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1 Growth dynamics of fast-growing tree species in mixed forestry and agroforestry
2 plantations

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9 ABSTRACT

10 In recent years, plantations of fast-growing tree species have emerged as a possible way to meet
11 the increasing demand for biomass for renewable energy in Europe. Agroforestry plantations
12 including fast-growing tree species could be an attractive option because they reduce land
13 competition for biomass and food production while providing forest benefits. Today, the species
14 interactions that determine whether a given mixture will be more productive than the
15 corresponding monocultures are still poorly understood. Our objective was to assess the
16 performance of fast-growing trees, i.e. poplar (*Populus nigra* × *P. deltoides*) and alder (*Alnus*
17 *glutinosa*), in association with herbaceous species either N₂-fixing species (succession alfalfa
18 (*Medicago sativa*) and clover (*Trifolium pratense*)) or graminoids (succession of wheat (*Triticum*
19 *aestivum*) – triticale (*Triticosecale*) – temporary grassland consisting of mixtures of perennial
20 ryegrass (*Lolium perenne*) and fescue (*Festuca ovina*)), respectively, and in association together.
21 We compared tree growth in mixed stands to growth in the respective tree monocultures. An
22 experimental plantation composed of three blocks including the different treatments was set up in
23 2014 in northeastern France. In the forest mixture, poplar and alder were planted in alternating

24 rows, and in the agroforestry plots, every second line of trees was replaced by the crops. No
25 fertilizers (of any kind) were used during the experiments. During six growing seasons, tree
26 growth (height and diameter at breast height) was monitored monthly in the agroforestry stands,
27 the forest mixture stand and the two tree monocultures. By the end of 2019, poplar stem height in
28 association with N₂-fixing crops (alfalfa, then clover) was higher than in the forest mixture and
29 the monoculture. During the warmest growing season with a marked dry period in June-July
30 (2018), poplar height growth rate in the agroforestry treatment was between three and five times
31 higher than for the poplars in the monoculture and the forest mixture. A facilitation process in the
32 agroforestry plantations could explain this result due to a significant enrichment of the soil in
33 nitrogen by the N₂-fixing crops. This result only appeared several years after tree planting, and
34 management actions were necessary in order to control the strong competition between crops and
35 trees during the early stages. In the forest mixture, poplars associated with alders were smaller
36 than in their monoculture, in spite of a stratification of the canopies of the two species. For alders,
37 tree growth did not appear to be affected by either an association with graminoids or with poplar.

38 *Keywords:* Mixed tree plantations; Agroforestry; Growth dynamics; Fast-growing tree species;
39 Interactions

40

41 **1. Introduction**

42 European Union leaders have agreed to increase the share of renewable energy in EU
43 energy consumption to 27% by 2030 (European Biomass Association, 2017). Between 2007 and
44 2017, renewable energy production increased by 64% in Europe; in 2017, wood (and other solid
45 biofuels) accounted for the largest share of renewable energy at 42% of primary renewable
46 energy production (Eurostat, 2019). In recent years, plantations of fast-growing tree species have
47 emerged to increase the contribution of biomass to renewable energy. Globally, these plantations

48 accounted for 2% of the forest area in the world in 2012 (Cateau et al., 2018); in Europe, there
49 were between 55,000 and 60,000 hectares of this type of plantation, mainly composed of poplars
50 and willows in 2012 (Mola-Yudego et al., 2017). Fast-growing tree plantations are often
51 monocultures (Liu et al., 2018). However, in the context of climate change and resource scarcity,
52 mixed-species plantations can be interesting and several advantages have been highlighted. In
53 particular, a higher stand production in mixtures than in monocultures (over-yielding or
54 transgressive over-yielding) can result from facilitation (i.e. at least one species increases a
55 resource availability for its companion species, especially interesting when mixing N₂-fixing
56 species and non-fixing species) or from complementarity/competitive reduction (Vandermeer,
57 1989). In addition, mixed plantations can be more resistant, particularly to diseases and pest
58 attacks (Chamagne et al., 2017; Powell and Bork, 2004). However, mixed plantations are not
59 always more productive than monocultures, and this highlights the need to carefully consider
60 species assemblages and specific site conditions (for reviews, see Piotta, 2008, and Marron and
61 Epron, 2019).

