices have to adapt the
50 modern forest to the ongoing environmental changes. Many studies had already focused on forest
51 management showing that thinning is efficient to mitigate soil water deficit (Bréda *et al.* 1995, Misson
52 *et al.* 2003, Sohn *et al.* 2013). Mixing species in forest stands also appeared to be beneficial to limit
53 growth reduction under drought event, yet depending on the species combination (Pretzsch *et al.*
54 2013, Thurm *et al.* 2016). Lately, a few observations mentioned a lower drought resistance for trees
55 growing on poor soils (Royo & Knight 2012, Sergent *et al.* 2014) putting in question the interest of soil
56 fertilization as a management option alleviating drought impact on forest trees.

57 As recently pointed out by Gessler *et al.* (2017), the role of soil fertility in drought survival of forest
58 trees has been surprisingly unstudied. Several nutrients have been identified to be involved in plant
59 drought response, generally from studies on herbaceous species or on tree species at sapling stages.
60 For instance, K is known as an important actor of stomatal control (Sardans *et al.* 2015) and Ca was
61 found to play a major role in cavitation resistance (Herbette & Cochard 2010). However, because of
62 numerous interactions between functions, or organs, these specific pieces of knowledge cannot be
63 readily assembled to forecast the overall effect of soil nutrients fertility on mature tree response to
64 drought. For example, higher N availability was associated with higher resistance to cavitation but this
65 could not compensate for concomitant lower root-to-leaf area ratio, and resulted in overall higher
66 probabilities of hydraulic failure in drought conditions (Ewers *et al.* 2000, Bucci *et al.* 2006).

67 Radial growth variations have long been considered as an integrative proxy of tree functioning and
68 were frequently studied in a context of soil water deficit (Becker *et al.* 1994, Bréda & Granier 1996).
69 Many studies also reported the effect of nutrient additions on radial growth (Spiecker 1991, Sikstrom
70 1997, Long *et al.* 2011) and at least one of them evaluated the influence of climate variations on
71 fertilization effect (Van der Perre *et al.* 2012). However, to our knowledge, no study tried yet to
72 determine whether fertilization could help to mitigate drought negative impacts on forest trees. In

73 addition to ring width, the carbon isotopes composition ($\delta^{13}\text{C}$) of tree rings, which integrates the
74 variations in gas exchange, provides a valuable indicator of tree water status (Brooks & Mitchell 2011)
75 and has already been used to monitor the tree physiological response to fertilization (Balster *et al.*
76 2009, Brooks & Coulombe 2009). Here again, no study related yet the effect of drought \times fertilization
77 interaction on tree-ring $\delta^{13}\text{C}$, but when $\delta^{13}\text{C}$ measurements were performed in the leaves, the
78 differences between N-fertilized and control trees did not appear to be weather dependant (Betson *et*
79 *al.* 2007).

80 Sessile oak (*Q. petraea* (Matt.) Liebl.) is a major species of the Western Europe forests, usually
81 considered as relatively drought tolerant (Friedrichs *et al.* 2009b). However, projections of its future
82 potential range under moderate warming push it away from its current distribution area by the end of
83 the century (Hanewinkel *et al.* 2013). In the past 50 years, several fertilization experiments were
84 conducted in France to increase its productivity. The current study took advantage of one of the oldest
85 trials, making retrospectively available 50-year long radial growth chronologies where both fertilization
86 and water deficit events took place.

87 The objectives of this study were to determine whether soil fertilization (NCa or NPKCaMg) could: i)
88 improve oak radial growth, ii) modify the relationship between growth and climate and iii) change
89 negatively or positively the resistance, recovery and resilience of oak trees to drought. To address
90 these questions, drought events were quantified by daily soil water balance modelling and relate to
91 interannual ring width variations. Growth chronologies were also used to calculate resistance, recovery
92 and resilience (Lloret *et al.* 2011) to drought-induced crises. In addition, the tree-ring $\delta^{13}\text{C}$ was
93 measured to evaluate potential differential gas-exchange processes between fertilized and control
94 trees.

95

96

97 **2. Material and methods**

98

99 *2.1. Site and experimental design*

100

101 The study was carried in an experimental site set up in 1969 in a sessile oak stand located in the forest
102 of Bercé, France (N 47° 48' 23.19", E 0° 23' 17.63"; alt. 153 m asl). The trial was composed of nine 0.33-
103 ha square plots, distributed in three blocks (see Garbaye *et al.* 1974 for a complete description). Each
104 block included three modalities of fertilization: 1) NCa, 2) NPKCaMg and 3) control. In August 1969,
105 1500 kg.ha⁻¹ of CaO from slaked lime, 200 kg.ha⁻¹ of P₂O₅ from scories, and 34 kg.ha⁻¹ and 120 kg.ha⁻¹
106 of MgO and K₂O, respectively, from Patentkali® were spread by hand. Nitrogen was supplied as
107 ammonitrate in May 1970 (120 kg N.ha⁻¹) and May 1971 (100 kg N.ha⁻¹). The stand was about 40 years
108 old at the year of the fertilization.

109 The soil is a stagnic luvisol, with a relatively low pH (3.7<pH_{0.5cm}<4.0), a high C/N (23.2 at 0-5cm depth)
110 and a low Ca content (<0.10 mmol_c.l⁻¹) (Garbaye *et al.* 1974, Bakker 1998).

111

112 *2.2. Sampling and measurements*

113

114 In each of the nine plots, five dominant trees were cored to the pith at breast height in April 2008. Two
115 cores were sampled from each tree: one intended for ring width measurements, the other one for
116 isotopes measurements. Tree-ring width was measured from the bark to the pith to the nearest 1/100
117 mm. Ring-reading mistakes were checked and corrected by crossdating the cores according to the
118 procedure described in Becker *et al.* (1994). During the crossdating step, each individual chronology
119 was compared to the average chronology (N=44) where 27 pointer years were identified from 1933 to
120 2007.

121

122 The $\delta^{13}\text{C}$ measurements were performed on four trees of each of the three blocks of the NCa and
123 control treatments. However, because of a poor quality core, only 11 trees were considered in the
124 control treatment instead of 12 in the NCa treatment. The assessment was limited to a period starting
125 five years before the fertilization event and ending five years after the drought event of 1976. Thus,
126 on each of the available 23 cores, all the rings corresponding to the years 1965 to 1980 were separated
127 with a scalpel under a microscope. From each ring, only the latewood was kept and placed for 48 hours
128 in a 50°C oven. The dried samples were finely ground with a ball mill (MM200, Retsch GmbH, Haan,
129 Germany) before a 1 ± 0.1 mg aliquot was weighted in a 4x6 tin capsule (Elemental Microanalysis
130 Limited, Devon, UK). The samples were analysed with a continuous-flow elemental analyzer (vario
131 ISOTOPE cube, Elementar, Hanau, Germany) coupled with an isotope mass spectrometer (IsoPrime
132 100, Isoprime Ltd, Cheadle, UK). Measurements were performed at the INRA facility in Functional
133 Ecology (SILVATECH OC 081). Stable carbon isotope ratio was expressed as the $^{13}\text{C}/^{12}\text{C}$ ratio relative to
134 the Pee Dee Belemnite standard ($\delta^{13}\text{C}$; ‰) The precision of the $\delta^{13}\text{C}$ measurements, calculated as the
135 standard deviation of 48 repetitions of a lab working standard, was 0.04‰.

