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Linking above- and belowground phenology of hybrid walnut growing along a climatic gradient in temperate agroforestry systems

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Awaz Mohamed, Alexia Stokes, Zhun Mao, Christophe Jourdan, Sylvie Sabatier, et al.. Linking above- and belowground phenology of hybrid walnut growing along a climatic gradient in temperate agroforestry systems. *Plant and Soil*, 2018, 424 (1-2), pp.103-122. 10.1007/s11104-017-3417-4 . hal-01837395

HAL Id: hal-01837395

<https://hal.science/hal-01837395>

Submitted on 26 May 2020

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Plant and Soil

Above and belowground phenological relationships in hybrid walnut growing along a climatic gradient --Manuscript Draft--

Manuscript Number:									
Full Title:	Above and belowground phenological relationships in hybrid walnut growing along a climatic gradient								
Article Type:	Special Issue S71 - Root Ecology								
Keywords:	Agroforestry; rhizotron; root elongation; initiation; mortality; longevity								
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Order of Authors:	Awaz Mohamed Alexia Stokes Zhun Mao Christophe Jourdan Sylvie-Annabel Sabatier François Pailler Stephane Fournier Lydie Dufour Yogan Monnier								
Order of Authors Secondary Information:									
Funding Information:	<table border="1"> <tr> <td>Meta program INRA-AAFCC</td> <td>Dr. Alexia Stokes</td> </tr> <tr> <td>Campus France (FR)</td> <td>Dr Awaz Mohamed</td> </tr> <tr> <td>Kurdish Institute</td> <td>Dr Awaz Mohamed</td> </tr> <tr> <td>Fondation de France</td> <td>Dr Yogan Monnier</td> </tr> </table>	Meta program INRA-AAFCC	Dr. Alexia Stokes	Campus France (FR)	Dr Awaz Mohamed	Kurdish Institute	Dr Awaz Mohamed	Fondation de France	Dr Yogan Monnier
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Abstract:	<p>Background and Aims Plant phenology is a sensitive indicator of plant response to climate change. Observations of phenological events belowground for most ecosystems are difficult to obtain and are less characterized than those aboveground. Very little is known about the relationship between shoot and root phenology, especially in the field. We examined the influence of environmental factors and root morphological traits on fine root production and mortality in relation with shoot phenology in hybrid walnut trees (<i>Juglans sp. L.</i>) growing in three different climates (oceanic, continental and Mediterranean) along a latitudinal gradient in France.</p> <p>Methods Eight rhizotrons were installed at each site for 21 months to monitor tree root dynamics. Root elongation rate (RER), root initiation quantity (RIQ) and root mortality</p>								

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	<p>quantity (RMQ) were recorded frequently using a scanner and time-lapse camera. Leaf phenology, phenological phases and stem radial growth were also measured. Fine roots were classified into orders and 0-1 mm, 1-2 mm and 2-5 mm diameter classes and fine root longevity and risk of mortality were calculated per class of diameter at each site during different periods over the year.</p> <p>Results Root growth was not synchronous with leaf phenology in any climate or either year, but was synchronous with stem growth during the late growing season. A distinct bimodal pattern of root growth was observed during the aerial growing season but growth was negligible during the rest of the year. Maximal mean root elongation rates (RER) ranged from 2-5 mm during the late growing season (when leaves were still functioning), depending on climate. Mean RER was driven by soil temperature measured in the month preceding root growth in the oceanic climate site only. However, mean RER was significantly correlated with mean soil water potential measured in the month preceding growth at both Mediterranean (positive relationship) and oceanic (negative relationship) sites. Root diameter had no effect on RER. Mean RIQ was significantly higher at both continental and Mediterranean sites compared to the oceanic site. Soil temperature was a driver of mean RIQ during the late growing season at continental and Mediterranean sites only. Mean RMQ increased significantly with decreasing soil water potential during the late aerial growing season at the continental site only. Mean root longevity at the continental site was significantly greater than for roots at the oceanic and Mediterranean sites. Roots in the 0-1 mm and 1-2 mm diameter classes lived for significantly shorter periods compared to those in the 2-5 mm diameter class. First order roots lived longer than lateral roots at the Mediterranean site only and first order roots in the 0-1 mm diameter class had 44.5% less risk of mortality than that of lateral roots for the same class of diameter.</p> <p>Conclusions We conclude that factors driving root RER were not the same between climates. However, soil temperature was the best predictor of root initiation at all three sites, but drivers of root mortality remained largely undetermined.</p>
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Comment citer ce document :

Mohamed, A., Stokes, A., Mao, Z., Jourdan, C., Sabatier, S., Pailler, F., Fourtier, S., Dufour, L., Monnier, Y. (2017) Root growth and mortality of fine roots along a climatic gradient in temperate agroforestry systems. *Plant and Soil*, 424 (1-2), 103-122. , DOI : 10.1007/s11104-017-3417-4



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19/4/2017

Dear Hans,

We would like to submit the attached manuscript, entitled “Above and belowground phenological relationships in hybrid walnut growing along a climatic gradient” for consideration as a full paper in *Plant and Soil* (Special issue Root Ecology – EcoSummit 2016). All co-authors have agreed to the final version of the manuscript, which has not been submitted elsewhere.

Our think our manuscript is suitable for *Plant and Soil* because of the need for detailed data when aiming to understand, quantify and model fine root dynamics in relation to soil carbon sequestration and ecosystem functioning. We also require a better understanding of root system growth and phenology, especially in the natural soil environment.

Thank you for your consideration of our manuscript. Please do not hesitate to contact me if you require further information.

Yours sincerely

Alexia

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1 Above and belowground phenological relationships in hybrid walnut
2 growing along a climatic gradient

3

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14 **Key words**

15 Agroforestry; rhizotron; root elongation; initiation; mortality; longevity

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17

18

19

20 **Abstract**

21 ***Background and Aims***

22 Plant phenology is a sensitive indicator of plant response to climate change. Observations of
23 phenological events belowground for most ecosystems are difficult to obtain and are less
24 characterized than those aboveground. Very little is known about the relationship between shoot
25 and root phenology, especially in the field. We examined the influence of environmental factors
26 and root morphological traits on fine root production and mortality in relation with shoot
27 phenology in hybrid walnut trees (*Juglans* sp. L.) growing in three different climates (oceanic,
28 continental and Mediterranean) along a latitudinal gradient in France.

29 ***Methods***

30 Eight rhizotrons were installed at each site for 21 months to monitor tree root dynamics. Root
31 elongation rate (RER), root initiation quantity (RIQ) and root mortality quantity (RMQ) were
32 recorded frequently using a scanner and time-lapse camera. Leaf phenology, phenological
33 phases and stem radial growth were also measured. Fine roots were classified into orders and
34 0-1 mm, 1-2 mm and 2-5 mm diameter classes and fine root longevity and risk of mortality was
35 calculated per class of diameter at each site during different periods over the year.

36 ***Results***

37 Root growth was not synchronous with leaf phenology in any climate or either year, but was
38 synchronous with stem growth during the late growing season. A distinct bimodal pattern of
39 root growth was observed during the aerial growing season but growth was negligible during
40 the rest of the year. Maximal mean root elongation rates (RER) ranged from 2-5 mm during the
41 late growing season (when leaves were still functioning), depending on climate. Mean RER
42 was driven by soil temperature measured in the month preceding root growth in the oceanic
43 climate site only. However, mean RER was significantly correlated with mean soil water

44 potential measured in the month preceding growth at both Mediterranean (positive relationship)
45 and oceanic (negative relationship) sites. Root diameter had no effect on RER. Mean RIQ was
46 significantly higher at both continental and Mediterranean sites compared to the oceanic site.
47 Soil temperature was a driver of mean RIQ during the late growing season at continental and
48 Mediterranean sites only. Mean RMQ increased significantly with decreasing soil water
49 potential during the late aerial growing season at the continental site only. Mean root longevity
50 at the continental site was significantly greater than for roots at the oceanic and Mediterranean
51 sites. Roots in the 0-1 mm and 1-2 mm diameter classes lived for significantly shorter periods
52 compared to those in the 2-5 mm diameter class. First order roots lived longer than lateral roots
53 at the Mediterranean site only and first order roots in the 0-1 mm diameter class had 44.5% less
54 risk of mortality than that of lateral roots for the same class of diameter.

55 **Conclusions**

56 We conclude that factors driving root RER were not the same between climates. However, soil
57 temperature was the best predictor of root initiation at all three sites, but drivers of root mortality
58 remained largely undetermined.

59 **1. Abbreviations**

60 RER: Root elongation rate, RMQ: Root mortality quantity, RIQ: root initiation quantity, EGS:
61 early growing season, LGS: late growing season, DS: dormant season, ψ : Soil water potential.

62

63 **2. Introduction**

64 Climate models predict that an increase in atmospheric CO₂ concentration, precipitation and
65 temperature could affect many biological phenomena and increase the frequency and magnitude
66 of extreme weather events (Solomon et al 2007). Changes in plant phenology are considered to
67 be a very sensitive and observable indicator of plant responses to climate change (Steinaker et
68 al 2010, Morin et al 2010). The timing of above and below ground phenological events is
69 important to assess ecosystem function and plant productivity (Fridley 2012, Richardson et al
70 2006). Aboveground phenological events include bud burst, leaf expansion and leaf fall, all of
71 which have attracted attention because of the role they play in determining species' responses
72 to climate change (Diez et al 2012). However, observations of phenological events
73 belowground, including timing of root initiation, peak growth, survivorship and cessation of
74 growth, are more difficult to obtain for most ecosystems and hence are less characterized
75 especially in natural conditions.

76 Fine root dynamics, defined as elongation rate (Germon et al 2016, Jourdan et al 2008),
77 production and mortality (Hendrick & Pregitzer 1993b, Mao et al 2013b, McCormack et al
78 2014), turnover (Anderson et al 2003), survivorship (Anderson et al 2003, Kern et al 2004) and
79 senescence (Huck et al 1987), play an essential role in ecosystem nutrient cycling and the global
80 carbon budget (C) cycle (Vogt et al 1995, 1998, Gill & Jackson 2000) because they regulate
81 the storage of large quantities of C. It is widely acknowledged that fine root phenology could
82 be strongly influenced by different factors (biotic and abiotic) throughout the year, and these
83 factors alter patterns of root growth and longevity. Several studies found strong effects of
84 abiotic factors on root elongation, such as soil temperature (Kuhns et al 1985, Wan et al 2002,
85 Tanner et al 2006, Steinaker & Wilson 2008, Steinaker et al 2010, Coll et al 2012), soil water
86 content (Green et al 2005, Metcalfe et al 2008, Misson et al 2006, Block et al 2006) or air
87 temperatures (M'bou et al 2008, Tierney & Fahey 2002; Fukuzawa et al 2013). For example,

88 Mao et al, (2013) studying *Picea abies* L. and *Abies alba* Mill. in montane and subalpine forest
89 ecosystems have found that root elongation (RER) was significantly correlated with soil
90 temperature above temperatures of $>1^{\circ}\text{C}$. Germon et al, (2016), studying walnut (*Juglans*
91 *regia* × *nigra* L.) trees in a Mediterranean climate also found that RER was positively and
92 significantly correlated with mean soil temperature. In contrast, other studies have found no
93 correlations with abiotic factors (Hendrick & Pregitzer 1993a, Hendrick & Pregitzer 1993b,
94 Hendrick and Pregitzer 1996a, Joslin & Wolfe 1998, Joslin et al 2000) and suggest that
95 endogenous factors, such as growth regulators (McAdam et al 2016), photoassimilate transport
96 and photosynthates availability (Sloan et al 2016, Tierney & Fahey 2002, Joslin et al 2000) are
97 the main drivers of growth. Abramoff and Finzi, (2015) also suggested that endogenous cuing
98 and allocation of stored carbohydrates were dominant drivers of root growth in Mediterranean
99 trees. Radville et al, (2016), studying Arctic shrub-graminoid communities, showed that root
100 growth occurred in near freezing temperatures and was not driven by soil temperature.

101 Although air temperature may be the most important environmental factor controlling the
102 timing of aboveground growth, as reported by a number of studies (Menzel 2003, Radville et
103 al 2016a, Wielgolaski 1999), the drivers of belowground phenology are less clear. We also have
104 a poor understanding of the relationship between root growth and leaf phenology (Pregitzer et
105 al 2000, McCormack et al 2014, Abramoff & Finzi 2015) and how this relationship is affected
106 by abiotic factors. More effort is needed in understanding such relationships. It is commonly
107 assumed that root and shoot growth are asynchronous (Steinaker et al 2010, Abramoff & Finzi
108 2015, Sloan et al 2016) with a peak of root growth in the early and late spring (Contador et al
109 2015, Germon et al 2016) or in the summer (Psarras et al 2000). However, several studies have
110 shown that root growth can occur in a single flush but often occurs in multiple flushes
111 throughout the growing season (Reich et al 1980, Harris et al 1995, Steinaker et al 2010)
112 depending on resource availability either during a single seasonal pulse or multiple periods of

113 favorable environmental conditions (McCormack et al 2014). In temperate forests, leaf growth
114 occurs several weeks before root growth (Steinaker & Wilson 2008, Abramoff & Finzi 2015,
115 Harris et al 1995). While Radville et al, (2016) in an arctic climate, and Abramoff and Finzi,
116 (2015) reviewing data from a subtropical climate, showed that root growth precedes shoot
117 growth by several weeks to several months (Radville et al 2016b, Broschat 1998).

118 Fine root turnover provides considerable amounts of C and nitrogen (N) to the soil (McCormack
119 et al 2012, Cox et al 1977, Hendrick & Pregitzer 1993b, Wells & Eissenstat 2001), often
120 exceeding the amounts returned by leaf litter fall in some ecosystems (Vogt et al 1986). Fine
121 root lifespan is considered an important root trait (Wang et al 2016), because it determines the
122 quantity of root organic matter transferred to soil (Guo et al 2008) as well as exerting an indirect
123 control on nutrient and water uptake efficiency (McCormack et al 2012). Root turnover varies
124 widely within and among species and across ecosystems (Majdi et al 2005) but a fundamental
125 understanding of the mechanisms that control fine root life span among different climates is
126 poorly understood. Most published studies have related root lifespan either to endogenous
127 factors such as root diameter and branch order (Guo et al 2008, Wang et al 2016), seasons of
128 initiation, nitrogen (N) concentration (McCormack et al 2012), root depth (Baddeley and
129 Watson 2005) or to climatic factors such as temperature, water and nutrient availability (Chen
130 & Brassard 2013; Green et al 2005). However, knowledge of the influence of environmental
131 factors on fine root life span remains limited. Understanding how endogenous and
132 environmental factors co-vary to influence root longevity is therefore important in order to
133 provide a better understanding of the contribution of fine roots to resource fluxes (Baddeley
134 and Watson 2005).

135

136 In this study, we examined root elongation, initiation, mortality and survivorship of walnut trees
137 (*Juglans L.*) growing in agroforest systems over 21 months along a climatic gradient in France.

138 We focused on relating root phenology to leaf and stem phenology. We aimed at determining
139 which factor most drives root growth over different phenological periods. We also characterized
140 the relationship between root and shoot phenology, particularly in response to both temperature
141 and precipitations. Rhizotrons were used to monitor monthly root growth and mortality in each
142 site. We hypothesized that (i) shoot and root phenology are asynchronous regardless of the
143 climate, (ii) the drivers of root growth and mortality are not the same between climates, (iii)
144 root diameter is linked to elongation rate and is altered over phenological periods and between
145 climates, and (iv) root longevity is altered among climates.

146 **3. Materials and methods**

147 **3.1 Study sites**

148 Root and shoot phenology of hybrid walnut (*Juglans nigra* × *regia* L.) were studied in three
149 agroforestry systems along a latitudinal gradient in France. Trees were intercropped with
150 pasture or crops (Fig. S1). The most northern site was located at Cormont, Pas de Calais, France
151 (50°33'27.87"N, 1°44'3.08"E, elevation 40 m a.s.l.). Climate was oceanic with a mean annual
152 temperature of 11°C and a mean annual rainfall of 777.9 mm (Météo France, see section 3.2.2),
153 thus the site is hereafter termed 'oceanic' (Fig S2). The agroforest comprised hybrid walnut
154 (*Juglans nigra* × *regia* L.), common walnut (*Juglans regia* L., 1753), ash (*Fraxinus* L.),
155 sycamore (*Acer pseudoplatanus* L.) and oak (*Quercus* L.), at 13 m x 7.5 m tree spacing,
156 intercropped with permanent pasture (ovine pasture). All trees were planted in 1999 at a total
157 current density of 100 trees ha⁻¹. The soil is silt loam (Table 1; Fig. S3) and at least 2.5 m deep,
158 with the presence of the water table at this depth in June. The site is situated next to La
159 Dordonne River. The mean diameter at breast height (DBH) of walnut trees at the site was 0.30
160 ± 0.03 m and mean height was 14.75 ± 3.50 m.