62 Since fast-growing tree plantations increase around the world and most often on land
63 used for food (Cossalter and Pye-Smith, 2003), using an agroforestry approach in this type of
64 plantations (Lamerre et al., 2015; Tariq et al., 2018; Seserman et al., 2019) could be an attractive
65 alternative for farmers. It could reduce land use competition for biomass and food production,
66 while providing forest benefits (Pretzsch et al., 2017). Tropical agroforestry plantations have
67 been widely studied since the last century (e.g. Rao et al., 1998), but in temperate climates,
68 studies of such plantations are still very marginal, even though agroforestry is in progress in
69 Europe (Burgess et al., 2005; Carrier et al., 2019; Swieter et al., 2019) and North America
70 (Thevathasan and Gordon, 2004; Reynolds et al., 2007; Borden et al., 2017). Many studies can be
71 found on the effects of trees on crops (Isaac et al., 2014; Bouttier et al., 2014; Inurreta-Aguirre et
72 al., 2018; Kanzler et al., 2019), but studies dealing with the effects of crops on trees are less

73 frequent in the literature (e.g. but see Balandier et al., 2007 for various species of grass associated
74 to wild cherry (*Prunus avium*)). In addition, when studies focus on the tree component in
75 agroforestry systems, they generally deal with overall tree productivity (Lamerre et al., 2015),
76 without more finely studying their growth dynamics, for example, or the interaction processes
77 between species.

78 These interaction processes are still poorly understood, especially when it comes to
79 interactions between herbaceous and woody species in agroforestry, which is at the crossroads of
80 forestry and agronomy. In any plantation, interactions between individuals of the same species
81 (intra-specific) or between individuals of two different species (interspecific) can be negative (i.e.
82 competition), positive (i.e. competitive reduction and facilitation) or neutral. The same types of
83 interactions can take place between the woody and herbaceous species in agroforestry plantations
84 (Everson et al., 2009; Jose et al., 2004). The herbaceous component may be negatively impacted
85 by the woody component with regard to the availability of resources such as light (Carrier et al.,
86 2019). The competition for light will become more intense as the trees mature due to the increase
87 in shading by the canopy (Inurreta-Aguirre et al., 2018). Thus, the yield of crops close to the trees
88 decreases. This was shown by Bouttier et al. in 2014 where the herbaceous cover (*Phleum*
89 *pratense* and *Trifolium pratense*) yield decreased by 75% near poplars (*Populus deltoides* ×
90 *Populus nigra*) in an intercropping system compared to control plots. Larger litter deposition
91 within 1 m of the tree strip can also cause a decrease in the yield of the underlying crop, but, in
92 Swieter et al., 2019, this negative impact did not affect overall crop yields. On the other hand, the
93 two components, herbaceous and woody, can be complementary in their use of resources such as
94 soil water. Indeed, trees have been shown to use water more efficiently when they are associated
95 with a crop, compared to when they are in monoculture. Fernández et al., 2008, found that pines
96 (*Pinus ponderosa*) used deeper water resources (below 20 cm) due to the presence of herbaceous
97 roots in the top 20 cm of the soil layer in agroforestry than did pines in a monoculture.

98 Facilitation can also occur in these systems. For example, Powell and Bork (2004) observed an
99 increase in overall available soil nitrogen in an agroforestry system composed of poplars
100 (*Populus tremuloides*) and alfalfa (*Medicago sativa*). The performance of species mixture
101 systems is the net result of the above- and belowground interactions between the associated
102 species.

103 The aim of our study was to compare the performance of fast-growing trees in different
104 mixtures and in their respective monocultures: i.e. poplar (*Populus nigra* × *P. deltoides*) and
105 alder (*Alnus glutinosa*), in association with herbaceous species either N₂-fixing species
106 (succession alfalfa (*Medicago sativa*) - clover (*Trifolium pratense*)) or graminoids species
107 (succession of wheat (*Triticum aestivum*) - triticale (*Triticosecale*) - temporary grassland
108 consisting of mixtures of perennial ryegrass (*Lolium perenne*) and fescue (*Festuca ovina*)),
109 respectively. We studied the effects of the different types of species mixtures on tree intra- and
110 inter-annual growth dynamics, compared to the respective tree monocultures. Our main
111 hypothesis was that trees would be larger and taller in mixture plots than in monoculture due to a
112 reduction in species competition and/or facilitation provided by the presence of N₂-fixing species
113 (alfalfa – clover and alder), which increase the soil in nitrogen and benefit the non N₂-fixing
114 species (graminoids and poplar).