136

137 *2.3. Climate data and water balance model*

138

139 Daily climate data were obtained from the Météo-France weather station of Le Mans (N 47° 56' 27",
140 E 0° 11' 23"; alt. 58 m asl; weather station n°72181001), 22 km from the study site. Mean annual
141 temperature and precipitation calculated over the period 1949-2009 were 11.9°C and 687mm,
142 respectively.

143 The soil water deficit was retrospectively calculated by using the Biljou© water balance model (Granier
144 *et al.* 1999) supplied with daily climate data: rainfall (mm), global radiation ($\text{J}\cdot\text{cm}^{-2}$), mean temperature
145 ($^{\circ}\text{C}$), wind speed ($\text{m}\cdot\text{s}^{-1}$) and relative air humidity (%) from Le Mans weather station. Daily sum of
146 insolation duration was used for the oldest period where global radiation measurements were not yet
147 available (*i.e.* 1956-1975). Required soil parameters of the studied stand included the soil bulk density

148 (g.cm⁻³), the fine root proportion and the extractible water by the trees (mm) for each identified soil
 149 layers (Table 1). The canopy parameters were the average dates of budburst and leaf fall (days of the
 150 year), and the average maximum leaf area index (LAI) achieved each year at full leaf expansion (Table
 151 1).

152

153

Soil properties	Layer 1	Layer 2
Depth and thickness (cm)	0-50	50-120
Texture	loam	clay-loam
Fine roots proportion (percent)	80	20
Extractable water (mm)	52	120
Water content at permanent wilting point (kg.kg ⁻¹)	0.08	0.18
Soil bulk density at field capacity (g.cm ⁻³)	1.15	1.47
Canopy parameters	budburst	leaf fall
Date (day of year)	90	299
Leaf Area Index (m ² .m ⁻²)	6.0	

154

155 **Table 1.** Stand parameters and soil properties used to run the Biljou© model. Soil extractable water
 156 was computed from observations made at the study site and in a nearby ICPForest - Level II plot
 157 (Brêthes & Ulrich 1997). Budburst and leaf fall dates were derived from Lebourgeois *et al.* (2002).

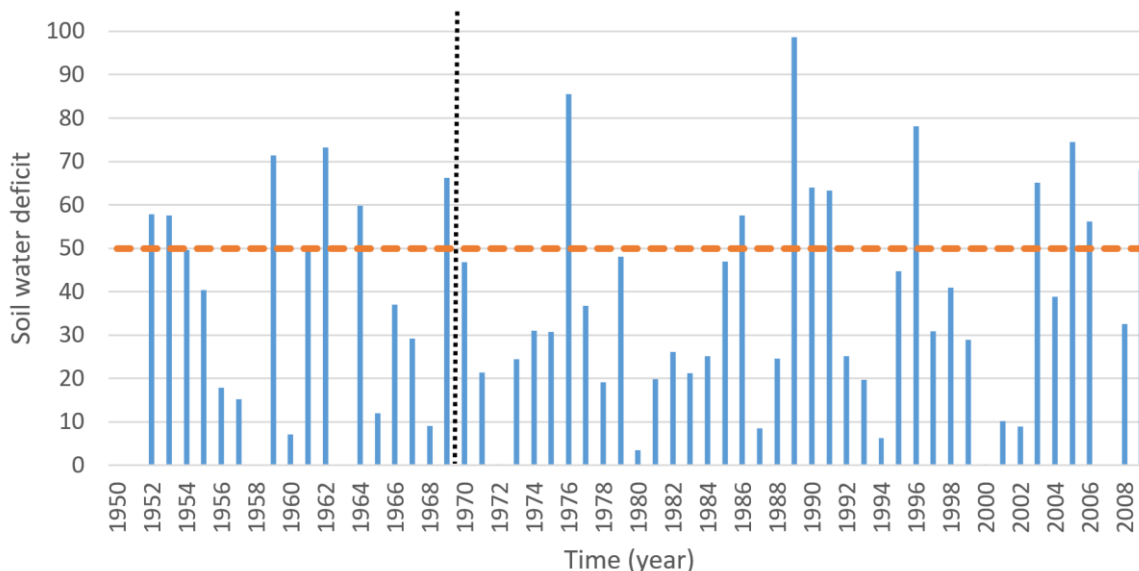
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159

160 Biljou© daily calculates the stand water balance from each elementary water flux that enters
 161 (precipitation) and goes out from the system (tree canopy transpiration and interception, soil and
 162 understorey evapotranspiration and runoff). Output variables are the above-mentioned fluxes, stand
 163 real evapotranspiration (ETR), potential evapotranspiration (PET) and relative extractible water (REW)

164 that fluctuates between 1 (field capacity) and 0 (permanent wilting point). Under a critical threshold
 165 of 0.4, the water availability is considered as stressful for most forest tree species and induces
 166 ecophysiological regulation of canopy conductance (Granier *et al.* 1999). The soil water deficit (SWD,
 167 dimensionless) was calculated as the sum of the daily differences between the threshold and the
 168 calculated REW values, divided by 0.4. SWD reflects then the intensity and duration of the soil water
 169 deficit period. SWD is usually integrated over the whole vegetative period (from budburst to leaf fall).
 170 However, since most of the sessile oak radial growth is achieved between June and August (Bréda &
 171 Granier 1996), several combinations of monthly values (*i.e.* June-July, July-August, June-July-August)
 172 were assessed to identify the best explaining variables on studied tree growth (see 2.5). To analyse the
 173 resilience, resistance and recovery to a drought event, we defined as severe a drought event with SWD
 174 greater or equal to 50 (Fig. 1). This limit was previously identified as likely to induce oak dieback (Bréda
 175 & Badeau 2008). When successive years exhibited $SWD \geq 50$, the SWD was cumulated over the whole
 176 crisis period (up to three years for the 1989-91 crisis, Table 2).

177
 178



179
 180 **Figure 1.** Yearly variation of soil water deficit (dimensionless) integrated over the whole vegetative
 181 period in the forest of Bercé from 1950 to 2007 calculated by the Biljou© model using daily climate

182 data from the Météo-France weather station of Le Mans. The vertical dotted line represents the
 183 fertilization year (1970). The horizontal dotted line represents the limit used to determine severe
 184 drought events (Bréda & Badeau 2008).