161 The second agroforest was located at Le Beil, Madic, Cantal, France (45°22'7.95"N,
162 2°28'1.46"E, elevation 530 m a.s.l.). Climate was continental with a mean annual temperature
163 of 9.95°C and a mean annual rainfall of 1174 mm (Météo France, thus this site is hereafter
164 termed 'continental' Figs. S1, S2). The agroforest comprised three transplanted tree species:
165 hybrid walnut (*J. major* MJ209 *x J. regia* L.), cherry (*Prunus avium*) and sycamore (*Acer*
166 *pseudoplatanus*), at 12 m x 8 m tree spacing, intercropped with permanent pasture (ovine or
167 bovine pasture). All trees were planted in 1994 at a density of 100 trees ha⁻¹. The soil is sandy,
168 particularly acidic, and attained an average maximum depth of 110 cm on a 5° to 10° (Table 1,
169 Fig. S3). The site is situated 300 m from Madic Lake. Mean DBH of all walnut cultivars at the
170 site was 0.20 ± 0.02 m and mean height was 12.09 ± 1.30 m.

171

172 The third agroforest was located at the Restinclières experimental site, 15 km north of
173 Montpellier, Department Hérault, France (43°43'N, 4°01'E, elevation 54 m a.s.l.). The climate
174 is sub-humid Mediterranean with a mean annual temperature of 15.4 °C and a mean annual
175 rainfall of 873 mm (this site is henceforth termed 'Mediterranean,' Figs. S1, S2). The study plot
176 comprised hybrid walnut trees (*Juglans regia* × *nigra* L. cv. NG23), at 13 × 4 m tree spacing,
177 intercropped with durum wheat (*Triticum turgidum* L. subsp. *durum* (Desf.) Husn). However,
178 rapeseed (*Brassica napus* L.) was also cultivated in 1998, 2001 and 2006, and pea (*Pisum*
179 *sativum* L.) in 2010 and 2016. All walnut trees were planted in 1995 in lines oriented east west,
180 and the current density is 110 trees ha⁻¹. The annual crop was fertilized with approximately 150
181 kg N ha⁻¹ yr⁻¹ (Cardinael et al 2015). The soil is a silty clay deep alluvial soil (25% clay and
182 60% silt) with a depth > 4m, and slope angle is <1° within the site (Mulia and Dupraz 2006).
183 The site is near the Lez river watershed and the depth from the soil surface to the water table
184 usually oscillates between 5 m in winter and 7 m in the summer (Cardinael et al 2015). More
185 details about the experimental site are available in (Dupraz et al 1999, Mulia and Dupraz 2006,

186 Cardinael et al 2015). Mean DBH of all walnut trees at the site was 0.24 ± 0.13 m and mean
187 height was 11.09 ± 2.50 m.

188

189 **3.2. Climatic data**

190 Global precipitation data for the three sites were obtained from Météo-France. Weather stations
191 were located at Le Touquet, (oceanic: $50^{\circ}30'48''\text{N}$, $1^{\circ}37'18''\text{E}$, elevation 5 m a.s.l.), Station
192 Naves (continental: $45^{\circ}19'12''\text{N}$, $1^{\circ}46'18''\text{E}$, elevation 450 m a.s.l.) and Restinclières
193 (Mediterranean: 43.702 N et $3,86$ E, elevation 100 m a.s.l.). Air temperatures were measured
194 in the shade at a height of 1.5m at each site and soil temperatures were measured in two soil
195 layers (10 and 60 cm) per site, using Thermochron iButtons (DS1921G) (Hubbart et al 2005).
196 All sensors were programmed to measure the temperature twice a day (2 a.m and 2 p.m). Soil
197 water potential (noted ψ hereafter) was measured using Irrometers (WaterMark, IRROMETER
198 Company, Inc. USA) installed at each site at depths of 10 and 60 cm.

199 **3.3. Rhizotron installation**

200 To measure tree root elongation and mortality along the climatic gradient, we installed
201 rhizotrons, also called root windows, in pits at each field site (Fig. S4). Rhizotrons comprised
202 transparent polyvinylchloride (PVC) sheets placed against the soil profile, through which root
203 growth dynamics can be observed (Reich, et al., 1980; Misra, 1999; Mao et al., 2014). In the
204 oceanic site, four trenches (2m long x 1 m wide x 2m deep) were dug in one row of trees and
205 each pit was located at 2 m from the tree trunk. One rhizotron was installed on each opposing
206 face of the trench (n = 8 rhizotrons).

207 In the continental agroforest (Madic), we dug eight (1 m long x 1 m wide x 1 m depth) trenches
208 in three rows of trees. Each trench was at a distance of 2 m from the nearest tree trunk. Eight
209 rhizotrons (50 cm long x 50 cm wide x 0.5 cm thick), were installed.

210 At the Mediterranean site, one pit (5 m length x 1.5 m width x 4 m depth) was dug in March
211 2012 between two walnut trees on the same tree row (Fig. S5) (Cardinael et al. 2015). The pit
212 was reinforced with wooden beams to avoid collapse of the pit walls. In June 2014, two
213 rhizotrons (100 cm long x 80 cm wide x 0.5 cm thick) were installed as well as eight smaller
214 windows (65 cm long x 30 cm wide x 0.5 cm thick) at depths of 20, 115, 220 and 320 cm.

215 Where the rhizotrons were to be placed on the soil wall, we gently removed the soil to make a
216 flat surface and cut all roots on the profile with secateurs. The soil removed during the digging
217 of the trenches was kept aside, and then sieved through a 5 mm sieve and air-dried for several
218 hours. The sieved and air-dried soil was then poured into the space between the window and
219 the soil profile and slowly compacted using a wooden plank. Rhizotrons were placed vertically
220 against the soil profile at an angle of 15°. This angle will permit the roots to grow downwards
221 due to positive geotropism (Huck & Taylor 1982; Mao et al 2013). Each rhizotron was covered
222 with foil backed felt insulation and black plastic sheeting to protect roots from light and
223 temperature variations. All pits were then covered with wooden boards and corrugated plastic
224 or a metallic roof to avoid damage from passing animals and to prevent direct rainfall and
225 sunlight on the rhizotrons. In the first three months after installation, no root growth was
226 recorded because soil disturbance during rhizotron installation causes over estimations of root
227 growth (Strand et al 2008, Mohamed et al. 2017).

228 ***3.4. Measurements of root growth***

229 To measure fine root growth dynamics, we either scanned rhizotrons or used a time-lapse
230 camera to automatically take pictures before then analyzing images (Mohamed et al 2017). In
231 the continental and Mediterranean sites, a scan of each rhizotron (between two and four images
232 per window depending on the size of the window) was taken at monthly intervals over 21
233 months using an Epson Perfection V370 flatbed scanner with a high optical resolution of 4800
234 dpi (Fig. S6).

235 At the oceanic site, a time-lapse camera (Cuddeback Attack, U.S.A.) was placed on a wooden
236 cleat in front of each rhizotron at a distance of 90 cm from the rhizotron (Fig. S6). Photographs
237 were taken daily at 2 a.m. and 2 p.m. for 21 months. The time-lapse cameras ran automatically
238 for several months at a time using alkaline batteries. In September 2014, the trench at the
239 Mediterranean site was flooded due to exceptionally strong rainfall, therefore all rhizotrons
240 were reinstalled in March 2015. No data were recorded from September 2014 to March 2015,
241 and data were recorded from March to June 2015 but not used in the statistical analysis.
242 Similarly, at the oceanic site, nearly all trenches were flooded due to strong rainfall in January
243 2015 and the proximity of the water table, and almost half the cameras were damaged. In March
244 2015, all cameras were replaced and no data were recorded from January 2015 to March 2015.
245 To avoid the same problem the following year, we removed cameras from November 2015 to
246 March 2016, therefore data are missing for this period also.

247 Monthly measurements of root emergence, mortality and elongation were carried out
248 immediately after roots were observed in each rhizotron (and after the first three months had
249 passed) until October 2014. Roots were classified into three diameter classes: (0-1) mm, (1-2)
250 mm, and (2-5) mm. However for measurements from the camera method, because of an
251 overestimation of diameters (Mohamed et al., 2017), we corrected the value of root diameter
252 by using the following equation:

$$253 \quad y = 0.43x$$

254 Where y represents the value corrected of root diameter, x represents the real value of the
255 diameter taken by the camera. 0.43 is the relative value corresponding to the mean gap between
256 scanner measurement and camera measurement. We also classified root topology into two
257 orders: 'parent' or 'child' (SmartRoot software). The effect of root topological orders at the
258 oceanic site was excluded from the analysis because a negligible number of lateral roots
259 emerged.

260 In previous studies, root mortality was assumed to occur when the root became darker in color
261 (West et al 2004) or when it disappeared (Baddeley & Watson 2005). In some studies, both
262 criteria were applied (Wells & Eissenstat 2001, Anderson et al 2009). In our study, color was
263 the only criterion applied (Mao et al 2013a), as root death can occur before its disappearance
264 (Hooker et al., 2000). We declared the root dead when it was turning black with no growth
265 between two or more successive sessions until the last observation date occurred.

266 **3.5. Image analysis**

267 Once images of root growth had been acquired, we conducted analysed images using the semi-
268 automated SmartRoot software (Lobet et al 2011). SmartRoot is an operating system
269 independent freeware based on ImageJ and using cross-platform standards (RSML, SQL, and
270 Java) for communication with data analysis softwares (Lobet et al 2011, Mathieu et al 2015).
271 Before analyzing roots, when necessary, images need “stitching” together (e.g. with Adobe
272 Photoshop CS3 software), if several have been taken for the same rhizotron (when the rhizotron
273 surface area was greater than the field of the scanner). In the case of this study, we transformed
274 all images to 8 bit gray scale and then inverted them using ImageJ software so that roots were
275 darker than the background of the image. The length and diameter of each root produced during
276 one interval time (i.e. one month) were calculated for each rhizotron (Mohamed et al. 2017).
277 Before analyzing a new sequence of images, SmartRoot provides the user with an icon to import
278 the traces of the same roots from the previous image data file to superimpose them on this new
279 image, which helps the estimation of the evolution of root length. This preceding image also
280 helps determine whether the root is live (walnut roots are usually cream in color) or dead
281 (turning black) (Huck & Taylor 1982, Mao et al 2013b).

282 **3.6. Aboveground phenology and radial growth**

283 We assessed the timing of shoot production through changes in the phenological phases of
 284 leaves throughout the year. We divided the year into three phenological periods, early growing
 285 season (from budburst to 100% leafing out of early green leaves), late growing season (100%
 286 leafing out to leaf-fall) and dormancy (leaf-fall to budburst, Fig. 1). Shoot phenological periods
 287 were recorded using a time-lapse camera (Wingscapes TimelapseCam8.0) at a resolution of 5
 288 megapixels in the oceanic and continental agroforests. One camera per site was placed on the
 289 trunk of one tree facing a line of trees. Photographs were taken daily at 12 a.m. and 12 p.m. At
 290 the Mediterranean site, shoot phenological periods were recorded visually using binoculars.
 291 During the bud-burst period, visual measurements were made daily.

292 We also measured the radial growth of tree trunks by installing dendrometers (Increment
 293 Sensor DB20) on eight trees per site. The dendrometers are girth bands, comprising a steel
 294 band, spring and nonius scale. Bands were placed on the stem; at a height of 1.3 m. Measured
 295 values are read at the nonius scale with 0.1 mm precision. Readings were made monthly at both
 296 continental and Mediterranean sites. However, readings were made only every three months at
 297 the oceanic site because of difficulties with site access. Tree height was recorded annually after
 298 leaf shedding using a hypsometer Vertex (Quebec, Canada).

299 **3.7. Root growth and mortality dynamics**

300 We used the following methods to estimate root elongation rate (RER), initiation and mortality:

301 (i) individual root growth was evaluated by calculating the difference between root length at $t-1$
 302 and at t . To determine daily RER, the mean of all individual root lengths produced between
 303 time t and $t-1$ was divided by the duration of the corresponding period:

$$305 \quad RER_{t-1, t} = \frac{len_{.t} - len_{.t-1}}{Pt_{-1, t}} \quad (\text{Equation 1})$$

306 where, $RER_{t-1, t}$ is the daily root elongation rate (in mm/day) from inventory time $t-1$ to t ; len_{t-1} and len_t are the lengths of the root n at inventory time $t-1$ and t , respectively; $p_{t-1, t}$ is the
307
308 period in days between inventory time $t-1$ and t .

309 (ii) Monthly mean root initiation quantity (RIQ), was calculated as the mean number of new
310 roots initiated between time t and $t-1$.

311 (iii) Monthly mean root mortality quantity (RMQ) was calculated as the mean number of dead
312 roots between t and $t-1$ only when alive roots were present.

313 **3.8. Statistical analysis**

314 All indicators of root dynamics, including mean RER (for growing roots only), mean RIQ and
315 mean RMQ (when the total number of alive roots was >0) were calculated using R software
316 Version 2.15.3 (R Development Core Team 2013). A Shapiro-Wilk test was performed before
317 each test to test if data followed a normal distribution and homogeneity of variances was
318 checked. For data not normally distributed, analyses were performed by a Kruskal-Wallis test.
319 Effects of season, site, diameter classes and topological orders were tested on each variable. A
320 post-hoc analysis was performed when the Kruskal-Wallis result was significant, using a
321 Nemenyi test of Kruskal Wallis at $p < 0.05$ to determine which levels of the independent variable
322 differed from each other level. Spearman's rank correlations (Spearman) were performed to
323 determine the relationship between the climatic variables (mean soil and air temperatures and
324 mean ψ) of the both the current and preceding months, and the mean RER, mean RIQ and mean
325 RMQ.

326 A Cox Proportional Hazard Model was used to analyze the effects of different varying factors
327 on root mortality and to calculate root longevity and risk of mortality. Factors used as variables
328 included sites, phenological period, diameter classes and topology orders. Different Cox Hazard
329 Models were performed for two topological orders: parent and child order (SmartRoot

330 software). We performed the statistical test only when the sample size was >20 for each
331 category (topology order, diameter classes, sites, time periods). All analyses were performed
332 using R software, Version 2.15.3 (R Development Core Team 2013) at a significance level of
333 <0.05.

334 **4. Results**

335 **4.1 Latitudinal gradient of meteorological and soil hydrological data**

336 Mean annual temperature over the two year period was 11.7°C (oceanic), 12.4°C (continental)
337 and 14.8°C (Mediterranean). Mean monthly air temperature over the same period was lowest
338 in December at all field sites (ranging from 3.1°C to 7.6°C; Fig. 1), and highest in July at the
339 oceanic (17.8°C), continental (20.6°C) and Mediterranean sites (24.3°C) (Fig. 2). Mean soil
340 temperatures during the early growing season at the oceanic site was 12.7°C, compared to
341 14.1°C and 11.9°C at the continental and Mediterranean sites, respectively. Mean soil
342 temperatures were 13.9°C (oceanic), 15.8°C (continental) and 17.9°C (Mediterranean) during
343 the late growing season and 9.6°C (oceanic), 10.8°C (continental), 6.7°C (Mediterranean)
344 during the dormant season.

345 Average annual precipitation over 2014 and 2015 was 910 mm (oceanic), 1056 mm
346 (continental) and 938 mm (Mediterranean) (Fig. 2). Rainfall at the Mediterranean site was
347 highly variable between the two years, with 1264 mm in 2014 and only 613 mm in 2015 (Fig.
348 2). A negative and significant ($p < 0.001$, $r = -0.40$) correlation was found between total annual
349 rainfall and ψ .

350 Mean annual soil water potential was significantly higher at the Mediterranean site than those
351 of continental and oceanic sites ($p < 0.0001$) and the oceanic site had a significantly higher ψ than
352 the continental site ($p < 0.001$).

353 Mean annual soil and air temperatures at the Mediterranean site were both significantly higher
354 than those at the continental and oceanic sites ($p < 0.001$) and the oceanic site had a significantly
355 greater mean soil temperature compared to the continental site ($p = 0.04$). However, no
356 significant differences were found in mean air temperature between oceanic and continental
357 sites ($p = 0.17$).