115 **2. Materials and methods**

116 *2.1. Study area*

117 The experimental plantation is located in an agricultural field at the experimental farm of
118 La Bouzule near Nancy, in northeastern France (48°44'19" N, 6°18'50" E, 219 m asl). The region
119 is characterized by a warm temperate climate, as shown in the Köppen-Geiger climate
120 classification world map (Kottek et al., 2006). The soil is a Vertic Stagnic Cambisol (IUSS

121 Working Group WRB 2006). The mean annual precipitation and temperatures were, respectively,
122 550 mm and 10.3°C between 2014 and 2019.

123

124 2.2. *Experimental design*

125 The experimental plantation was installed in the spring of 2014 and is 448 m long and 73
126 m wide, for a total area of 3.27 ha (Fig. 1.). The plantation consists of three blocks, each
127 containing three types of treatments: (i) two kinds of agroforestry, (ii) one forest mixture and (iii)
128 two tree monocultures or two agricultural plots, each plot measuring approximately 0.15 ha (Fig.
129 1.). The agroforestry plots were composed of herbaceous species associated with woody species.
130 From 2014 to 2017, the alder plots were planted with cereals (spring wheat (*Triticum aestivum*)
131 rotated with a winter wheat and triticale (*Triticosecale*); and the poplar plots with alfalfa
132 (*Medicago sativa*); then from 2018, temporary grassland mixing perennial ryegrass (*Lolium*
133 *perenne*) and fescue (*Festuca ovina*) replaced the cereals and clover (*Trifolium pratense*)
134 replaced the alfalfa. The forest mixture plot was composed of alternating rows of poplar and
135 alder. The cereals and the temporary grassland are grouped together under “graminoids”,
136 hereafter. The forest plots (tree monocultures and the forest mixture) were planted at a density of
137 2000 trees per hectare (2.5 m between the rows and 2 m between the trees in a given row) while
138 the agroforestry plots had a density of 1000 trees per hectare, every other row of trees being
139 replaced by crops (5 m between the rows and 2 m between the trees) (Fig. 1.). Tree planting was
140 realized with 30-cm-long poplar cuttings of the Euramerican poplar clone Dorskamp (*Populus*
141 *deltoides* × *Populus nigra*) and one-year-old rooted alder (*Alnus glutinosa*) seedlings measuring
142 from 50 to 80 cm in height. A total of 3649 trees were planted, corresponding to 1836 poplars
143 and 1813 alders. The plantation design leaves sufficient room at the extremity of the rows
144 necessary for the agricultural machinery to pass along. The orientation of tree lines and the
145 spatial distribution of treatments have been chosen to minimize wind and shelter effects (Figure

146 1). To reduce border effects, one border row around each plot was not included in the
147 measurements. In the internal plots, we took into account 732 poplars in monoculture, 697 alders
148 in monoculture, and 440 poplars and 440 alders in the agroforestry and forest mixture. Grass
149 strips of 1 m in overall width were present at the base of the tree lines in agroforestry treatments
150 (0.5 m on each side of the trees). Mechanical and chemical weed control was realized on the tree
151 rows in 2014 and 2015. The plantation was neither watered nor fertilized. No pruning
152 management was performed. In 2019, total tree mortality was 5%, mostly in block 3 where soil
153 was shallower.