185

186 2.4. Resistance, Recovery and Resilience calculations

187

188 The resistance, recovery and resilience indexes were calculated from ring widths according to Lloret *et*
 189 *al.* (2011). Briefly, the resistance (Rs) is a quantification of the diminution of growth during a crisis due
 190 to soil water deficit above the severe drought event limit. It is calculated as the ratio of growth during
 191 crisis (one or several years of soil water deficit >50) to growth before crisis. Recovery (Rc) represents
 192 the capacity of trees to grow after a drought event. It is calculated as the ratio of growth after crisis to
 193 growth during crisis. Resilience (RI) is the capacity of trees to resume their pre-crisis growth level. It is
 194 calculated as the ratio of post- to pre-crisis growth. Ring widths during, before and after drought were
 195 averaged over one to ten years to calculate the per-, pre- and post-crisis of growth, depending on the
 196 duration of the drought event and of the periods between two successive drought events; Table 2
 197 presents the six identified drought-induced crisis and the corresponding pre- and post- periods for
 198 growth calculations.

199

Crisis	Crisis Duration	Pre-Crisis	Post-Crisis	Cumulated <i>SWD</i>	Maximum <i>SWD</i>
1	1952-1954	1950-1951	1955-1958	197	58
2	1959-1964	1955-1958	1965-1975	261	73
3	1976-1977	1965-1975	1978-1988	122	85
4	1989-1992	1978-1988	1993-1994	251	99
5	1995-1996	1993-1994	1997-2002	123	78

200

201 **Table 2.** Characteristics of the six drought-induced crises of growth detected in the tree-ring width
202 chronologies: crisis years, pre- and post-crisis periods, soil water deficit (*SWD*) cumulated over the
203 crisis period and maximum yearly *SWD* observed during the crisis period. Both cumulated and
204 maximum *SWD* were calculated over the entire vegetative period (from budburst to leaf-fall).

205

206 2.5. Data analysis

207

208 As no age trend was observed on ring width over the studied period and in order to prevent any
209 dampening of the fertilization effect, raw ring widths were displayed and used in further calculations.

210 The effect of fertilization on the radial growth and on the $\delta^{13}\text{C}$ was tested year by year by using analysis
211 of variance also including a block effect and its interaction with the fertilization effect. Post-hoc Tukey's
212 tests were used to assess differences between the three fertilization modalities. The effect of
213 fertilization on resistance, recovery and resilience was tested with a one-factor ANOVA for each crisis
214 independently. A mixed model was applied to test the effect of the treatment over the whole
215 chronology. The treatment and the crisis were then defined as fixed effects and the tree as random
216 effect. Measurements made on rings from a same tree were considered as repeated measurements
217 linked together with an autoregressive structure. The effect of fertilization on the relationship between
218 *Rs*, *Rc* and *Ri* and water deficit was tested using ANCOVA.

219 The relationships between climate and radial growth of the control trees were assessed through
220 multiple linear regressions. A set of 16 variables, including several combinations of monthly mean
221 temperatures from April to June and Biljou© *SWD* outputs (monthly *swd* from June to August and *swd*
222 cumulated from June to August for current and previous years), were centred (*i.e.* subtracting the
223 mean) and scaled (*i.e.* dividing by the standard deviation), and tested in order to determine the best
224 dendrobioclimatic model. The model was calculated on the control trees using stepwise regressions

225 where significant regressors were selected according to the Mallows criteria. The selected model was
226 then applied to the ring width chronologies of the fertilized trees and parameters coefficients and
227 goodness of fit were compared to the control ones.

228

229

230 **3. Results**

231

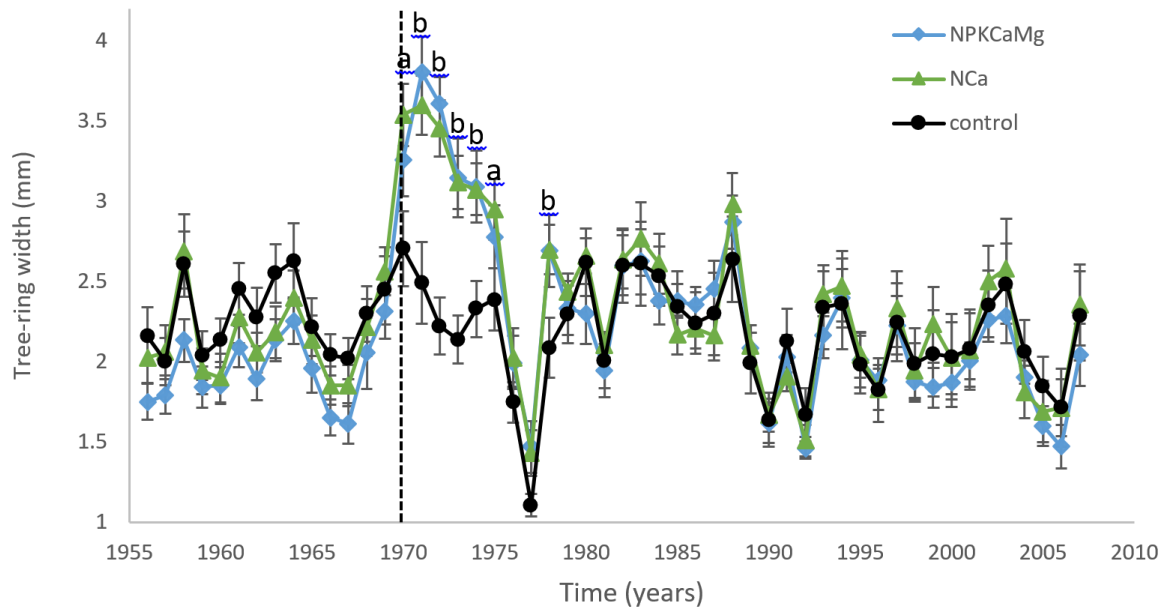
232 *3.1. Radial growth differences between fertilized and control trees*

233

234 Compared to the control trees, the fertilized trees showed an increase in radial growth that started
235 immediately after the fertilization, in 1970, maximised in the first three years (on average +42% ring
236 width for NCa and +45% ring width for NPKCaMg) and lasted for nine years, until 1978 (Fig. 2). After
237 1971, though, the differences in ring width between fertilized and control trees grew smaller and
238 became not significant in 1976 and 1977, when the overall growth dramatically decreased due to the
239 first extreme drought event since fertilisation (Fig. 1). The two fertilization treatments had rather
240 similar effects on radial growth although only the NCa trees appeared with a significantly increased
241 growth in 1970 and 1975. However, one can notice a slightly (but not significant) lower average ring
242 width for the NPKCaMg trees during the 20 years preceding fertilization that might have persisted
243 afterwards. A slight block effect was observed in 1973 ($F=5.0$, $P=0.01$), 1975 ($F=3.4$, $P=0.04$) and 1977
244 ($F=4.3$, $P=0.02$).

245

246



247

248 **Figure 2.** Growth chronologies of sessile oaks according to treatments. The vertical dotted line
 249 represents the fertilization year (1970). Different letters indicate significant differences among
 250 treatments ($P < 0.05$), a: NCa is different from control, b: both NCa and NPKCaMg are different from
 251 control. Vertical bars represent standard errors of the mean.