358 **4.2 Leaf phenology**

359 The date of budburst differed among sites: the Mediterranean trees in 2015 had an earlier
360 budburst (18 April 2015) than the continental and oceanic climates by 15 days and 27 days,
361 respectively. In 2016, this difference increased to 21 and 28 days, respectively (Table 2). The
362 Mediterranean trees had an earlier leaf unfolding date (2 June 2015) than the continental and
363 oceanic climates by 3 and 16 days, respectively. Mediterranean trees had later leaf fall (18
364 November 2014 and 12 November 2015) than the continental (6 days in 2014 and 15 days in
365 2015) and oceanic sites (10 days in 2014 and 9 days in 2015).

366 **4.3 Stem phenology**

367 The timing of root growth was synchronous with that of stem growth during the late growing
368 season (from June to November) in both study sites (Fig. 3). Stem radial growth started when
369 trees had 100 % of leaf unfolding (the onset of late growing season). Root and stem growth had
370 an antagonistic growth pattern (Fig. 3), i.e. peaks of root growth occurred inversely to those of
371 stem growth. Stem growth then dropped sharply with leaf fall. The length of the radial growing
372 season was shorter than that of roots by 86 days and 73 days at both continental and
373 Mediterranean sites, respectively.

374 **4.4 Root elongation rate (RER)**

375 Mean RER for growing roots at all sites was influenced significantly by season, with a bimodal
376 distinct flush of root growth observed during the aerial growing season (Fig. 4), and negligible

377 growth during the rest of the year. Peaks of mean RER always lagged behind those for budburst.
378 In 2015, mean RER was initiated before budburst in both oceanic (28 days) and continental (26
379 days) climates. However at the Mediterranean site, budburst preceded root elongation by 28
380 days in 2015. Mean RER peaked in June (Mediterranean) or July (oceanic and continental; Fig.
381 2), before decreasing and then peaking to a lesser extent in August for the Mediterranean site,
382 and September for the oceanic and continental sites (Fig. 4). When mean RER (during all
383 observation periods) and between all sites was compared, mean RER was significantly higher
384 ($p = 0.01$) at the oceanic site compared to the continental site only.

385 No significant relationships were found between RER and root diameter classes. No significant
386 differences were found in RER of any roots between the early and dormant seasons.

387 When all root data were combined, mean RER was positively and significantly correlated with
388 the mean air and soil temperatures of the month preceding the RER measurement at the oceanic
389 ($P < 0.0001$, $r_s = 0.55$) and continental ($P < 0.0001$, $r_s = 0.48$) sites only (Fig. 5a,b). Mean RER was
390 correlated with mean ψ at the oceanic site only (Fig. 5c, $P < 0.001$, $r_s = 0.55$). However, when
391 mean RER of roots growing during the aerial growing season was examined, positive and
392 significant correlations were found between mean RER and soil temperature (Fig. 6a, $p = 0.002$,
393 $r_s = 0.61$) and mean RER and air temperature (Fig. 6b, $p = 0.004$, $r_s = 0.48$) of the month preceding
394 growth at the oceanic site only. The mean RER was significantly correlated with mean ψ in
395 both oceanic (negatively) (Fig. 6c, $p = 0.004$, $r_s = -0.48$) and Mediterranean (positively) (Fig. 6c,
396 $p = 0.05$, $r_s = 0.50$) sites only.

397 **4.5 Comparing and above and belowground phenology**

398 Phenological periods of growth differed between sites. In 2015, the Mediterranean climate had
399 a longer aerial growing season (208 days) than continental and oceanic climates by 30 days and
400 36 days, respectively. In 2014, the dormant season was shorter at the Mediterranean site (151

401 days) compared to continental (172 days) and oceanic sites (188 days). However, in 2015, the
402 length of the growing season was similar in oceanic and Mediterranean climates but the dormant
403 season was longer by 36 days at the continental site (Table 2). The duration of the growing
404 season of roots was longer than that for leaves for the oceanic (38 days), continental (62 days)
405 and Mediterranean (8 days) sites (Table 2). Root growth was not synchronous with leaf
406 phenology in any climate or either year. However, root elongation was synchronous with trunk
407 growth in the three climates (Fig 4).

408 **4.6 Mean monthly root initiation and mortality quantities**

409 Mean RIQ was always highest during the late growing season compared to the other seasons.
410 The first peak of root appearance at each site was 3 months after rhizotron installation (October
411 2014 at both the oceanic and continental sites and in June 2015 at the Mediterranean site). In
412 2015, peaks of mean RIQ were found in June at the oceanic site (1.17 ± 2.32 roots), in July at
413 the continental site (3.6 ± 6.02 roots) and in October at Mediterranean site (1.71 ± 3.29 roots;
414 Fig. 7). Each peak of mRIQ was followed immediately by a peak of mRMQ in all climates
415 during the late growing season (Fig. 7). A significantly lower number of roots was initiated
416 ($p=0.02$) at the oceanic site (0.66 ± 1.87 roots) compared to both continental (0.7 ± 5.3 roots)
417 and Mediterranean climates (1.9 ± 4.9 roots). No significant differences in mean RIQ were
418 found between continental and Mediterranean sites.

419 No significant differences in mean RMQ were found between climates between early and late
420 growing seasons. Mean RMQ was significantly higher in the late growing season compared to
421 the dormant season ($p = 0.009$).

422 During the late growing season, mean RIQ was not correlated with mean ψ in any of the three
423 climates (Fig. 8). Significant negative correlations were found between mean RIQ and mean
424 soil temperature of the preceding month at the continental ($P < 0.001$, $r_s = -0.28$) and

425 Mediterranean ($P < 0.001$, $r_s = -0.54$) sites only (Fig. 8). Mean air temperature of the preceding
426 month was negatively correlated ($p = 0.002$, $r_s = -0.37$) with mean RIQ in the Mediterranean
427 climate only (Fig. 8). However, mean RMQ increased rapidly with the increase of mean soil
428 temperature and mean ψ and peaked when ψ was maximal at the continental site only (Fig. 9).
429 However, mean RMQ was not correlated with mean soil or air temperatures or mean ψ in either
430 oceanic or Mediterranean sites (Fig. 9). When all factors were considered together, mean RIQ
431 and mean RMQ of first order roots (parent) was significantly greater than lateral order (child)
432 roots at the continental site only ($p < 0.001$).

433

434 **4.7 Root longevity and risk of mortality**

435 Cox's proportional hazards regressions showed that when all root diameter classes were
436 grouped together, mean root longevity at the continental site was significantly greater than for
437 roots at the oceanic ($z = 7.7$, $p < 0.001$) and Mediterranean ($z = 14.2$, $p < 0.001$) sites. The longevity
438 of roots at the Mediterranean site was significantly shorter than at the oceanic site (Fig. 10a,
439 Table 3). Compared to the continental climate, the risk of mortality was 2.7 times greater for
440 roots from the Mediterranean site and 2.1 times greater for roots from the oceanic site. The
441 phenological period had an important effect on root longevity at continental site but not at
442 oceanic and Mediterranean sites during the observation period. At the continental site,
443 compared to the dormant season, the risk of mortality was 1.8 times more during the early
444 growing season and 1.7 times more during the late growing season (Fig. 10b). No significant
445 differences in longevity were found between growing seasons at the other two sites. Root
446 diameter classes had the largest effect on root longevity compared with other factors. When
447 lateral roots were excluded from the analysis (for all growth periods combined), roots in the 0.1
448 mm diameter class lived for significantly shorter periods compared to those in the 2-5 mm
449 diameter class at continental ($z = -1.65$, $p = 0.006$) and Mediterranean ($z = -3.36$, $p = 0.0007$) sites

450 only. However, no significant differences in longevity were found between roots from the 0-1
451 mm and 1-2 mm diameter classes (Fig. 10c). At the continental site, roots in the 2-5 mm
452 diameter class had 38% less risk of mortality than roots in the 0-1 mm diameter class. At the
453 Mediterranean site, roots in the 2-5 mm diameter class had 61% less risk of mortality than those
454 from 0-1 diameter class. When all factors were considered together, except for topological
455 order, first order roots lived longer than lateral roots at the Mediterranean site ($z = -3$, $p = 0.005$)
456 but not at the continental site. At the Mediterranean site, first order roots in the 0-1 mm diameter
457 class had 44.5 % less risk of mortality ($z = -3.04$, $p = 0.002$) than that of lateral roots for the same
458 class of diameter, but no differences in longevity were found at the continental site. First order
459 roots in the 1-2 mm diameter class had significantly longer longevity ($z = -2.7$, $p = 0.005$) than
460 lateral roots of the same class of diameter at the Mediterranean climate, but not at the continental
461 site.

462 **5. Discussion**

463 We did not find any significant differences between climates with regard to the phenology of
464 root dynamics throughout the year. Walnut hybrids had a distinct bimodal pattern of root growth
465 during the aerial growing season in all three climates, with much less root growth during the
466 aerial dormant season.

467 *Temperature and soil water potential effects on root growth dynamics*

468 Mean RER of walnut trees was positively correlated with both mean soil and air temperatures
469 at the oceanic and continental sites only. It is surprising that we did not find any relationships
470 between mean RER and temperature at the Mediterranean site, as Germon et al (2016) found a
471 highly significant and positive correlation between RER and soil temperature for the same stand
472 of walnut cultivars. However, mean RER was significantly and positively correlated with mean
473 air and soil temperatures during the late growing season, where the highest peaks of root growth

474 were found at the oceanic site only. Mean RER at the oceanic site was also significantly and
475 negatively correlated with mean soil ψ of the preceding month, i.e. as was also found by Joslin
476 et al., (2001) for oak (*Quercus prinus* L.) and white oak (*Quercus alba* L.) growing in a
477 subtropical climate. However, mean RER at the Mediterranean site was significantly but
478 positively correlated with mean soil ψ , similar to results for *Abies balsamea* L. (Olesinski et al
479 2011) and *Quercus alba* L. seedlings (Reich et al 1980). At the continental site, the absence of
480 correlations of RER with any climatic factors is in conflict with other studies which indicate
481 that air and soil temperatures are the prominent factors driving RER (Misra 1999, Hendricks et
482 al 2006, Mao et al 2013b, McCormack and Guo 2014, Germon et al 2016, Gill & Jackson 2000),
483 especially during the growing season in temperate climates. In our study, for all climates, soil
484 temperature never reached below 3°C or above 21°C during the entire study period. Most root
485 elongation occurred when the soil temperature was within the range 9 - 17°C. Our results are
486 contradictory to those found by Heninger and White (1974) and Lyr (1996) who showed that
487 the highest rates of root growth of deciduous trees under non limiting moisture conditions
488 were usually found when soil temperatures were above 20°C. Here we found that the highest
489 rate of elongation occurred when temperatures were between 14 - 17°C. At the oceanic site,
490 soil temperature varied little throughout the year, with few extreme values, whereas the
491 continental site had large seasonal differences in soil temperature. Mean soil ψ at the
492 Mediterranean site was significantly lower than at the oceanic and continental sites. Soil ψ can
493 limit root elongation by either excessive water resulting in anaerobic conditions or inadequate
494 water to support growth (Joslin et al 2001). Previous studies have shown that walnut seedlings
495 have a low resistance to water stress and are sensitive to waterlogging both between and within
496 cultivars (Mapelli et al 1995), a phenomenon that we demonstrated (waterlogging occurred in
497 the oceanic site and water stress in occurred in the Mediterranean site).

498 Our results demonstrated a decline in RER with the decrease of mean soil ψ at the
499 Mediterranean site, suggesting that soil water is limiting for root growth in the superficial
500 layers, as found for other broadleaf species (e.g. Wan et al., 2002 studying *Gutierrezia*
501 *sarothrae*). However, at the oceanic site, our results showed that RER augmented with the
502 decrease of mean soil ψ and declined with the increase of mean air and soil temperatures, also
503 found by Joslin et al, (2001) in *Quercus prinus* L.. Our results indicate that at the oceanic site,
504 soil temperature played a major role in driving root elongation, as also found by (Germon et al
505 2016, Mao et al 2013b, McCormack and Guo 2014) and that soil ψ played an indirect role, but
506 as both factors co-vary during the late growing season, it is difficult to disentangle their distinct
507 effects on root growth.

508 Our results suggest that, once soil temperature is favorable for roots, and if there are no extreme
509 occurrences of temperature throughout the year, then other limiting factors will drive root
510 growth. For example, root growth decreased substantially irrespective of soil temperature
511 during a period of drought (Reich et al, 1980) (similar to the climatic conditions at our
512 Mediterranean site).

513 Surprisingly, and contrary to the observations of previous authors (e.g. Germon et al, (2016)
514 working on walnut cultivars, Mao et al, (2013) studying *P. abies* and *A. alba* and Kern et al
515 (2004) studying *Populus deltoides* Bartr), mean RER was not related to root diameter. While
516 trees growing at the continental site produced many short-lived lateral roots, no lateral root
517 initiation occurred at the Mediterranean and oceanic sites. Soil conditions could have played a
518 role because strong soil acidity has been showed to increase heavy metal solubility and hinder
519 the development of lateral roots (Kahle 1993). The lower phosphorus content at the continental
520 site would also influence root architecture and lateral root development, as roots increase their
521 exploration and scavenging of the soil (Rao et al. 2015).

522 Mean RIQ and mean RMQ were related to annual variations in soil temperature, except for
523 the first peak of root initiation which occurred three months after rhizotron installation at the
524 three sites regardless of the phenological period (Johnson 2001, Baddeley & Watson 2005) .
525 We consider this result as an artefact of the rhizotron method, which led to an overestimation
526 of the fine root production (Hendrick & Pregitzer 1996a, Majdi 1996, Majdi et al 2005, Green
527 et al 2005, Metcalfe et al 2008). The second peak of mean RIQ was found during the late
528 growing season, regardless of climate, and was followed immediately by a peak in mean RMQ.
529 Therefore, the major pulse of hybrid walnut root production is inherently programmed to occur
530 during the late growing season (June-November) with significantly less production in the aerial
531 dormant season, as also found in many deciduous tree species in temperate zones (e.g., Joslin
532 2000; Hendrick & Pregitzer, 1996a,b, Joslin et al 2000). Psarras et al, (2000), also found a peak
533 of root emergence in *Malus sylvestris* (L.) in late June and early July, which coincided partially
534 with major phases of shoot and fruit growth.

535 In our study, mean RIQ was significantly higher at the continental site compared to the two
536 other sites during the late growing season. A first possible reason is to link to the phenomenon
537 responsible for the higher development of lateral roots. Another explanation for this greater
538 productivity is that soil and air temperatures and ψ were optimal for growth during the late
539 growing season. Mean RIQ was correlated with mean soil temperature at the Mediterranean
540 and continental sites only, as was expected (Comas et al, 2005, Mao et al 2013a), but the lack
541 of significant relationships at the oceanic site is not understood. However, air temperature at
542 the three sites were correlated with mean RIQ during the late growing season. These results are
543 consistent with the observations of Radville et al (2016a), Fukuzawa et al (2013) and Steinaker
544 et al (2010), who demonstrated that temperature was a main driver of root initiation in temperate
545 environments. Tierney et al, (2003) also showed that mean fine root production of sugar maple
546 trees was strongly associated with mean air temperature but not soil moisture or nutrient

547 availability. However, in a literature review, Abramoff & Finzi (2015) suggested that for
548 Mediterranean trees, endogenous factors and the allocation of stored carbohydrates were
549 dominant drivers of root growth.

550 We found that mean RMQ did not differ significantly between sites and was highest during the
551 late growing season. These results are contrary to those of Kern et al, (2004), working on
552 *Populus deltoides* Bartr. in a continental climate, who found that mortality was greatest after
553 the end of the growing season. Mean RMQ was correlated with both mean soil temperature and
554 mean ψ at the continental climate only. Our results are in agreement with the finding of Harris
555 et al (1995), studying *Acer saccharum* in a moderate continental climate, who showed that root
556 mortality increased in warmer soil temperatures. We consider the peak of mortality as a
557 consequence of a trade-off between competing plant sinks to balance carbohydrate availability.
558 These results suggest that, if other factors are equal, the growth of new roots and the death of
559 existing roots are accelerated with the increase of soil temperature.

560

561 *Above and belowground phenological relationships*

562 The timing of root growth was asynchronous with that of budburst at all sites, and the spring
563 root flush occurred several weeks after budburst. As both budburst and root emergence are very
564 sensitive to local temperatures (Du and Fang 2014, Tierney and Fahey 2002), a rapid increase
565 in air temperature in April/May would stimulate budburst quickly. Soil is buffered against rapid
566 changes in air temperature, therefore the subsequent cambial activity in roots would take longer
567 to occur, and root flushes will usually occur after bud burst (Pregitzer et al 2000). Maximal root
568 and radial stem growth both took place during the late growing season. Peaks of stem and root
569 radial growth at the Mediterranean site occurred later in the season (September) than at both
570 other sites (July), possibly linked to precipitation events after the hot, dry summer.