154 [Insert Fig. 1. here]

155

156 *2.3. Monitoring of soil and climate conditions*

157 In 2014, initial soil characterization was carried out on soil cores (0-60 cm in depth,
158 diameter of 8 cm) sampled in the central inter-row of each plot (Clivot et al., 2019). On average,
159 soil composition was 60.9 % clay, 34.8 % silt and 4.4 % sand, between 0 and 60 cm in depth. The
160 pH was 7.4 on average and the exchange acidity (Al^{3+} and H^+) was 1. There was some spatial
161 variability over the site in the soil parameters, with increasing pH and carbon content from block
162 1 to block 3 (Fig. 1.), whereas soil depth decreased due to an outcrop of rocky material
163 (calcareous) near the soil surface in block 3. To monitor soil mineral nitrogen, three soil cores
164 were sampled (0-15 cm in depth, diameter of 8 cm) in the central inter-row of each of the five
165 modalities (i.e. poplar and alder monocultures, poplar and alder agroforestry, forest mixture) in
166 July 2018. The soil mineral nitrogen was extracted with 1M KCl (45 min of agitation at 20°C, 1:4
167 soil/solution ratio) and filtered on a Whatman 42 paper disc. The mineral nitrogen in the soil
168 extracts was analyzed by continuous flow colorimetry (Skalar analyzer).

169 Instruments to monitor environmental conditions were set up in the plantation in 2014,
170 and include a rainfall gauge (ARG100, Campbell Scientific, Inc., Logan, UT, USA) and a
171 thermistor (HMP45C probe, Campbell Scientific, Inc., Logan, UT, USA). Volumetric soil water
172 content (SWC, %) was monitored hourly with water content reflectometers (CS615, Campbell
173 Scientific, Inc., Logan, UT, USA) inserted into the soil at an equal distance between two trees in
174 the row at depths of 10, 30 and 80 cm (Fig. 1.). Meteorological and SWC data were recorded and
175 stored on data loggers (CR3000, Campbell Scientific, Inc., Logan, UT, USA).

176

177 *2.4. Tree dimension measurements*

178 Tree growth was assessed by measuring the stem height and diameter at breast height
179 (DBH) of all the trees at the end of each growing season. In addition, a representative sample of
180 tree height classes was defined in 2015. During growing seasons (April to August), tree growth
181 was monitored every three weeks for 20 poplars and 20 alders in each treatment in the three
182 blocks, for a total of 360 individuals: 20 trees \times 2 species \times 3 blocks \times 3 treatments (monoculture,
183 agroforestry, forest mixture). Height was estimated from the base of the tree to the last bud of the
184 tallest stem with a graduated pole accurate to the nearest centimetre from 2015 on. DBH was
185 measured with a digital caliper to the nearest millimetre from 2017 on.

186

187 *2.5. Inter- and intra-annual height growth dynamics*

188 In order to visualize inter-annual tree growth dynamics, height growth rate (cm day^{-1}) was
189 calculated for each tree and each year following equation (1):

$$190 \quad HGR_{inter} (\text{cm day}^{-1}) = \frac{(H_{final} - H_{initial})}{\Delta time} \quad (1)$$

191 where

192 HGR_{inter} is the inter-annual height growth rate,
193 H_{final} = the last height value of the growing season,
194 $H_{initial}$ = the first height value of the growing season,
195 Δ_{time} = the time interval between bud break (beginning of April) and bud set (end of
196 August).

197 For intra-annual height growth dynamics, height growth rate (cm day^{-1}) was defined as
198 the height difference between two successive measurement dates during the growing season,
199 divided by the time between the two dates (equation 2):

$$200 \quad HGR_{intra} (\text{cm day}^{-1}) = \frac{(H_{n+1} - H_n)}{(T_{n+1} - T_n)} \quad (2)$$

201 where

202 HGR_{intra} is the intra-annual height growth rate,
203 H_n = the height value at time n,
204 H_{n+1} = the height value at time n+1,
205 T_n = the date at time n,
206 T_{n+1} = the date at time n+1.

207 Only the data for 2018 are presented and discussed for intra-annual dynamics, because
208 2018 weather conditions were quite specific, the year being warmer than the other years, with
209 less precipitation (Fig. 2.) and with a net decrease in SWC during the summer (Fig. A1.). Growth
210 rate data for the years 2016, 2017 and 2019 are available as supplementary files (Figs. A2., A3.
211 and A4.).