252

253

254 Removing the time decreasing effect of fertilization on radial growth appeared necessary to assess the
 255 relationship between growth and climate correctly. A negative exponential model was fitted to the
 256 average growth chronology, for the two fertilization modalities independently (Fig. 3). These models
 257 were applied on a period starting at the first year of fertilization (*i.e.* 1970) and ending at the last year
 258 of the chronologies (*i.e.* 2007). Slightly different models were obtained for NCa (equation 1; $F=20.23$,
 259 $P<0.0001$, $\text{pseudo-}R^2=0.54$) and NPKCaMg (equation 2; $F=24.67$, $P<0.0001$, $\text{pseudo-}R^2=0.59$):

260

$$rw = 1.605 \cdot \exp(-0.186 \cdot t) + 2.115 \quad \text{equation 1 (NCa),}$$

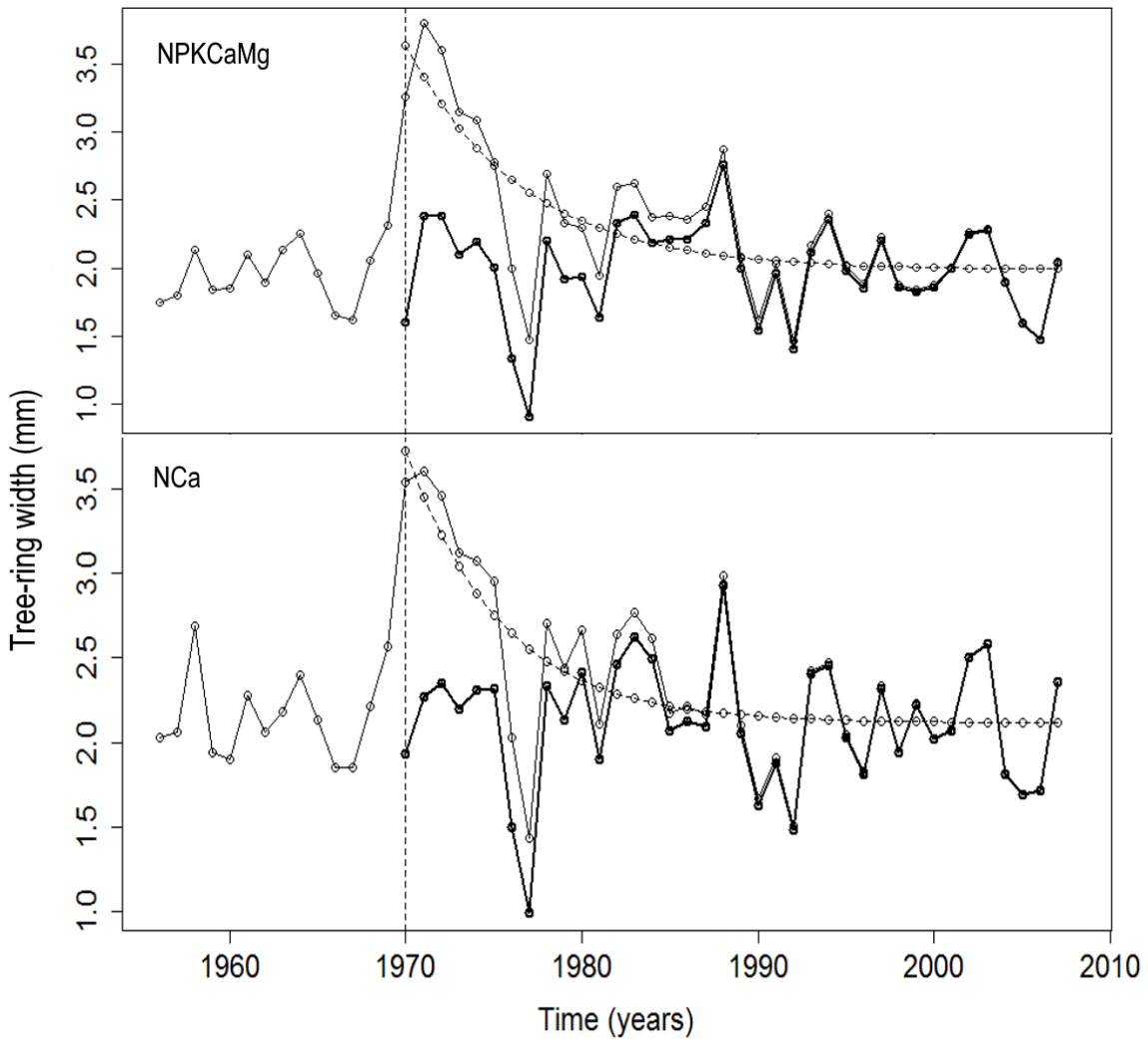
261

$$rw = 1.657 \cdot \exp(-0.153 \cdot t) + 1.986 \quad \text{equation 2 (NPKCaMg),}$$

262

where rw is the ring width (in mm) and t is the time (in year).

263 The residuals of these two models were used in the following calculations.



264

265 **Figure 3.** Model of the diminution of growth after fertilization. Thin solid line: measured growth, dotted
266 line: growth model, thick solid line: standardized growth, vertical dotted line: year of fertilization.

267

268 3.2. Relationships between radial growth and climate

269

270 The best dendrobioclimatic model retained by the stepwise multiple regression for control trees
271 (equation 3; $F=11.98$, $P<0.0001$, $\text{adj-}r^2=0.54$; Tab. 3) included four variables, sorted in decreasing order
272 of significance as follows: (i) the previous-year soil water deficit in June *pyswd6*, (ii) the current-year
273 soil water deficit cumulated from June to August *swd678*, (iii) the current-year May average

274 temperature *tmean5* and (iv) the tree-ring width of the previous year *pyrw*, corresponding to the first-
 275 order autocorrelation of growth:

$$276 \quad rw = 2.160 - 0.145*swd678 - 0.181*pyswd6 - 0.057 tmean5 + 0.069*pyrw \quad \text{eq. 3 (control)}$$

277 This model performed rather well when applied to the standardized radial growth of the fertilized trees
 278 (NPKCaMg: adj-r²=0.49; NCa: adj-r²=0.49). However, nor *pyrw* (first-order autocorrelation) in the NCa
 279 treatment, neither *tmean5* in both fertilization modalities appeared significant. The water deficit
 280 parameters *swd678* and *pyswd6* were significant for both fertilization modalities but the values of
 281 these parameters were smaller than for the control (Tab. 3). The relationships between modelled and
 282 observed (standardized) ring widths were not different between treatments (Fig. 4).