571 Our results suggest a trade-off between competing plant sinks (Radville et al 2016a). For
572 example, fine root growth was likely fueled by non-structural carbohydrates (NSC) stored
573 before the onset of the aerial growing season, as suggested by Gaudinski et al, (2009) and Najar
574 et al (2014). The decrease in fine root elongation observed in August (oceanic and continental
575 sites) and July (Mediterranean site) may be due to NSC being used for radial growth and fruit
576 production. NSC production from photosynthesis would then increase during the summer,
577 fueling a second root flush, before leaf senescence in November. The decrease in photosynthetic
578 rates at the end of the growing season would result in less NSC being available for radial
579 growth, which decreases rapidly in September – October (Radville et al 2016a, Du and Fang
580 2014, Abramoff & Finzi 2015). Minor root elongation can occur during aerial dormancy at all
581 sites, using local NSC stocks as energy for growth.

582

583 *Root longevity and risk of mortality*

584 We showed that root longevity differed significantly between climates and roots lived longest
585 at the continental site. Fine roots at this site were significantly thicker and root diameter was
586 correlated to longevity, as also shown by e.g., Anderson et al, (2003) and Wells and Eissenstat,
587 (2001). Roots in the 0-1 mm and 1-2 mm diameter classes lived for significantly shorter periods
588 compared to those in the 2-5 mm diameter class at continental and Mediterranean sites only.
589 Thicker roots have lower N concentration, lower surface area and higher C content than finer
590 roots and thus longevity is increased because of a decrease in metabolic activity (McCormack
591 et al 2012, Guo et al 2004, 2008, Baddeley & Watson 2005).

592 As root traits may be prominent drivers of ecosystem processes (McCormack et al, 2015), and
593 as root topological order can influence traits, considering root topology when studying root
594 survivorship is considered fundamental (Guo et al, 2008). In our study, first order roots lived
595 longer than lateral roots at the Mediterranean site only and first order roots in the both 0-1 mm

596 and 1-2 mm diameter classes had 44.5% less risk of mortality than that of lateral roots for the
597 same class of diameter, as also found by McCormack et al (2012). Guo et al, (2008) also showed
598 in longleaf pine (*Pinus palustris*. Mill.) that higher order roots had 46% greater longevity than
599 roots one order lower. We suppose that first order roots live longer than lateral roots because
600 of the greater resource investment in their construction. Finer lateral roots cost less to construct,
601 and so can grow quickly when needed for soil exploration and resource capture.

602 The risk of root mortality at the continental site was significantly greater during the growing
603 season compared to the aerial dormant season, as also found in apple (*Malus sylvestris*. L)
604 (Psarras et al 2000). However, our results are contrary to those of Wang et al, (2016), who found
605 that the mortality hazard ratio of *Picea abies* and *Abies alba* initiated in the late growing season
606 was reduced by 26.8% compared to roots that emerged in the early growing season. Root
607 longevity usually decreases with increasing temperature (King et al 1999, Majdi et al 2005),
608 therefore, as temperature fluctuations were more extreme at the continental site, roots may die
609 more quickly as summer temperatures increase rapidly. As root density was higher during
610 growing season at the continental site, soil herbivores and pathogens may be more active (Guo
611 et al 2008).

612

613 In conclusion, although root studies have increased significantly in recent years, it is still
614 difficult to draw any firm conclusions about how variations in climate will affect root dynamics
615 and in turn how changes in dynamics might affect plant production or carbon cycling in soil.
616 The main reason may be the difficulty to generalize this impact in the face of broad variability
617 in responses among plant species, biomes and climates, as well as the variability introduced by
618 methodology (Norby and Jackson, 2000). Our results call for further analyses on the role of site
619 conditions (e.g. soil, altitude, topography and plant genotype) in determining tree responses to
620 climate variability. An interesting next step would be to focus on better understanding how

621 edaphic and climatic factors interact in natural environments to influence the fine root
622 phenology of plants at various temporal and spatial scales. In addition, the seasonal phenology
623 of trees is a main driver of C allocation from shoots to roots, thus further research is also
624 required to evaluate more precisely the relationship between the internal dynamics of tree C
625 and nutrient resources and root phenology.

626 **Acknowledgments**

627 Thanks are due to Jérôme Nespoulous, Luis Merino Martin and Merlin Ramel (INRA) for
628 technical assistance, to Camille Béral (Agroof) for help finding field sites and to the farmers
629 M. Queuille and M. Becue for letting us work in their agroforests.

630 **Competing interests**

631 The authors declare that they have no competing interests.

632 **Funding**

633 Funding for a Ph.D. bursary was provided by Campus France and the Kurdish Institute, France
634 (AM), la Fondation de France (YM) and fieldwork was funded by the FOARDAPT project,
635 INRA metaprogram AAFCC (Adaptation of Agriculture and Forests to Climate Change),
636 France.

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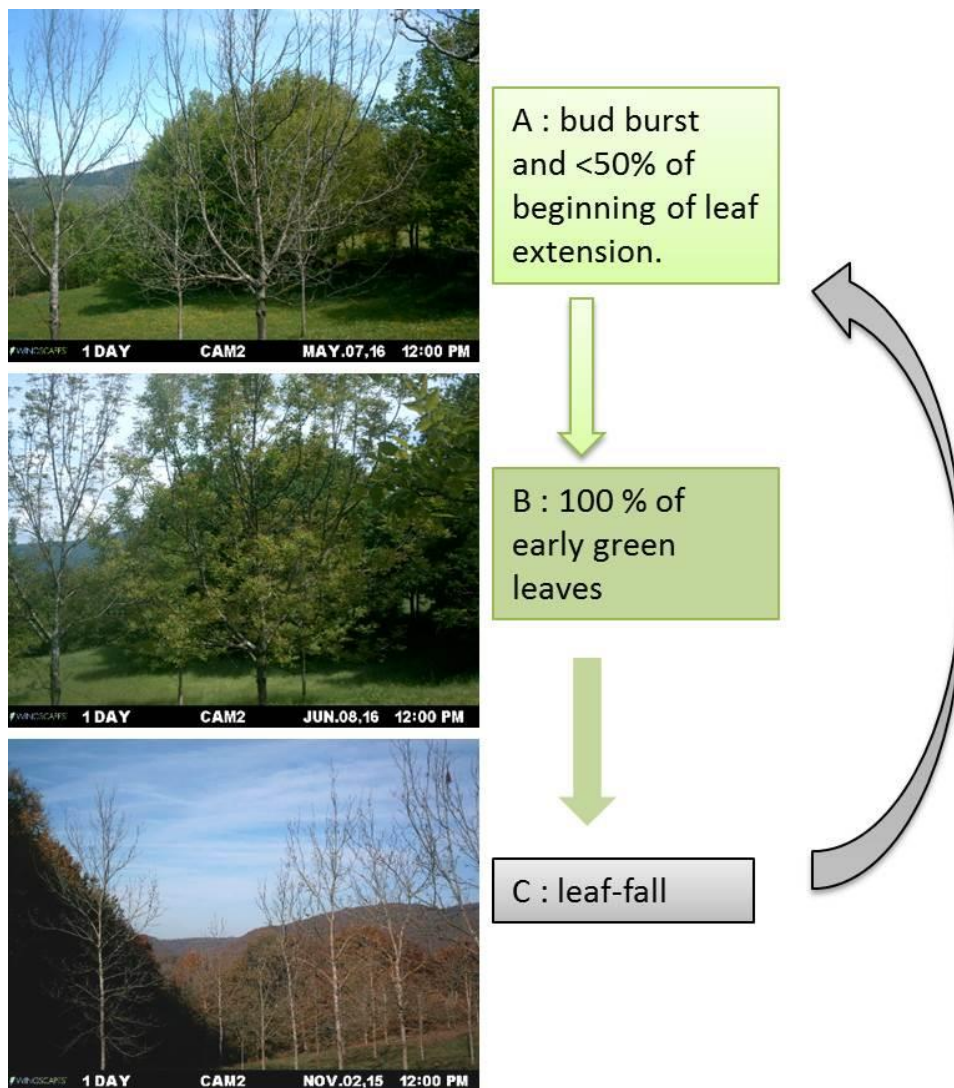
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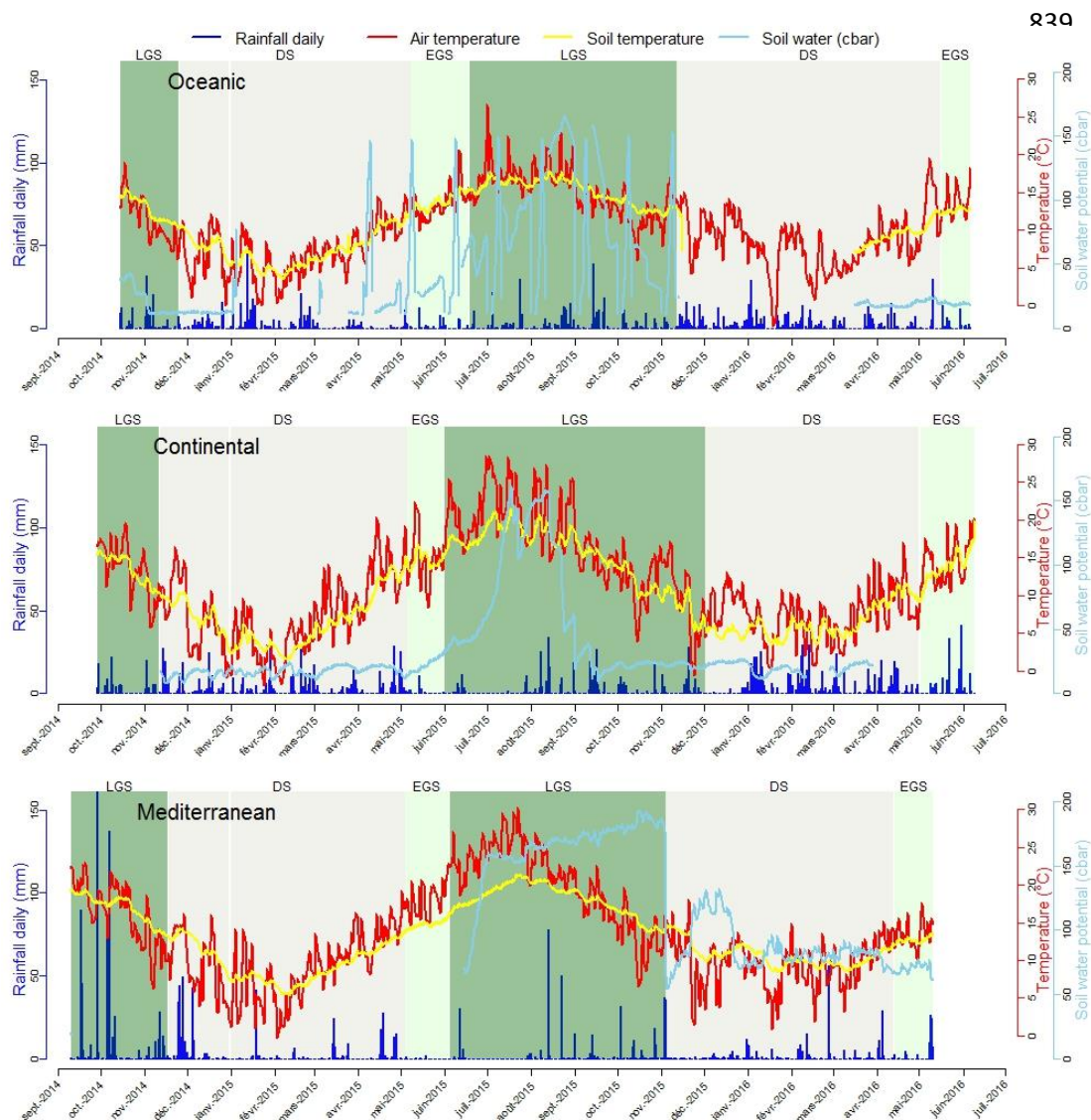
832 **7. Figures**

833



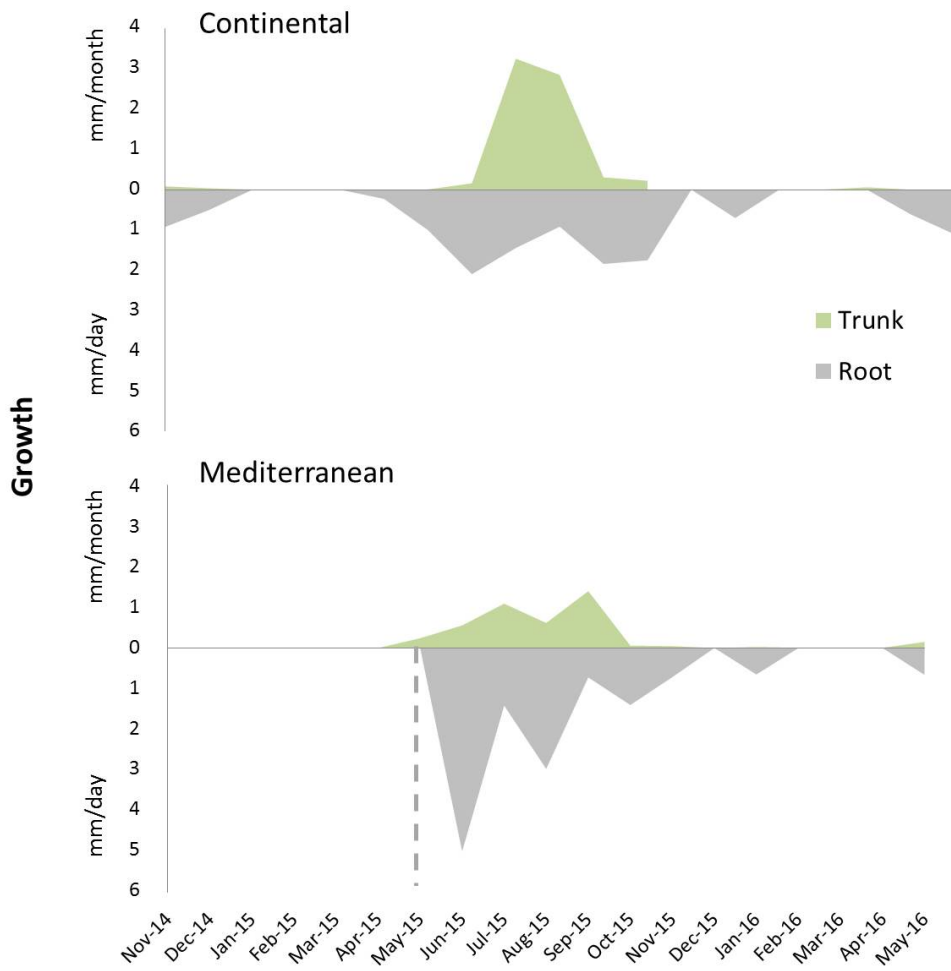
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836 Figure 1. The three leaf phenological phases observed throughout the year (bud-burst, 100% leafing,
 837 leaf-fall).