212

213 *2.6. Calculation of competition indices*

214 For each tree, the height to DBH (h/d) ratio (m cm^{-1}), which is a measure of tree shape,
215 was calculated and used as an indicator of the level of competition (Forrester et al., 2004;
216 Ghorbani et al., 2018). In the forest plots only (mixture and monocultures), we also used the
217 Hegyi index to evaluate the strength of neighboring competition (Hegyi, 1974). This index is
218 typically used to characterize local competition (Vanclay, 2006) and was calculated following
219 equation (3) (according to Prevosto, 2005):

$$220 \quad IC_i = \sum_{\substack{j=1 \\ j \neq i}}^n \frac{d_j}{d_i L_{ij}} \quad (3)$$

221 where

222 IC_i is the competition index of subject tree i ,

223 d_i = the DBH of subject tree i ,

224 d_j = the DBH of competitor tree j ,

225 L_{ij} = the distance between subject tree i and competitor j ,

226 n = the number of competitors (total = 8 neighboring trees: 2 in the same row and 3 each

227 in the two adjacent rows).

228

229 *2.7. Estimation of leaf nitrogen*

230 In 2018, ten fully expanded sun-exposed leaves were collected per treatment and per
231 species once a month in June, July and August. The leaves were oven-dried at 60°C for at least
232 48h, then ground to powder. Nitrogen concentrations (N_{leaf} , mg g^{-1}) were measured with an
233 elemental analyzer (NA-1500, Carlo Erba, Italy) from a sample of 2.0 ± 0.1 mg of dry powder.

234

235 *2.8. Statistical analyses*

236 Statistical tests were done with the free R software, version 4.0.0 (R Development Core
237 Team, 2019). Means were expressed with their standard errors. Statistical tests were considered
238 significant at $*P \leq 0.05$, $**P \leq 0.01$ or $***P \leq 0.001$.

239 We used the non-parametric Kruskal Wallis test to assess the effect of the species \times
240 treatment interaction on volumetric soil water content (SWC) at different depths (10 cm, 30 cm,
241 80 cm) for each year. When a significant effect was recorded ($P \leq 0.05$), we used the Wilcoxon
242 test for pairwise comparisons.

243 The effects of species, treatment (three treatments: monoculture, agroforestry, forest
244 mixture), date and their interactions (species \times treatment, species \times date, treatment \times date, species
245 \times treatment \times date) were tested on growth parameters (height, diameter, HGR_{inter} and HGR_{intra})
246 and on competition indices (Hegyi index, h/d ratio). A mixed-effect model, incorporating both
247 fixed and random effects, was adjusted to the data (lmer function of the lme4 package) with the
248 Maximum Likelihood (ML) method, to test the fixed effects. The model had the following form:

249
$$\text{Variable} \sim \text{Species} * \text{Treatment} * \text{Year} + (1 | \text{ID})$$

250 Species, treatment and date were defined as fixed effects; ID, corresponding to each tree
251 measured, was defined as a random effect.

252 As no date effect on leaf nitrogen contents during the 2018 growing season was recorded,
253 only the following effects were tested with a two-way ANOVA: species, treatment and their
254 interaction. We used the non-parametric Kruskal Wallis test to assess the effect of the modality
255 (five modalities: poplar and alder monocultures, poplar and alder agroforestry, forest mixture) on
256 soil organic nitrogen contents in 2018. When a significant effect was recorded ($P \leq 0.05$), the
257 Wilcoxon test was used for pairwise comparisons.

258

259 **3. Results**

260 *3.1. Climate variation over time*

261 During growing season (April through August), cumulative rainfall ranging between 197
262 mm and 413 mm (mean 265 mm) and daily temperatures between 15.2°C and 17.5°C (mean
263 16.1°C) were recorded at the experimental site. From 2016 to 2019, cumulative rainfall during
264 growing season decreased year after year, with 413 mm in 2016 compared to 197 mm in 2019.
265 Year 2018 was the warmest year with an average air temperature of 17.5°C during the April-
266 August period (11.2°C over the whole year). Very little precipitation was recorded in June and
267 July 2018, compared to the other years.