283

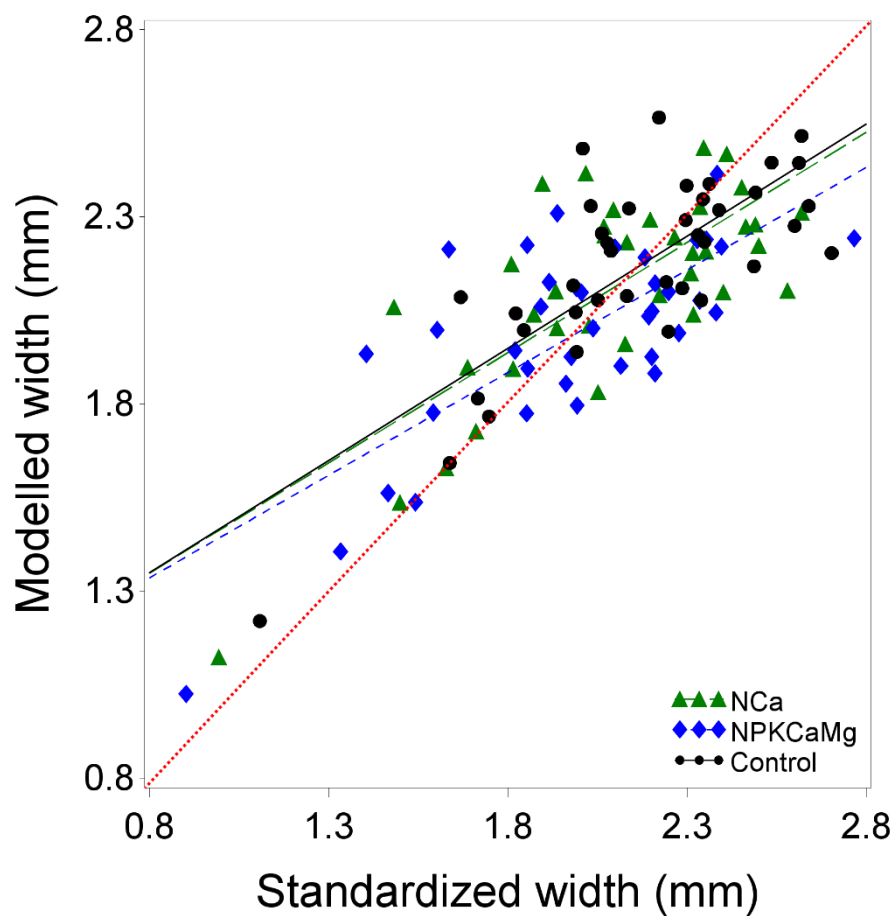
Treatments	Model parameters				
	<i>swd678</i>	<i>pyswd6</i>	<i>tmean5</i>	<i>pyrw</i>	<i>intercept</i>
Control	est: -0.145	est: -0.181	est: -0.063	est: 0.070	est : 2.156
	r ² : 0.15	r ² : 0.43	r ² : 0.10	r ² : 0.07	-
	t=-3.76	t=-4.66	t=-1.64	t=1.60	t=27.26
	p<0.001	p<0.001	p: 0.11	p: 0.12	p<0.0001
NCa	est: -0.199	est: -0.193	est: -0.027	est: 0.031	est : 2.113
	r ² : 0.23	r ² : 0.39	r ² : 0.02	r ² : 0.01	-
	t=-4.27	t=-4.08	t=-0.61	t=0.65	t=48.67
	p<0.001	p<0.001	p: 0.55	p: 0.52	p<0.0001
NPKCaMg	est: -0.193	est: -0.171	est: -0.030	est: 0.078	est : 2.008
	r ² : 0.20	r ² : 0.38	r ² : 0.03	r ² : 0.07	-
	t=-4.25	t=-3.75	t=-0.69	t=1.60	t=45.60
	p<0.001	p<0.001	p: 0.50	p: 0.12	p<0.0001

284

285 **Table 3.** Contribution and significance of the parameters selected for the dendrobioclimatic model:
286 *swd678*: current-year soil water deficit of June, July and August; *pyswd6*: previous-year soil water
287 deficit of June; *tmean5*: current-year mean temperature of April; *pyrw*: previous-year tree-ring width.
288 For each parameter, estimated values, partial- r^2 , t-value and associated p-values are displayed.

289

290



291

292

293 **Figure 4.** Relationship between observed (standardized) and modelled tree-ring widths in the control
294 (black dots), NCa (green triangles) and NPKCaMg (blue diamonds) treatments. Regression lines are
295 displayed in addition to the 1:1 (red dotted) line.

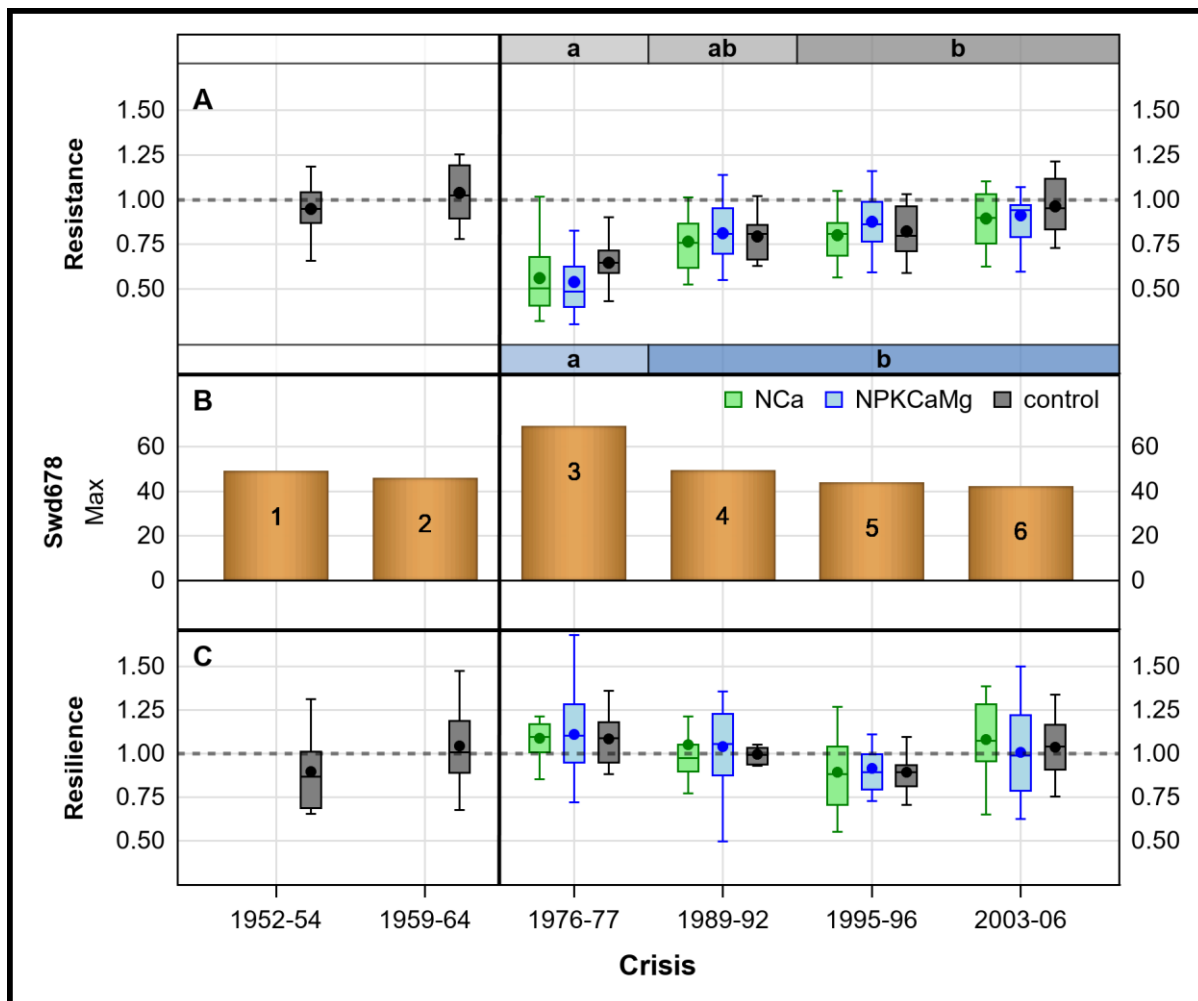
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297