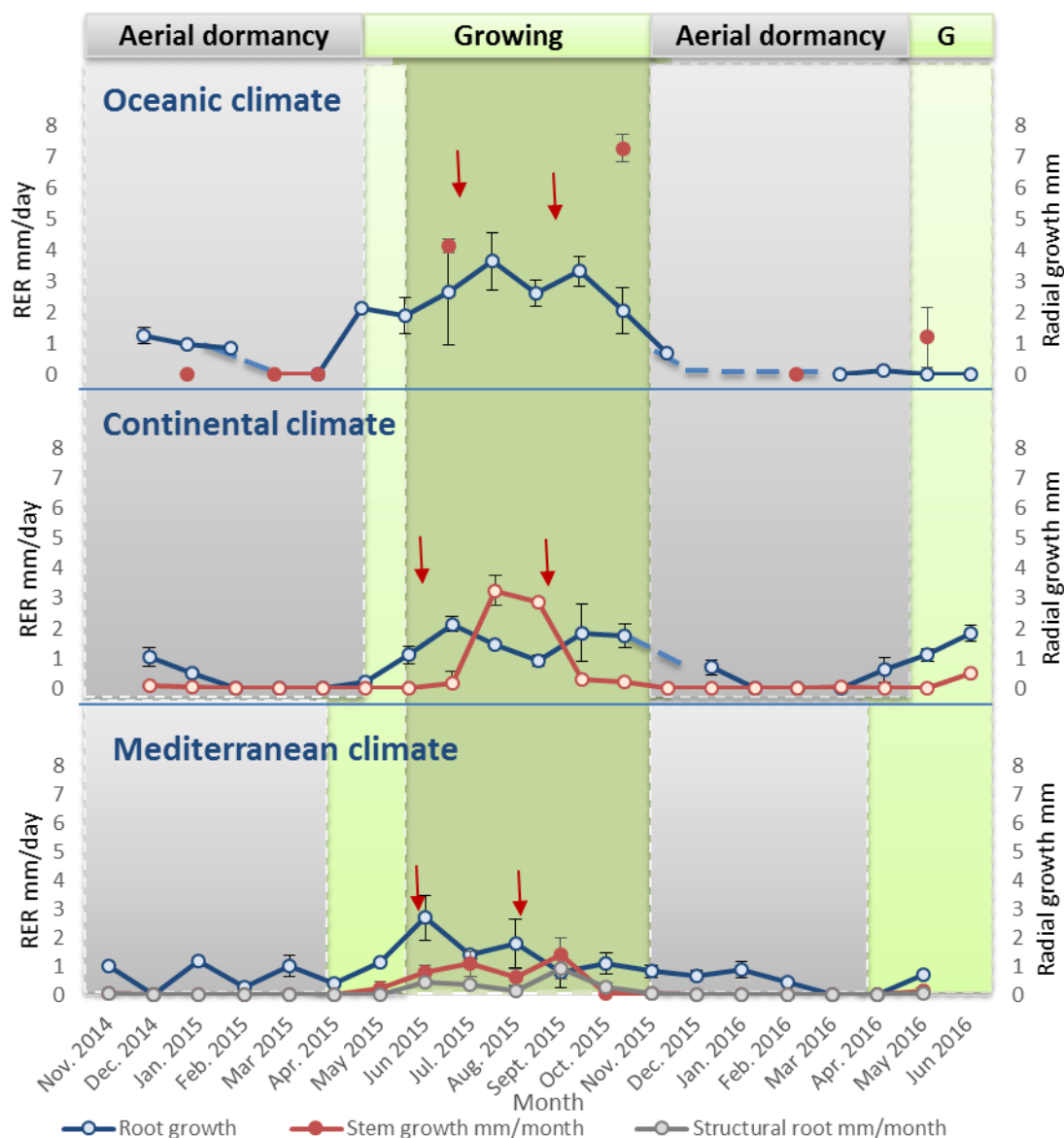


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857 Fig 2. Soil (yellow line) and air (red line; measured at a height of 1.5 m above rhizotrons)
 858 temperatures, daily precipitation (blue bars) and soil water potential (light blue line) at a)
 859 oceanic, b) continental and c) Mediterranean field sites over the observation period from
 860 September 2014 to June 2016. Different background colors correspond to different
 861 phenological periods: “LGS” is late growing season (green) “EGS” is early growing season
 862 (light green), “DS” is dormant season (gray).



878 Fig 3: Comparison of root elongation rate (RER, grey area) and trunk radial (green area) growth
 879 peaks in Mediterranean and Continental sites, over the observation period from November 2014
 880 to May 2016. The starting date for RER measurements in Mediterranean site is shown with a
 881 vertical dotted line. Detailed stem radial growth data are not available for the oceanic site.



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883

884 Fig. 4. Mean root elongation rate (RER, blue line) and trunk radial growth (red line) at a)

885 oceanic, b) continental and c) Mediterranean field sites over the observation period from

886 September 2014 to June 2016. Different background colours correspond to different

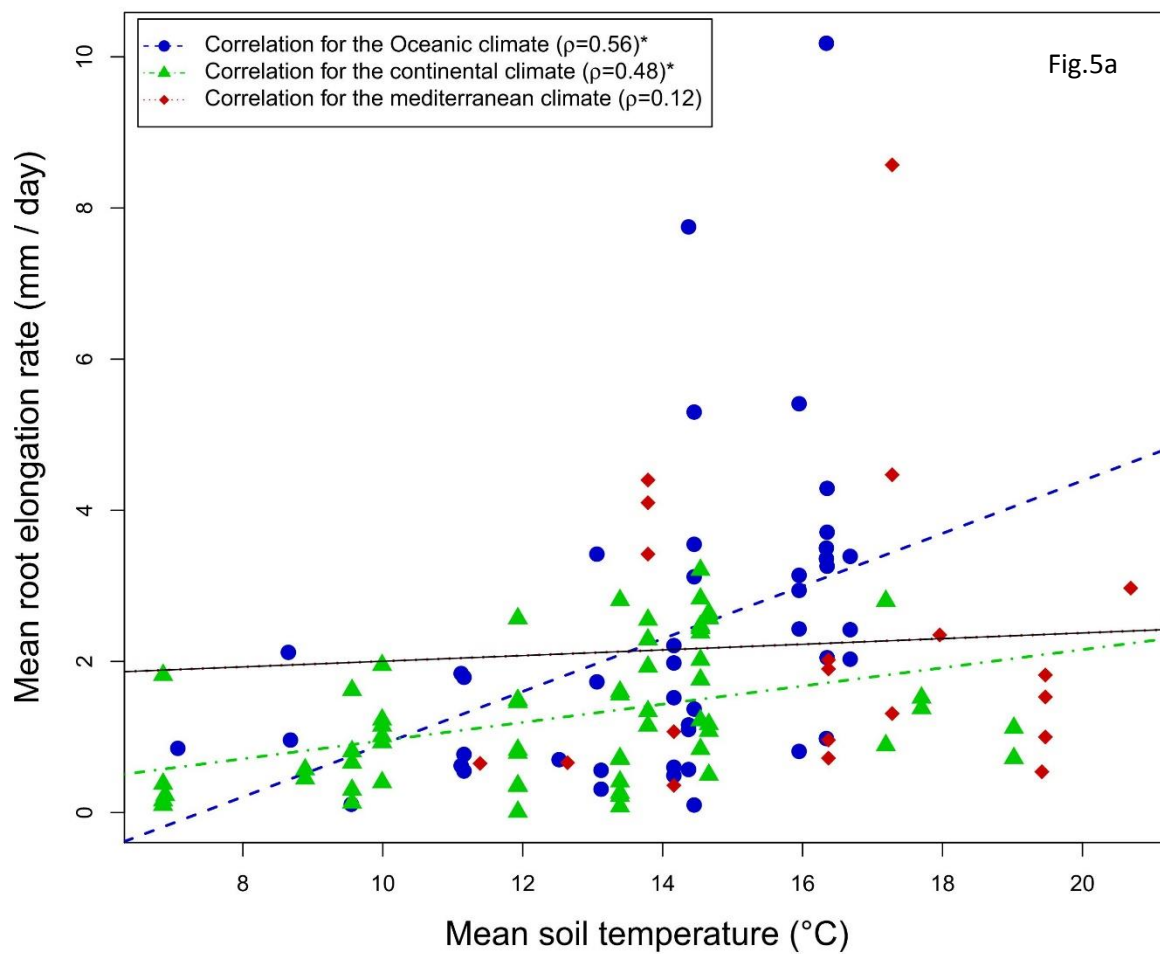
887 phenological periods: “LGS” is late growing season (green) “EGS” is early growing season

888 (light green), “DS” is dormant season (gray). Missing data/ flood damage is shown with a dotted

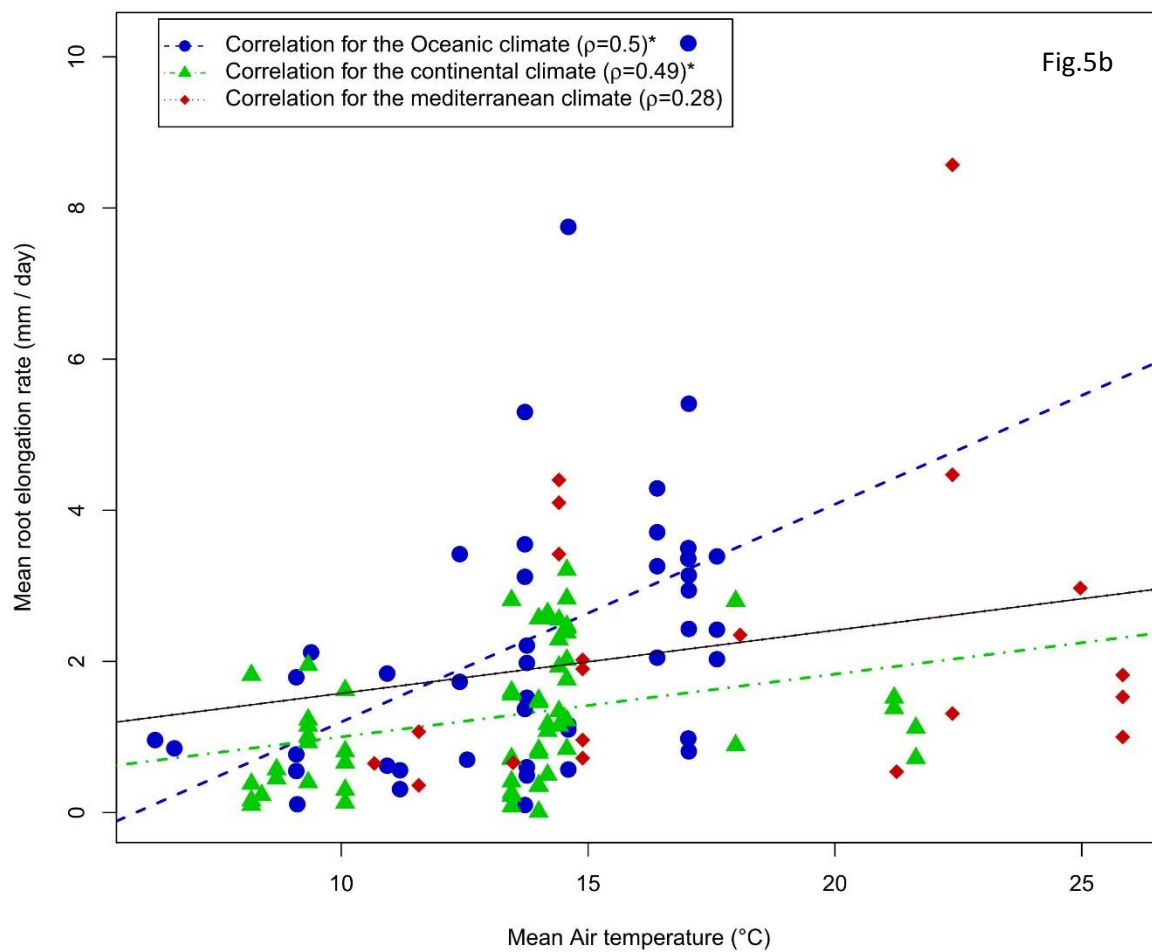
889 line over the dashed curves. Vertical bars represent standard deviations (not shown when

890 smaller than the symbol size).

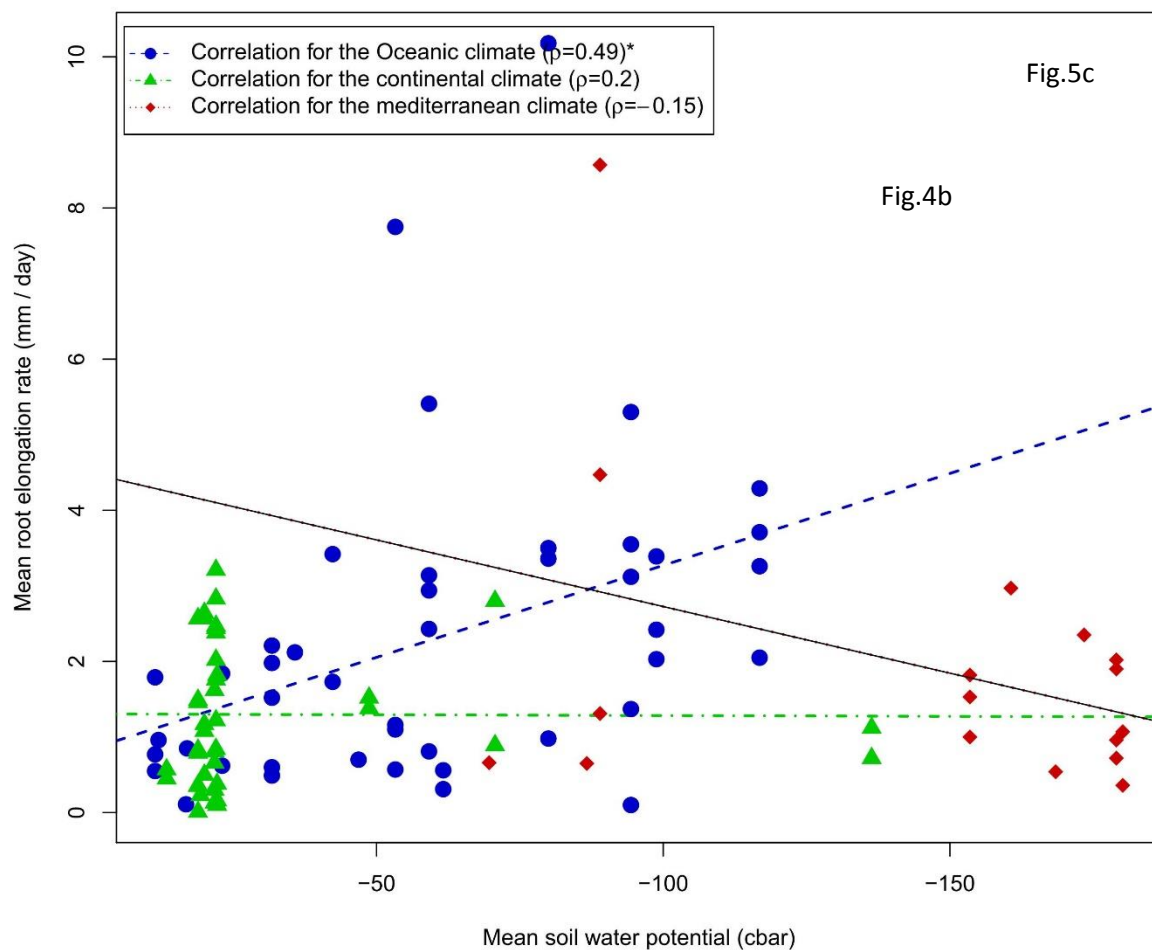
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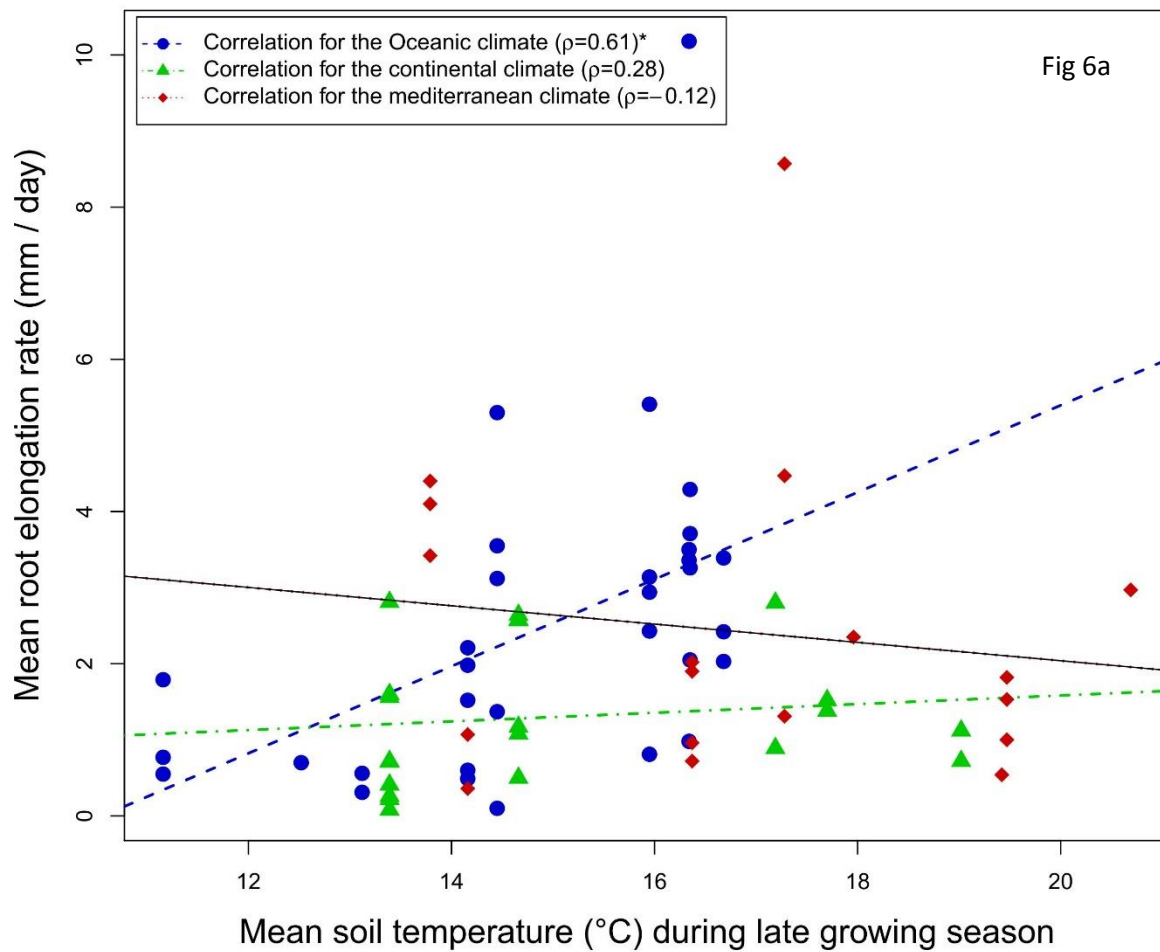