268 [Insert Fig. 2. here]

269 In 2017, SWC at 10 cm deep was significantly different between species ($P \leq 0.001$) and
270 treatments ($P \leq 0.001$) (Table 1). The soil was moister for poplars in agroforestry and the forest
271 mixture with a SWC of 30.5% and 28.7% (mean values during the growing season), respectively,
272 than for poplars in the monoculture with 20.4%. For alders, soil moisture was 10% higher in the
273 forest mixture than in agroforestry. Soil moisture was also higher in the alder rows (39.3%) than
274 in the poplar rows (28.7%) in the forest mixture. In 2018, although the difference was not
275 significant, the soil was moister for poplars in agroforestry than for poplars in monoculture, with
276 a SWC of 36.5% versus 27.7%, respectively. In 2017, SWC at 30 cm deep was significantly
277 higher in agroforestry than in forest mixture for poplars (41.2% versus 27.3%) and, for alders, it
278 was significantly higher in agroforestry (38.9%) than in forest mixture and monoculture (24.6%
279 and 25.7%, respectively).

280 [Insert Table 1 here]

281

282 *3.2. Soil and leaf nitrogen contents*

283 In July 2018, average N-NO₃⁻ in the soil was significantly higher in poplar agroforestry
284 than in the other modalities ($P \leq 0.01$; Table 2). Average levels of leaf nitrogen (N_{leaf}) were higher
285 for alders than for poplars ($P \leq 0.001$), except for the poplars in agroforestry. In agroforestry, the
286 poplars also had slightly higher, though non-significant, N_{leaf} values compared to the poplars in
287 the monoculture and in forest mixture (Table 2).

288 [Insert Table 2 here]

289 3.3. Tree dimensions

290 From 2015 to 2017, poplars were taller in forest plots than in agroforestry and, in 2017,
291 reached a height of 276 cm in monoculture and 250 cm in forest mixture versus 223 cm in
292 agroforestry (Fig. 3.). However, the poplars in agroforestry caught up with the poplars in the
293 forest mixture at the end of 2017 and with the poplars in monoculture in 2018. At the end of the
294 2019 growing season, agroforestry poplars were significantly taller than the poplars in the forest
295 treatments, with 475 cm versus 382 cm in forest mixture and 437 cm in monoculture. At this
296 time, alder heights were not significantly different among treatments (Fig. 3.). From 2015, the
297 poplars in the forest treatments were taller than the alders in any treatment (i.e. 158 cm for
298 poplars in monoculture compared to 101 cm for alders in monoculture, in 2015). From 2018,
299 agroforestry poplars were also significantly taller than alders in any treatment (Fig. 3.).

300 [Insert Fig. 3. here]

301 A significant treatment \times date effect was recorded for poplars in terms of DBH: while
302 poplars in monoculture had the largest diameter in 2017 and poplars in agroforestry the smallest,
303 by 2019 the latter exhibited a significantly larger diameter than the poplars in the forest plots
304 (Table 3). At the end of 2019, alder DBH was not significantly different among treatments.
305 Regardless of year and treatment, poplar stems were about 10 to 20 mm larger than alder stems.

306 [Insert Table 3 here]

307 3.4. Growth dynamics

308 3.4.1. Inter-annual growth dynamics

309 For poplars, a significant treatment effect on height growth rates was found each year,
310 except in 2016 (Fig. 4.). In 2015, poplars had slower growth in agroforestry plots than in forest
311 mixture: 0.3 cm day⁻¹ and 0.4 cm day⁻¹, respectively ($P \leq 0.05$). Inversely, in 2017, the
312 agroforestry poplars were the ones with the highest growth rate: 0.5 cm day⁻¹ for agroforestry vs.
313 0.3 cm day⁻¹ for forest mixture ($P \leq 0.001$). In 2018, agroforestry poplars had a height growth rate
314 almost twice as high as the poplars in the forest mixture and in monoculture, with an average
315 height increase of 0.8 cm per day versus 0.4 cm per day and 0.5 cm per day for forest mixture and
316 monoculture, respectively ($P \leq 0.001$). In 2019, the same trend as in 2018 was found between
317 agroforestry (0.8 cm day⁻¹) and forest mixture (0.4 cm day⁻¹; $P \leq 0.05$), but there was no longer a
318 significant difference between agroforestry and monoculture (0.6 cm day⁻¹). For alders, there was
319 a significant treatment effect in 2016 ($P \leq 0.001$) and in 2017 ($P \leq 0.01$): agroforestry alders had a
320 height growth rate higher than the alders in forest treatments. A significant date effect was also
321 found for both poplars and alders: for poplars, height growth rates were lower in 2015 and 2017
322 than in the other years ($P \leq 0.001$); for alders, height growth rates were lower in odd years than in
323 even years ($P \leq 0.05$).