298 3.3 Resistance, recovery and resilience

299

300 The fertilized trees did not show any significant differences of resistance (Rs), recovery (Rc) and
301 resilience (RI) compared to the control trees (and between them), neither when tested crisis by crisis
302 during the post-fertilisation period (Rs: $0.35 < F < 1.37$, $0.26 < P < 0.71$; Rc: $0.56 < F < 2.43$, $0.10 < P < 0.58$; RI:
303 $0.08 < F < 0.40$, $0.67 < P < 0.93$), nor when tested over the whole chronology (Rs: $F=1.13$, $P=0.33$; Rc:
304 $F=2.37$, $P=0.11$; RI: $F=0.18$, $P=0.83$). For the control trees, significant differences occurred between the
305 crises with resistance (Fig. 5) and recovery (not shown) varying from 0.65 and 1.72 in crisis 3 to 1.04
306 and 0.95 in crisis 2, respectively (Rs: $F=11.62$, $P < 0.0001$; Rc: $F=19.96$, $P < 0.0001$). For the fertilized
307 trees, the resistance significantly increased from crisis 3 to 6 (NCa: $F=20.45$, $P < 0.0001$; NPKCaMg:
308 $F=15.34$, $P < 0.0001$) whereas the recovery significantly decreased (NCa: $F=18.63$, $P < 0.0001$; NPKCaMg:
309 $F=26.16$, $P < 0.0001$). The resilience remained rather stable for the control trees, varying slightly but
310 significantly from 0.90, observed for crises 1 & 5, to 1.09 for crisis 3 (RI: $F=2.42$, $P=0.04$; however, the
311 Tukey post-hoc test did not detect significant differences as shown in Fig. 5). Whereas not any
312 significant differences in resilience were observed between crises for the NCa trees (RI: $F=2.44$,
313 $P=0.11$), slight significant differences were observed across crises for the NPKCaMg trees (RI: $F=3.79$,
314 $P=0.035$). The resistance was significantly and negatively correlated to the intensity of drought,
315 expressed as the maximum reached during the crisis by the water deficit for the months of June to
316 August ($SWD678_{max}$), for the fertilized trees (NCa: $R^2=0.95$, $P=0.025$, $N=4$; NPKCaMg: $R^2=0.999$,
317 $P=0.0005$, $N=4$) but not for the control trees ($R^2=0.61$, $P=0.068$, $N=6$). The recovery was significantly
318 and positively related to $SWD678_{max}$ for both fertilized trees (NCa: $R^2=0.98$, $P=0.011$, $N=4$; NPKCaMg:
319 $R^2=0.98$, $P=0.0084$, $N=4$) and control trees ($R^2=0.80$, $P=0.016$, $N=6$). Not any significant relationship was
320 observed between resilience and $SWD678_{max}$, whatever the treatment. Resistance decreased and
321 recovery increased when soil water deficit increased whatever the treatment, resulting in resilience
322 being close to one the whole time.



323

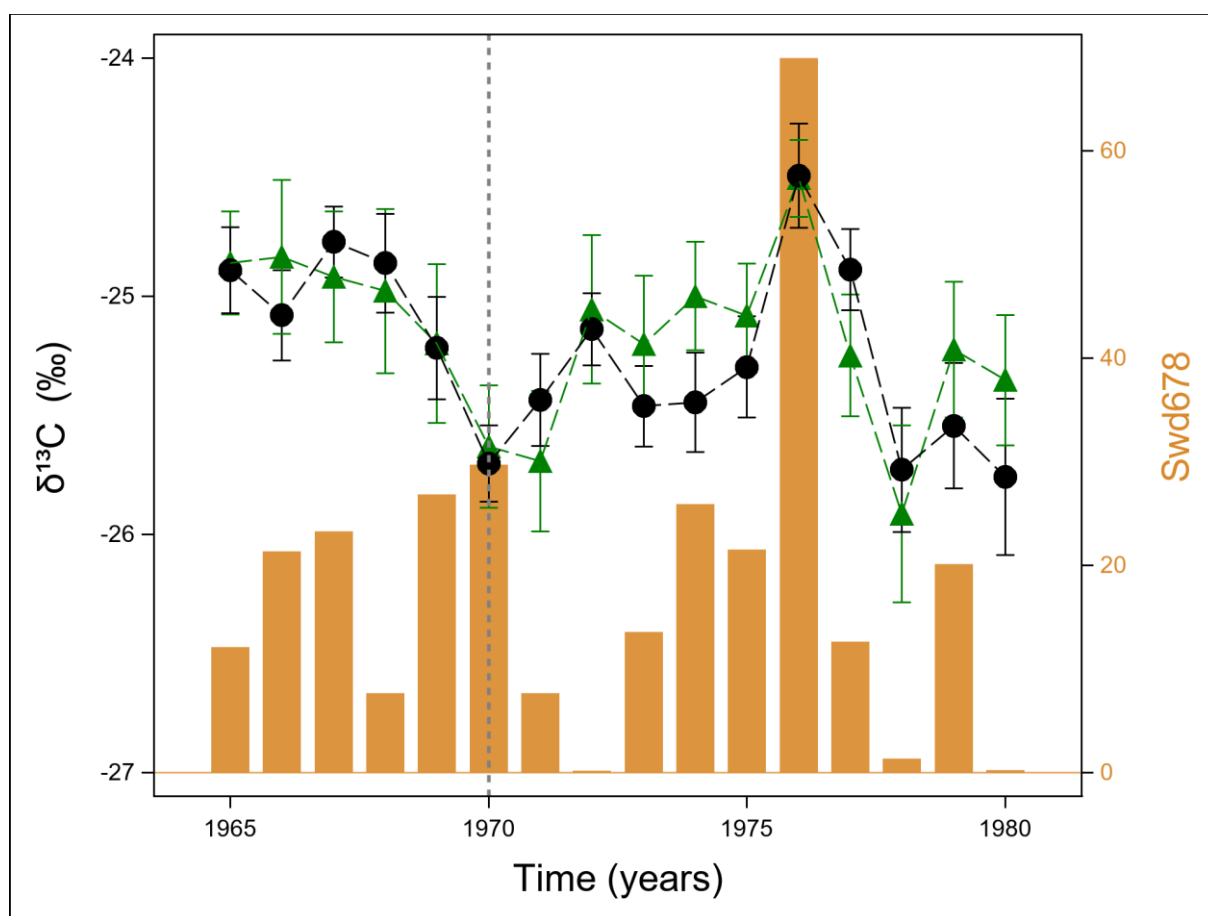
324 **Figure 5.** (A) Resistance (dimensionless) and (C) resilience (dimensionless) of oaks according to the
 325 treatment (grey= control, green= NCa, blue= NPKCaMg) and the crisis chronologically sorted. Panel (B)
 326 displays $Swd678_{max}$ (dimensionless), the maximum June-August water deficit observed during the
 327 crisis. The numbers indicate the chronological order of the crisis according to table 2. The boxplots
 328 displayed the mean, median, first and third quartiles, minimum and maximum values after removing
 329 the outliers. The letters a and b represent the significant differences between crises for the control
 330 (grey) and fertilized (blue) trees, respectively.