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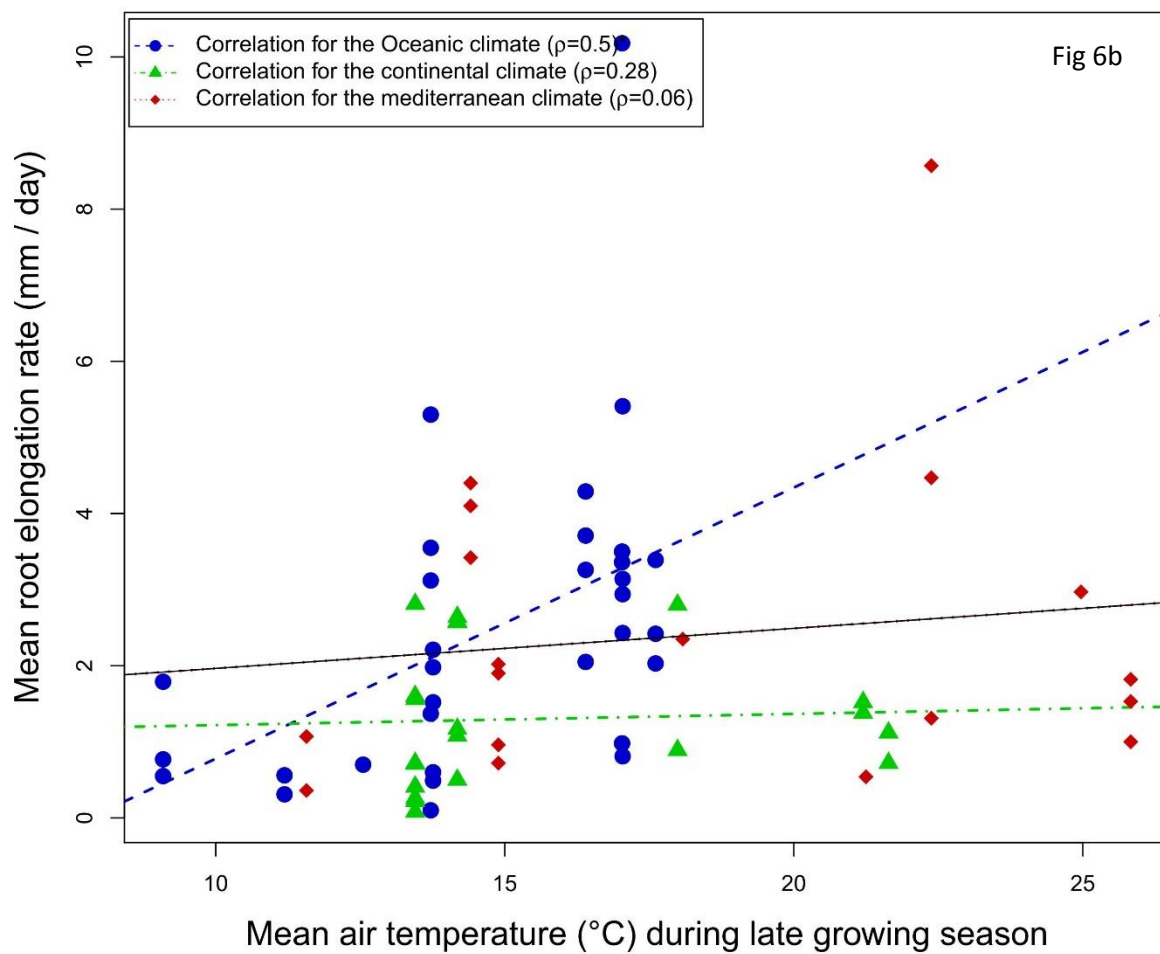
895 Fig 5: Correlations (for all periods combined together) between mean root elongation rate
 896 (RER) and (a) mean soil temperature, (b) mean air temperature and (c) mean soil water potential
 897 at the oceanic (green triangles and dot-dashed line), continental (blue circles and dashed line)
 898 and Mediterranean (red diamonds and dotted line) sites.

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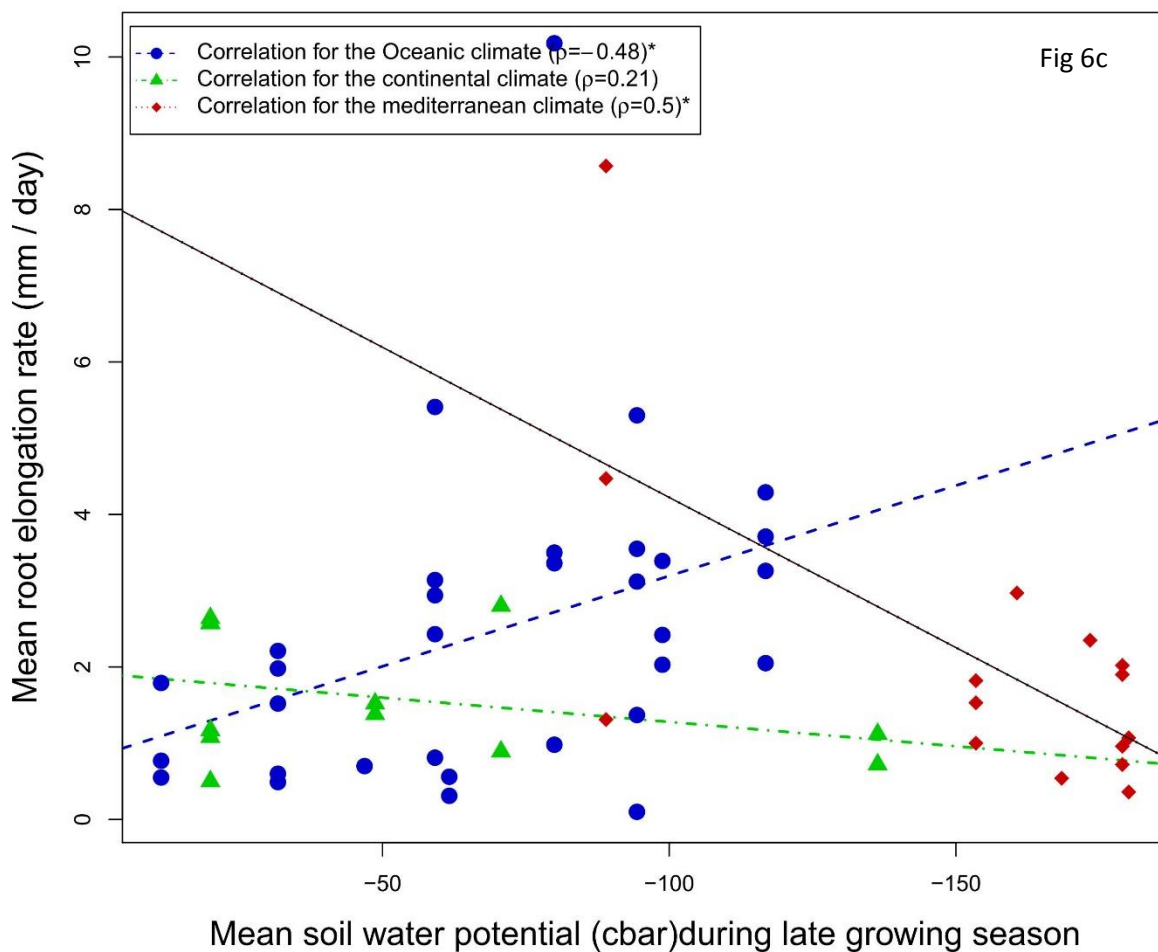
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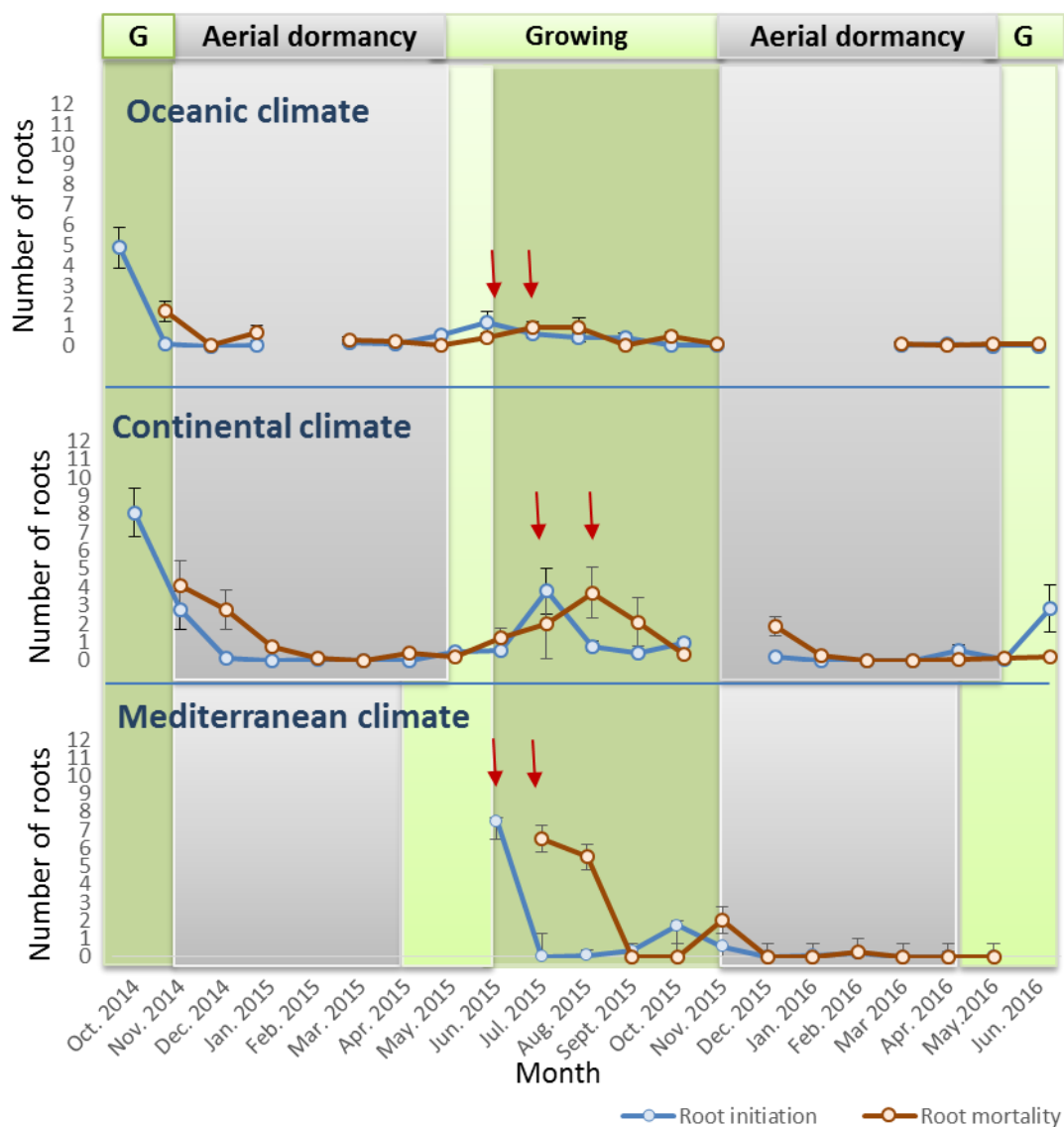


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905 Fig 6. Correlations (for late growing season only) between mean root elongation rate (RER)
 906 and (a) mean soil temperature, (b) mean air temperature and (c) mean soil water potential at the
 907 oceanic (green triangles and dotdash line), continental (blue circles and dashed line) and
 908 Mediterranean (red diamonds and dotted line) sites. Vertical bars represent standard deviations
 909 (not shown when smaller than the symbol size).