324 [Insert Fig. 4. here]

325 3.4.2. Intra-annual growth dynamics

326 For each species and in each treatment, average growth in height per day was the fastest at
327 the beginning of June with between 1.3 cm (the lowest value observed for poplars in agroforestry
328 and in monoculture) and 2 cm (the highest value observed for agroforestry alders). A species
329 effect was also observed in early June: alders in forest mixture had significantly higher height

330 growth rates ($P \leq 0.05$) than did poplars in the same treatment (1.75 cm day⁻¹ versus 1.4 cm day⁻¹
331 on average, respectively).

332 During summer, there was a significant species \times treatment effect on HGR_{intra} only in
333 2018 (Table A1). In July and August, agroforestry poplars exhibited a higher height growth rate
334 than did the poplars in monoculture and forest mixture ($P \leq 0.001$, Fig. 5., Table A1). Indeed, in
335 July, poplar growth in agroforestry was between three and five times higher than for poplars in
336 monoculture and forest mixture, respectively. In August, poplar growth in the forest plots nearly
337 stopped while the agroforestry poplars continued to gain 0.4 cm per day on average. For alders,
338 there was no significant treatment effect on height growth rates in 2018: the alders in each
339 treatment followed the same dynamics, i.e. a peak in growth in early June followed by a
340 gradually decreasing rate. In September, poplar and alder height growth stopped in all treatments.

341 [Insert Fig. 5. here]

342 3.5. Intra- and inter-specific competition

343 3.5.1. Hegyi index

344 Irrespective of the year, there was a significant species \times treatment effect with a
345 significantly higher Hegyi index for poplars in monoculture and alders in forest mixture than for
346 poplars in forest mixture and alders in monoculture (4.57 and 5.72 versus 4.05 and 4.21,
347 respectively, in 2017; Fig. 6.). A significant date effect was also found. For alders, the gap
348 between monoculture and forest mixture was more pronounced in 2019 than in 2017 and 2018,
349 with a significant increase in the Hegyi index in forest mixture (5.95 in 2019 versus 5.72 in 2017
350 and 5.61 in 2018). For poplars, the contrary was observed (although the trend was non
351 significant): the gap between monoculture and forest mixture was less pronounced than in 2017
352 and 2018, with a decreasing index in the monoculture (4.82 in 2019 versus 5.57 in 2017).

353 [Insert Fig. 6. here]

354 3.5.2. Height to DBH (*h/d*) ratio

355 There was a significant date effect irrespective of treatment and species, with *h/d*
356 decreasing over time (Table 4). Each year, the species × treatment interaction was significant. In
357 2017, there was a higher *h/d* ratio for poplars in agroforestry than for poplars in monoculture and
358 forest mixture; alders in all treatments also had a higher *h/d* ratio than poplars in monoculture and
359 forest mixture (Table 4). From 2018, there was a clear decrease in *h/d* for both poplars and alders
360 in agroforestry. In 2019, agroforestry poplars showed a lower ratio than monoculture poplars with
361 a value of 1.25 m cm⁻¹ versus 1.53 m cm⁻¹, respectively. Agroforestry alders had a lower *h/d* than
362 alders in forest mixture with a value of 1.36 m cm⁻¹ versus 1.58 m cm⁻¹, respectively. The *h/d* was
363 lower for poplars than for alders in forest mixture (1.41 m cm⁻¹ vs. 1.58 m cm⁻¹).