331

332 *3.4. Mean $\delta^{13}C$ chronologies*

333

334 Fertilized trees did not show any statistically significant differences in their values of $\delta^{13}\text{C}$ compared to
335 the control ones. However, a slight increase was noticeable between 1973 and 1975, a period of
336 moderate soil water deficit a few years after fertilization (Fig. 6). $\delta^{13}\text{C}$ was significantly and positively
337 related to *Swd678* ($R=0.53$, $P=0.03$, $N=16$) without significant differences between treatments.
338
339



340
341
342 **Figure 6.** Variation of soil water deficit from June to August and carbon isotope composition ($\delta^{13}\text{C}$)
343 between 1965 and 1980 according to treatments (black: control, green: NCa). The dotted line
344 represents the fertilization year. Vertical bars represent the standard errors of the mean.

345
346

347 **4. Discussion**

348

349 *4.1 The fertilization had an immediate positive effect on radial growth that rapidly attenuated*

350

351 The supply of fertilizers dramatically increased the radial growth of the oak trees. Contrary to other
352 forest trials that often displayed a slightly delayed and gradual growth enhancement (Lebourgeois *et*
353 *al.* 1993, Picard *et al.* 1999), the growth increase started the growing season that immediately followed
354 the fertilization. Nitrogen fertilization generally has a positive and rapid effect in stimulating tree
355 growth (Spiecker 1991, Becker 1992, Sikstrom 1997, Brooks & Coulombe 2009) but depressive effect
356 were also observed (Picard *et al.* 1999). This enhancing effect is usually short-termed (Sikstrom 1997)
357 likely because new limiting factors (*e.g.* nutrients, light) rapidly appear (Elvir *et al.* 2006). On the
358 contrary, the improving effect of liming (*e.g.* Ca addition) in deficient soils classically occurs after
359 several years and lasts a longer time (Spiecker 1991, Long *et al.* 2011). In the slightly Ca-deficient soil
360 we studied, it then appeared that the fertilization effect on radial growth was dominated by the
361 relatively important quantity of supplied N (*i.e.* 220 Kg N.ha⁻¹). The Ca supply may have prevented the
362 acidifying effect of N addition although the slake lime form was likely not the most efficient buffer. The
363 lack of significant differences in growth between treatments in 1976 and 1977 was also consistent with
364 observations that NPP response to N-fertilization nullified in dry years (Lim *et al.* 2015). The addition
365 of P+K+Mg to the NCa dose (similar in both fertilization treatments) had no additional effect on radial
366 growth, likely because the availability of these elements was optimal in the original soil and remained
367 optimal after the addition of the NCa dose.

368

369 *4.2 The fertilization did not change the growth response to drought*

370

371 One of the most severe water deficit observed in Europe in the late decades (*i.e.* the 1976 drought)
372 occurred only six years after the fertilization application, while its effect was still clearly visible on the
373 radial growth. Yet, the drought response of fertilized and control trees, assessed from two different
374 and complementary approaches, appeared identical.

375 By relating the ring width variations to the climatic observations, the first approach (*cf.* 3.2) led to the
376 identification of the principal variables constraining the radial growth. Summer soil water deficits of
377 the current and previous years were the main factors controlling the ring width of the studied trees,
378 as it is commonly observed on sessile oaks (Lebourgeois *et al.* 2004; Friedrichs *et al.* 2009a, 2009b;
379 Michelot *et al.* 2012; Trouvé *et al.* 2014). In addition to climate variables, the between-year variations
380 in ring width also appeared to be influenced by the previous-year growth, confirming the importance
381 of lag effects on oak radial growth (Lebourgeois *et al.* 2004, Misson *et al.* 2004) that cannot be
382 summarized by the only water deficit.

383 The relative contributions of these different variables to the dendroclimatic model applied to the three
384 treatments were rather similar (Tab. 3, Fig. 4). The slightly better goodness of fit observed for the
385 control trees was expected, since the variable selection was performed on this population only. The
386 real duration of the fertilization effect on the tree physiology was difficult to evaluate. Its legacy on
387 radial growth ceased before the second climatic crisis occurred, in 1989. However, the leaf chemical
388 contents of the NPKCaMg trees were still different from the control ones in 2014 (Durand *et al.*
389 submitted). Depending on the effective durability of the fertilization, considering the whole 1970-2007
390 period in the dendroclimatic analysis could have dampened the potential treatment effects.

391 In the second approach (*cf.* 3.3), each climatic crisis was considered independently. However, even if
392 a gradual and significant increase in resistance was observed over the four crises that followed the
393 fertilization event, fertilized and control trees displayed equivalent performances (Fig. 5). This
394 resistance increase from crisis n°3 to crisis n°6 was likely mainly due to a concurrent decrease in
395 drought intensity (characterized by the variable $SWD678_{max}$ in this study). The expected negative

396 relationship observed between resistance and drought intensity (also seen in Zang *et al.* 2014 on other
397 tree species) appeared weaker for the control than the fertilized trees but the identification of these
398 differences was based on a very restricted number of observations (n=6 and 4, respectively). The
399 recovery indexes mirrored the resistance ones, as already observed (Zang *et al.* 2014; Gazol *et al.*
400 2017), by showing a positive significant relationship with $SWD678_{max}$ but no differences between
401 fertilized and control trees. Because of the way the indexes are calculated, the fact that recovery and
402 resistance behave oppositely, logically involves that the growth levels were the same before and after
403 the crisis, thus that the resilience value is 1. Thus, consistently with the observations made on
404 resistance and recovery, the average resilience appeared remarkably stable over the whole studied
405 period for the three treatments. This is coherent with the observations of Merlin *et al.* (2015) or Trouvé
406 *et al.* (2017), the latter observing that the dominant trees of *Q. petraea* stands resumed their pre-1976
407 growth level between 1978 and 1980. Such a stable resilience was generally mentioned for species
408 growing in their optimal ecological conditions (*Abies alba* and/or *Fagus sylvatica* in Zang *et al.* 2014;
409 Metz *et al.* 2016; Diaconu *et al.* 2017, Vitali *et al.* 2017) and contrasted with those observed for species
410 growing at the edge of their distribution range (*Picea abies* in Zang *et al.* 2014; Lloret *et al.* 2011).