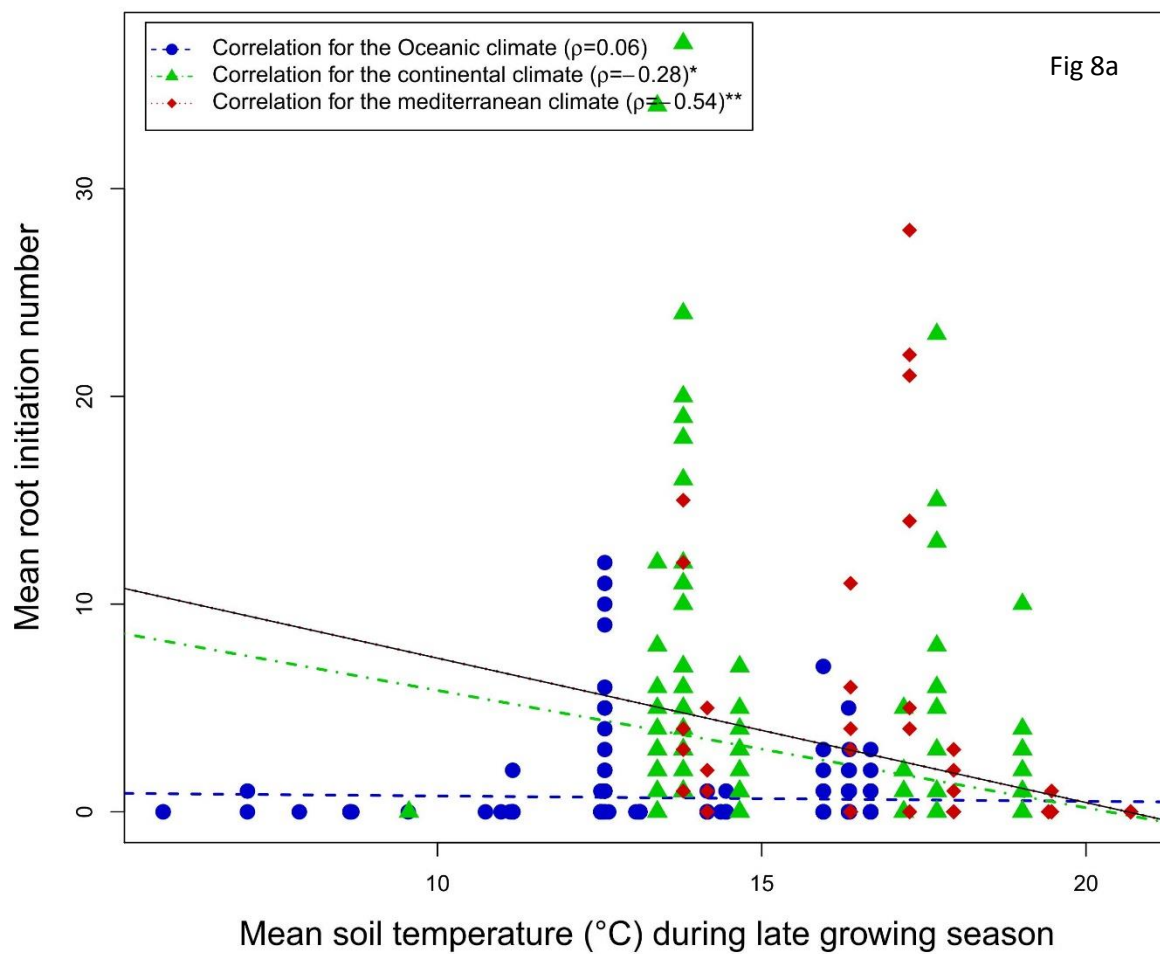
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912 Fig 7. Mean root initiation quantity (RIQ, blue line) and mean root mortality quantity (RMQ, red line) between time t and $t-1$, per 0.25 m^{-2} rhizotron (red line) at a) oceanic, b) continental
 913 and c) Mediterranean field sites over the observation period from September 2014 to June 2016.
 914 Different background colors correspond to different phenological periods: “LGS” is late
 915 growing season (green) “EGS” is early growing season (light green), “DS” is dormant season
 916 (gray). Missing data/ flood damage is shown with a dotted line over the dashed curves.
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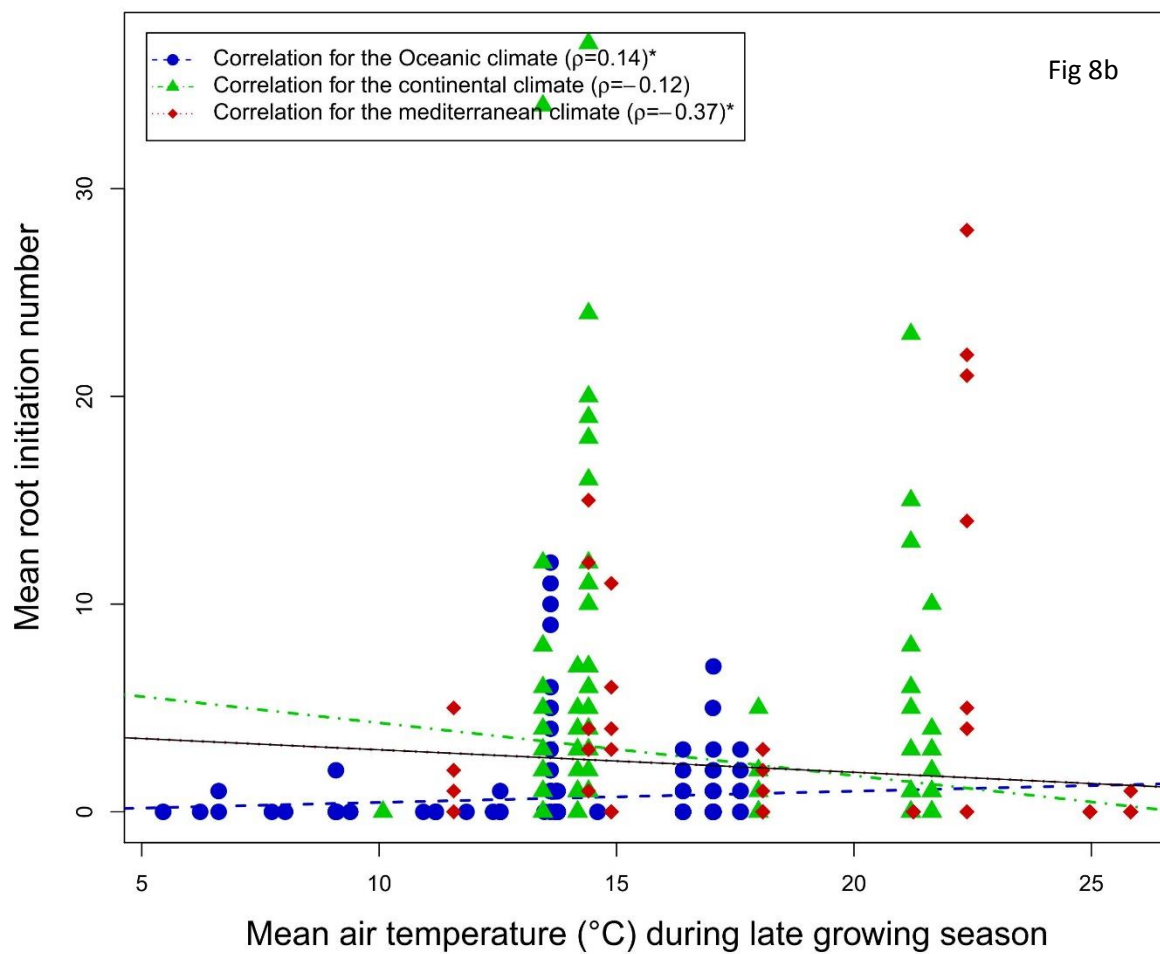
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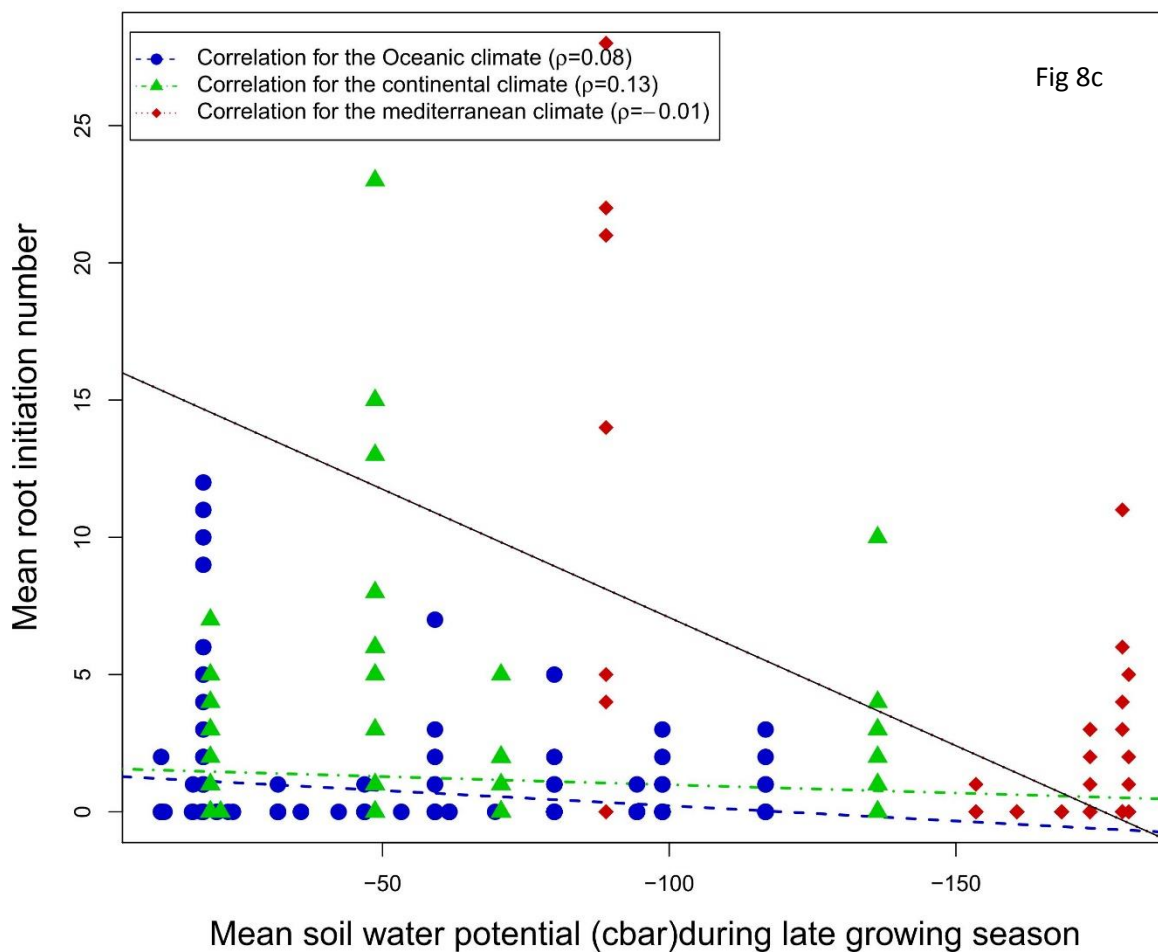
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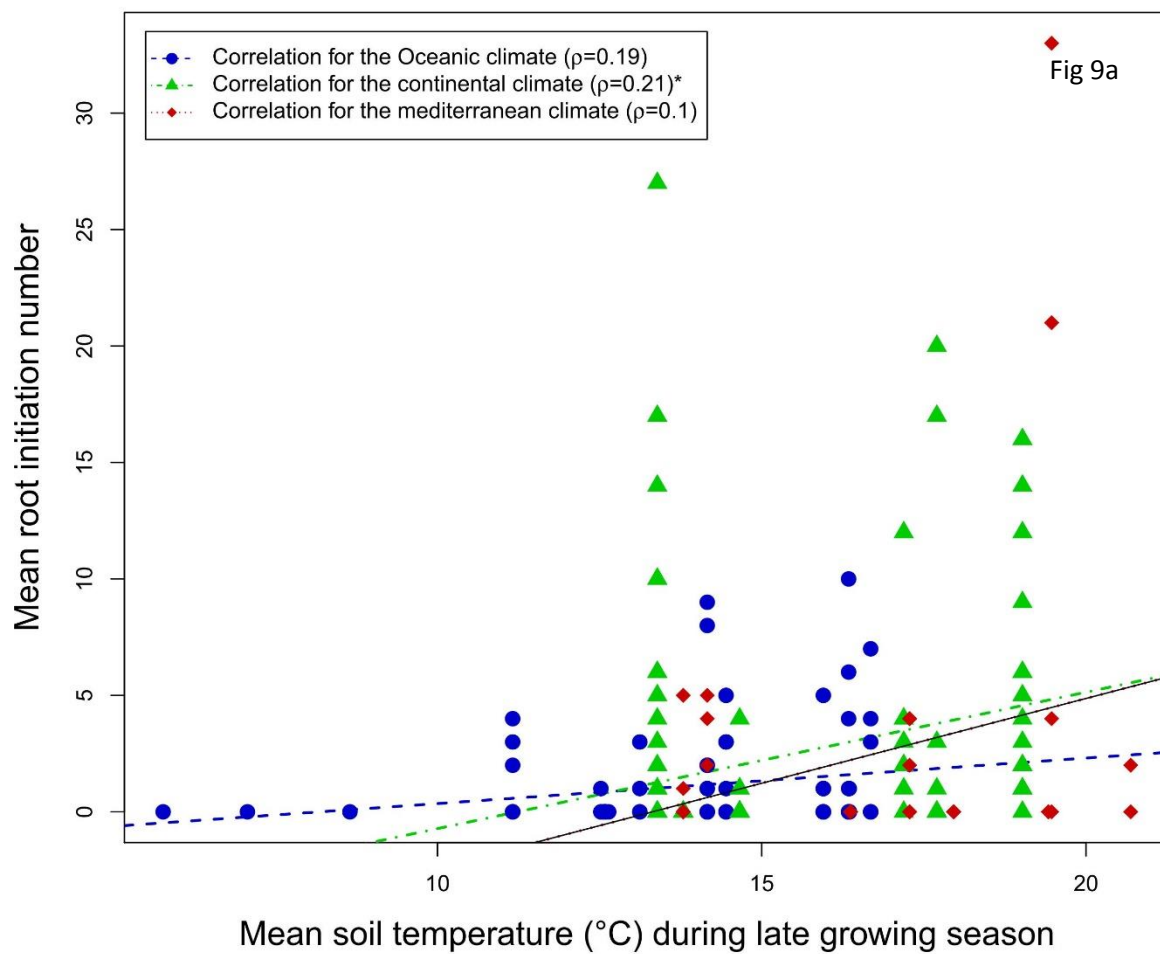
925 Fig 8. Correlations (for late growing season only) between mean root initiation (RIQ) and (a)
 926 mean soil temperature, (b) mean air temperature and (c) mean soil water potential at the oceanic
 927 (green triangles and solid line), continental (blue circles and dotted line) and Mediterranean
 928 (red diamonds and dashed line) sites.