411

412 *4.3 Which processes led to the increase of radial growth without changing the responses to drought*
413 *and climate?*

414

415 Based on the short lasting effect on radial growth and on the absence of differences between the two
416 fertilization modalities (*NCa* and *NPKCaMg*), we hypothesized that growth stimulation resulted mainly
417 from nitrogen inputs in this study. The simultaneous input of Ca was planned to prevent any
418 acidification processes and associated nutrients loss to occur. As N is paradoxically both a common
419 limiting factor for plant productivity and a pollutant deposited worldwide, its effect on plant physiology
420 have been largely studied. Yet, increasing the N availability affects many different plant processes that

421 can compensate each other, especially on large-size and long-lived plants as forest trees. Identifying
422 the processes that ended to increase the radial growth of the oak trees without changing their
423 response to drought is thus not straightforward. Water relations, water-use efficiency then carbon
424 allocation are successively discussed below.

425 In the current study, the $\delta^{13}\text{C}$ of the rings built after the fertilization event were not significantly
426 different between the NCa-fertilized and the control trees (although slightly higher in fertilized trees).
427 It suggested that (i) the fertilization did not change the leaf gas exchanges or (i) that stomatal
428 conductance and photosynthesis rate changed in parallel. Such a lack of significant effect of N
429 fertilization on tree-rings $\delta^{13}\text{C}$ was already observed on *Pseudotsuga menziesii* (Balster *et al.* 2009) or
430 *Picea abies* (Krause *et al.* 2012) although, in most cases, N-fertilization was found to induce a short-
431 time increase in $\delta^{13}\text{C}$, being interpreted as an increase in photosynthesis (Brooks & Mitchell 2011) or a
432 reduction in stomatal conductance (Brooks & Coulombe 2009). As a decrease in C assimilation
433 (required if a decrease in stomatal conductance is considered) is not likely to occur in fertilized trees,
434 we hypothesize that the fertilization, in the current study, either did not change the leaf gas exchange,
435 or led to equivalent increases in C assimilation and stomatal conductance. When water availability is
436 not limiting, the increase in leaf area index (LAI) generally observed in response to N inputs could be
437 accompanied with (Green & Mitchell 1992, Clearwater & Meinzer 2001) or without (Samuelson *et al.*
438 2014; Krause *et al.* 2012) an increase of the photosynthetic rate (resulting from an increase of the total
439 amount of Rubisco). Both changes would lead to an increase in the tree-level C assimilation that can
440 explain the observed increase in radial growth. As a matter of fact, several studies tend to show that
441 the stimulated growth is the result of a two-phases response, with an initial increase in photosynthetic
442 rate and growth efficiency followed by a longer phase of elevated LAI and C allocation changes (Brooks
443 & Coulombe 2009; Lim *et al.* 2015). When water availability is limited, a higher (N-induced) LAI, by
444 increasing rainfall interception and quantity of transpired water, tends to accentuate drought intensity
445 and cause hydraulic imbalance. N-fertilized trees are thus expected to decrease their stomatal
446 conductance, which turns into a $\delta^{13}\text{C}$ increase, in a first step (Brooks & Coulombe 2009, Samuelson *et*

447 *al.* 2018). After a few years, trees eventually recovered their hydraulic balance by adjusting leaf and
448 sapwood area to the available water supply. In the current study, it is noticeable that the slight (but
449 not significant) increase in $\delta^{13}\text{C}$ occurred on fertilized oaks during years without water deficit and
450 disappeared in 1976.

451 Coming to carbon allocation, Gessler *et al.* (2017) suggested that a high nutrient availability might have
452 a detrimental effect on tree drought recovery because of preferential biomass allocation aboveground.
453 Indeed, increasing the quantity of available Ca has been shown to decrease the C allocation to the root
454 system, thus favouring the allocation to aboveground biomass (Fahey *et al.* 2016). Regarding N
455 availability, its effect on fine root dynamics is still controversial with some results showing an increase
456 in root production (Shi *et al.* 2017) and turn-over with N availability and others showing no systematic
457 changes (Beets & Whitehead 1996, Dzedek *et al.* 2016) or even decrease (Nadelhoffer 2000). Even if
458 fertilization does not change root production, the N-induced stimulation of the aboveground
459 production generally leads to a decrease of the C fraction allocated to the roots (Beets & Whitehead
460 1996; Ewers *et al.* 2000; Lim *et al.* 2015).

461 In addition to these possible changes in the distribution of growth between above- and below-ground
462 compartment, fertilization could also change C allocation between growth and other functions,
463 particularly respiration, storage or reproduction. Indeed, rather than an augmentation of carbon
464 assimilation, the increase of growth could be explained by a diminution of carbon loss by respiration.
465 However, as the fertilization is known to improve leaf production and increase N storage in tissues,
466 both maintenance and growth respirations are also expected to increase (Manter *et al.* 2005). The
467 fertilization could also decrease the C amount dedicated to storage (Ludovici *et al.* 2002; Goodsman *et*
468 *al.* 2010), reproduction and defence functions (Hoft *et al.* 1996) for the benefit of the radial growth. In
469 the experiment carried at Bercé, though, the fertilization had enhanced the acorn production (Garbaye
470 & Leroy 1974). It can therefore be concluded that under the conditions of the Bercé site, fertilization

471 temporarily stimulates aerial growth without inducing imbalances that could modify resilience and
472 resistance to severe drought episodes.

473

474

475 **5. Conclusion**

476

477 The objectives of the study were to determine if soil fertilization (NCa or NPKCaMg) can i) improve
478 trees growth, ii) modify the relationship between growth and climate and iii) change negatively or
479 positively the resistance, recovery and resilience of trees to drought. The radial growth of the sessile
480 oaks increased dramatically the first year following fertilization, peaked the year after then declined
481 progressively for the next six years when fertilized and control trees eventually converged. These
482 results suggested that fertilization led to a temporary increase in carbon acquisition (or aboveground
483 production) and that the involved morphological and physiological changes did not alter the capacity
484 of trees to cope with drought. The resilience of the sessile oaks in Bercé, a site with high soil available
485 water, fertilized and control alike, was high and rapid confirming the drought tolerant behaviour of
486 this species (Bréda *et al.* 1993). From this study, it is not possible to conclude that the fertilization could
487 not improve the oak resilience. Such a conclusion could only be drawn from experimental designs
488 where the resilience of control trees is lessened, for instance because of drier conditions (*i.e.* lower
489 available water) or poorer soil fertility than those encountered in Bercé. It is however noteworthy here
490 that fertilization increased wood production without weakening trees in their response to drought.
491 Fertilization could be an efficient way to shorten the time needed to reach harvest diameters, reducing
492 the exposure time of trees to climatic hazards. For the future forest management, soil fertilization
493 could be, associated with a control of stand LAI (by thinning), an efficient lever to adjust nutrient and
494 water demands.

495

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497

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