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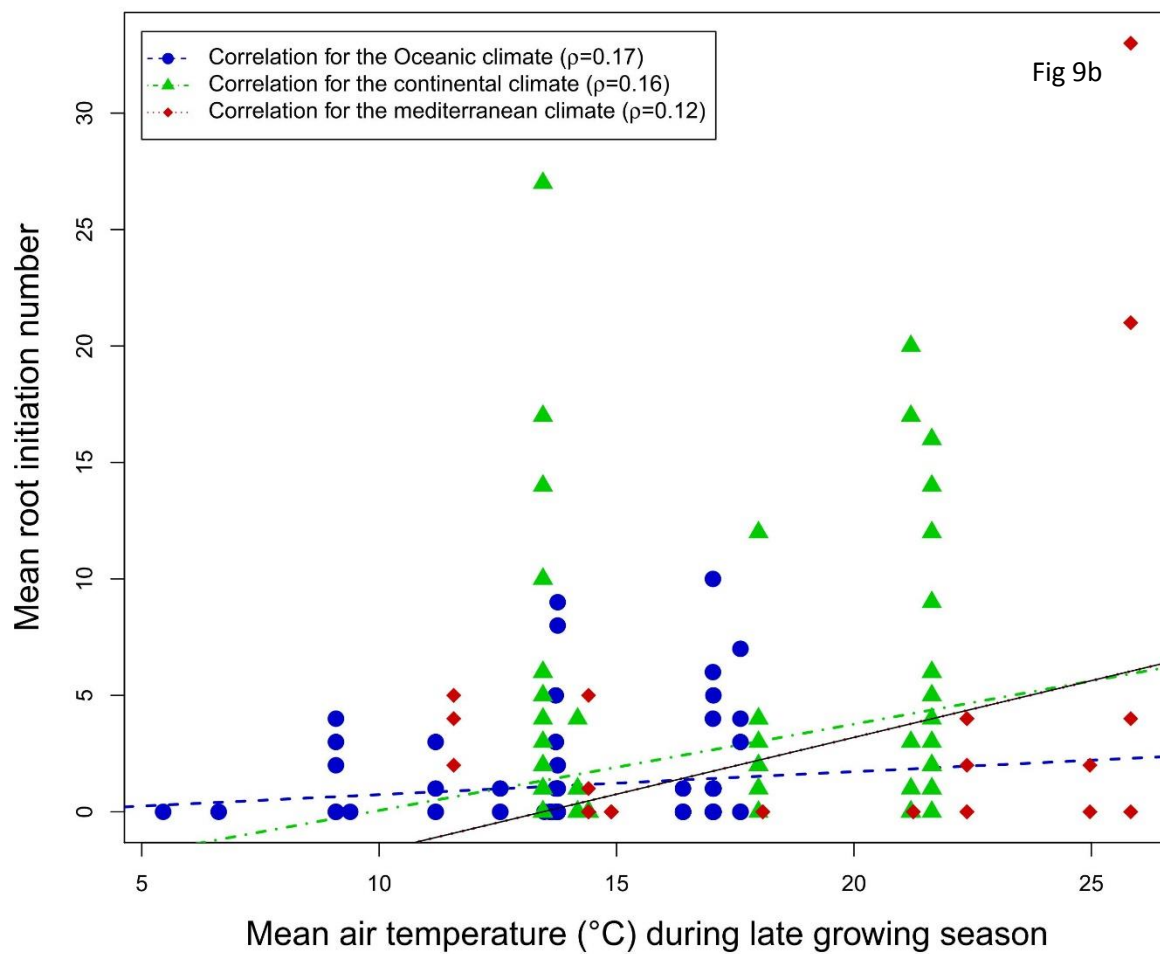
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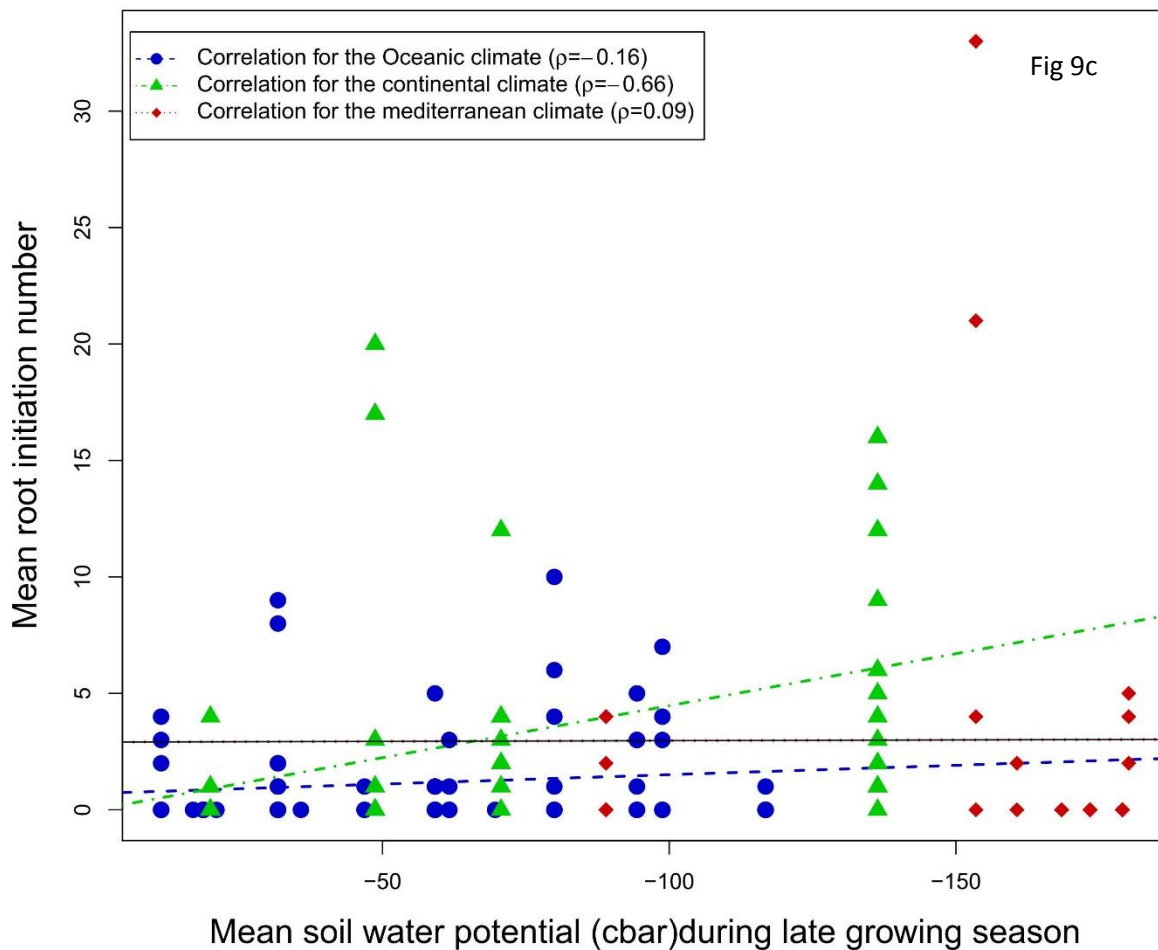
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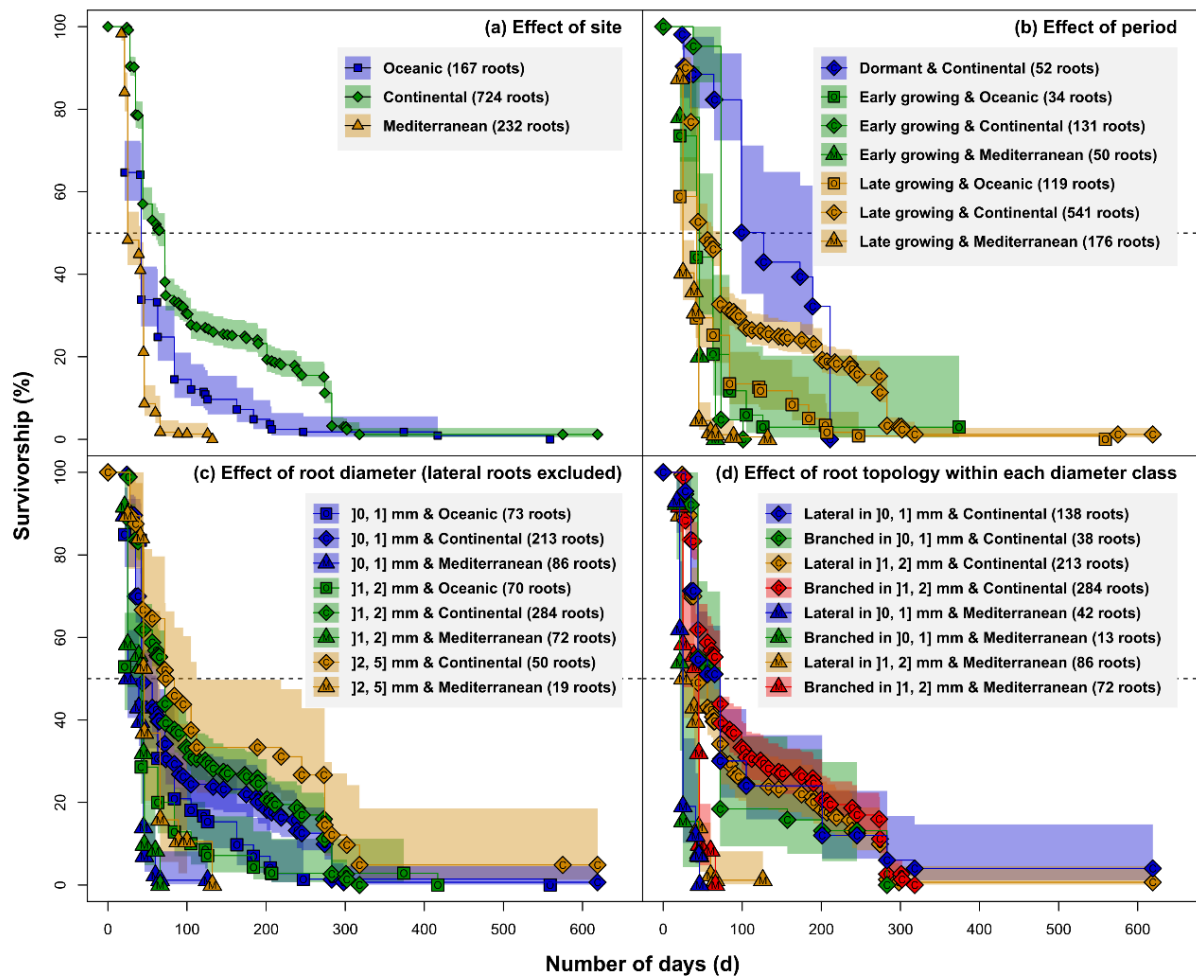
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941 Fig 9. Correlations (for late growing season only) between mean root mortality (RMQ) and (a)
 942 mean soil temperature, (b) mean soil water potential at the oceanic (green triangles and solid
 943 line), continental (blue circles and dotted line) and Mediterranean (red diamonds and dashed
 944 line) sites.

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950

951 Fig 10. Cox's hazard regression relationships for estimating root longevity and risk of mortality
 952 in relation to (a) climate (oceanic - squares, continental - diamonds and Mediterranean -
 953 triangles), (b) phenological periods (early growing season, late growing season and dormant
 954 season), (c) root diameter classes (0-1) mm , (1-2) mm and (2-5) mm and (d) root topological
 955 order (first and second order roots) over the observation period from October 2014 to June
 956 2016. Different shades represent the interval confidence of each curve corresponding to the
 957 color of that curve.

958

959 Table 1: Soil physical and chemical characteristics at each site. Data are means \pm standard
 960 deviation (S.D.)

Soil properties												
	Chemical								Texture (%)			
	pH	N (g/Kg)		C/N		P (g/Kg)		K (g/100g)		Clay	Silt	Sand
		Mean	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean			
Oceanic	6.9	0.17	0.1	9.19	1.5	0.15	0.1	1.5	0.1	17.6	66.3	16.1
Continental	4.7	0.22	0.1	9.76	1.4	0.04	0	2.82	0.2	15.1	22.6	62.3
Mediterranean	8.4	0.9	0.1	10.7	0.7	-	-	-	-	25.0	60.0	15.0

961

962

963 Table 2. The length (in days) of different phases of the growing season for both shoots and roots
 964 in the three climates

Phenological growth periods	Early growing season		Late growing season		Dormant season		Total growing season	
Shoot								
Year	2015	2016	2015	2014-	2015-	2015		
				2015	2016			
Oceanic								
Date	15 May	12 May	18 Jun	08 Nov	03			
Length	34	-	138	188	Nov	172		
					191			
Continental								
Date	3 May	5 May	05 Jun	12 Nov	28 Oct			
Length	33	36	145	172	190	178		
Mediterranean								
Date	18 Apr	14 Apr	02 Jun	18 Nov	12			
Length	45	-	163	151	Nov	208		
					154			
Root								
Oceanic	210			100	154	210		
Continental	240			118	124	240		
Mediterranean	216			-	126	216		

965 - no observation recorded

966

967 Table 3: Correlations between mean soil and air temperatures, mean soil water potential of the preceding month and root elongation rate (RER),
 968 root initiation quantity (RIQ) and root mortality quantity (RMQ) in at the three sites during the late growing season.

Variable	oceanic		continental		Mediterranean		
	ρ	P	ρ	P	ρ	P	
Soil	RER	0.61	<0.001**	0.28	0.21	-0.12	0.61
temperature	RIQ	0.06	0.38	-0.28	<0.001**	-0.54	<0.001**
	RMQ	0.19	0.08	0.21	0.02*	0.10	0.54
Air temperature	RER	0.48	0.005**	0.28	0.21	0.06	0.78
	RIQ	0.14	0.04*	-0.12	0.06	-0.37	<0.001*
	RMQ	0.17	0.11	0.16	0.08	0.12	0.48
Soil water	RER	-0.48	0.005**	0.21	0.51	0.50	0.05*
	RIQ	0.08	0.23	0.13	0.11	-0.01	0.86
	RMQ	-0.16	0.14	-0.66	<0.001***	0.06	0.64

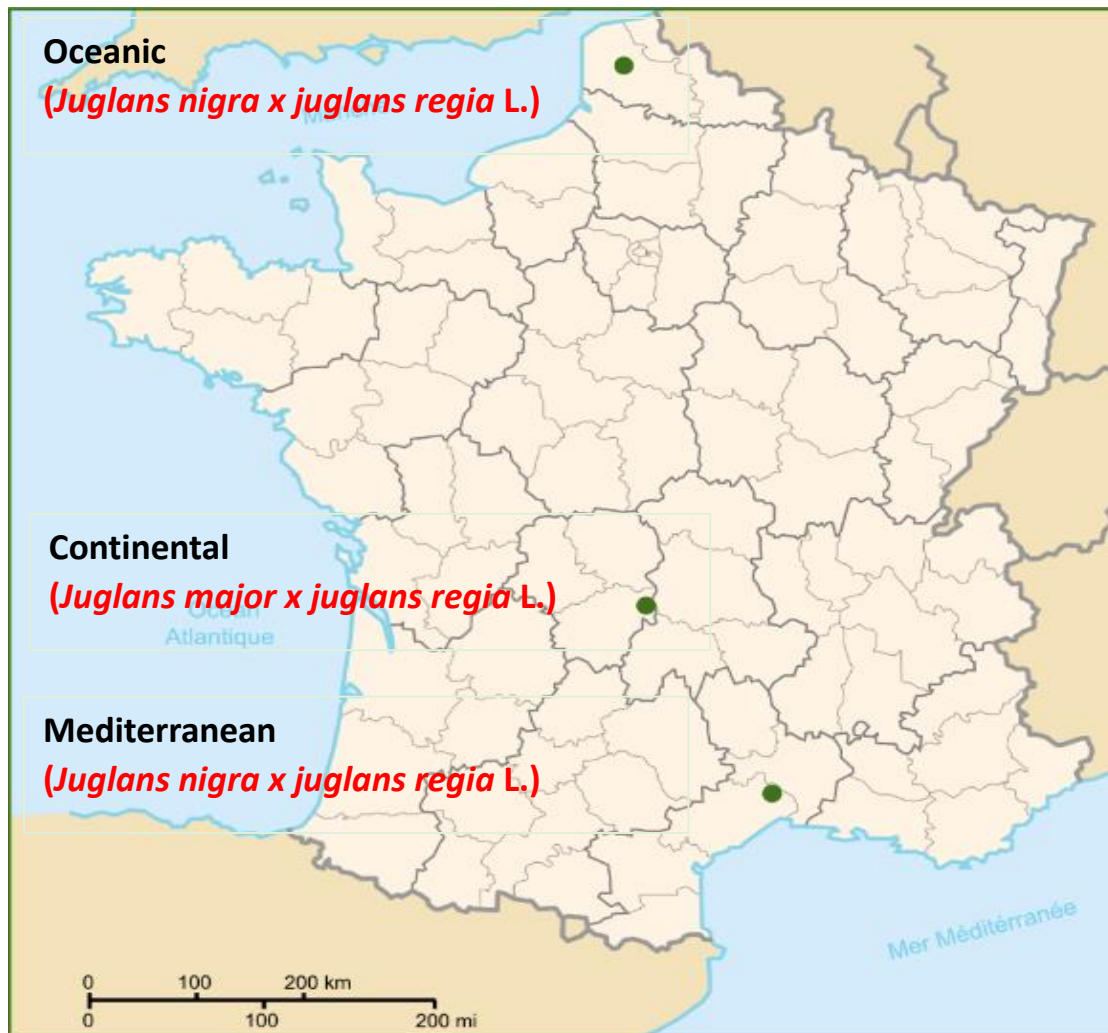
969

8. Supplementary Material

Figure S1: Aerial view of the three sites from Google Earth images 2016



Figure S2 Geographic location of each site along the latitudinal gradient in France



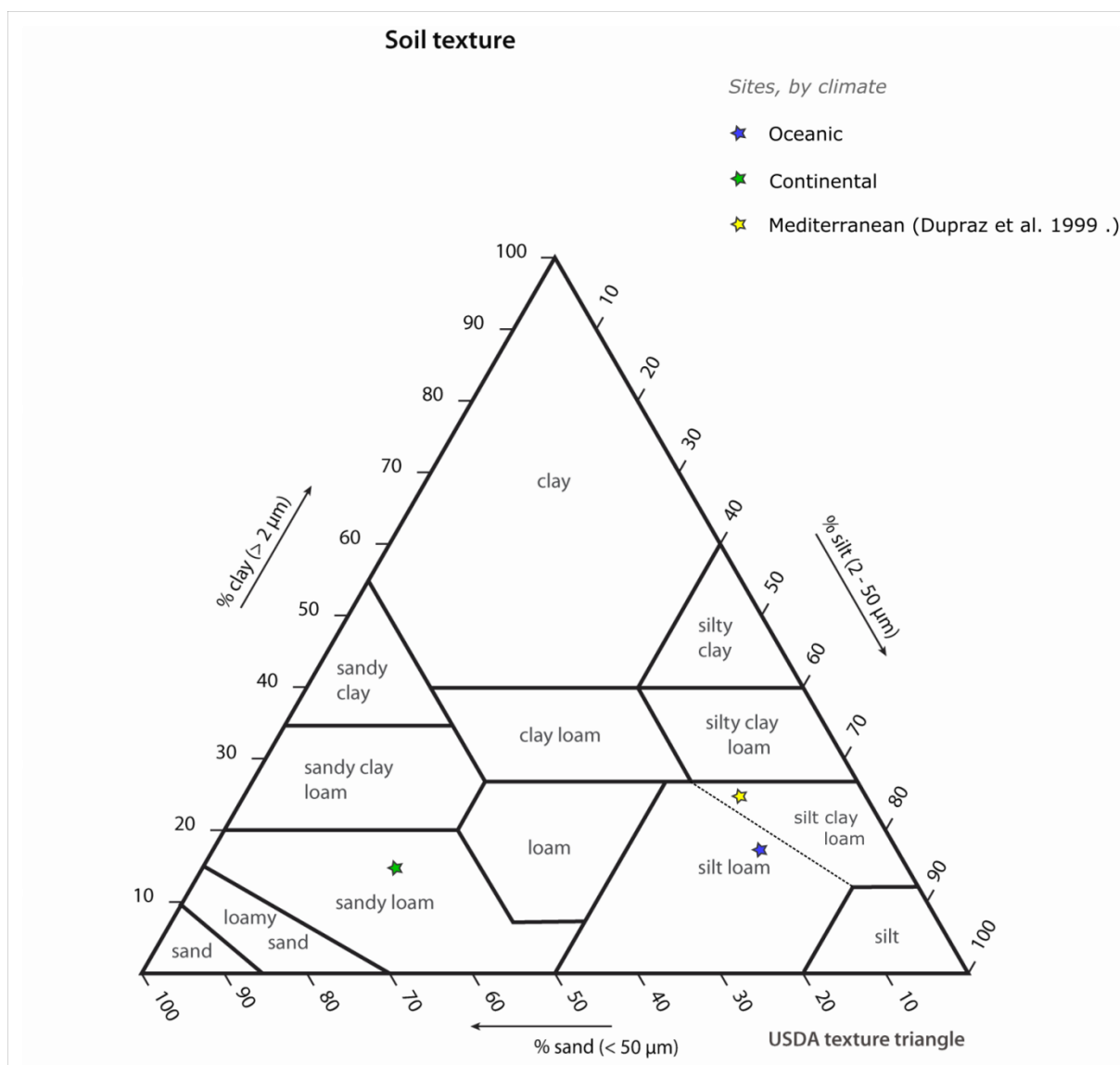


Fig S3: Soil texture at each site

Figure S4 Trenches with rhizotrons at the continental and oceanic sites



Figure S5 Trench with rhizotrons at the Mediterranean site



Figure S5 Techniques used to obtain images of roots in rhizotrons



Flatbed scanner (Epson Perfection V370)



Time lapse camera (CUDDEBACK ATTACK)



Circular scanner (CI-600 Digital Root Imager)