364 [Insert Table 4 here]

365 4. Discussion

366 We investigated how the performance of fast-growing trees, i.e. poplar and alder, in
367 monocultures is affected when the species are associated in mixed stands and when they are
368 associated with herbaceous species (with an alfalfa-clover succession for poplar and with
369 graminoids for alder). In particular, we present six years of growth monitoring of a large number
370 of trees. Our main hypothesis was that interspecific competition in mixture plots (both mixed
371 forest stands and tree-crop mixtures) would be less strong than intra-specific competition in tree
372 monocultures, due to ecological niche sharing between species and/or facilitation processes
373 caused by the presence of N₂-fixing species (alfalfa, clover, alder) in the mixtures. We therefore
374 expected that the trees would grow faster and be larger and taller in mixtures than in
375 monocultures.

376 4.1. Climate conditions

377 The weather conditions measured from 2016 to 2019 were contrasted among years.
378 Conditions were particularly dry during the 2018 growing season with a drastic decline in
379 precipitation during precisely those months where tree growth is usually high (June-July).
380 Moreover, both mean annual temperature and April-August temperatures were, on average,
381 higher in 2018 than in the other years. This resulted in a marked decrease in SWC in July and
382 August 2018: in August, at 10 cm in depth, the minimum value was measured for poplars in
383 monoculture with a SWC of 15% and the maximum value was recorded for poplars in
384 agroforestry with a SWC of 28%, corresponding respectively to 41% and 77% of field capacity
385 (Fig. A1.).

386 4.2. Trends over time

387 4.2.1. Agroforestry vs. monoculture

388 Shortly after planting, the agroforestry poplars exhibited a delayed growth rate compared
389 to the poplars in the monoculture and forest mixture. This may be due to belowground
390 competition between the poplars and the alfalfa immediately after planting. Indeed, crops can
391 reduce the nutrient and water available to trees, thereby reducing their growth (Burgess et al.,
392 2005); this is especially true for legumes such as alfalfa, which can have deep, competitive roots
393 like trees (Dawson et al., 2001). Similar results were highlighted by Gakis et al. (2004), who
394 showed that trees (*Acer pseudoplatanus* and *Pinus sylvestris*) associated with legumes (*Trifolium*
395 *repens*) had a lower height and a smaller stem diameter than in monoculture. Moreover, Powell
396 and Bork (2004) showed that the height and diameter of poplars (*Populus tremuloides*) were
397 reduced by 30% when they were associated with alfalfa (*Medicago sativa*) during the early stages
398 of development. In our study, alfalfa was replaced by clover during the fifth growing season
399 (2018). At this stage, the trees were well established and the belowground competition with the
400 crop was probably less strong. Indeed, in 2019, the agroforestry poplars had an average height

401 and diameter greater than the poplars in the monoculture. Moreover, from 2018 on, the height
402 growth rate of the agroforestry poplars was consistently higher than for the monoculture poplars.

403 After six years of growth, the monoculture poplars exhibited a higher *h/d* ratio than did
404 the agroforestry poplars. This result suggests that the intra-specific competition in the
405 monocultures was more intense than the interspecific competition faced by the trees in
406 agroforestry. Our results are in line with those of Rivest on *Populus spp.* for intercropping with
407 soybean (*Glycine max*) and cereals (Rivest et al., 2009). In the latter study, shortly after planting,
408 the intercrop was not beneficial to poplar growth, but after four years, DBH and stem height were
409 higher in agroforestry than in the monoculture. The authors argued that these results were mainly
410 due to the effect of intercrop fertilization applied during their study. At our experimental site, the
411 crops were not fertilized but the alfalfa and then the clover, which are both N₂-fixing species,
412 may have had a positive effect on poplar growth. Indeed, the diameter increment of the poplars in
413 the agroforestry treatment was approximately 15 mm per year between 2017 and 2019, vs. 8 mm
414 in the monoculture. Similarly, Taghiyari and Efhami (2011) showed a positive effect on the
415 diameter increment of *Populus nigra* in mixtures with alfalfa, with an average annual increment
416 of 13.8 mm over ten growing seasons vs. 12.2 mm without alfalfa. Recently, Shults et al. (2020)
417 also showed an increase in soil N-NO₃⁻ ranging between 150 and 220% in a poplar (*Populus*
418 *nigra* × *P. maximowiczii*) short rotation plantation intercropped with clover (*Trifolium pretense*)
419 compared to a bare-soil control; this increase caused a 25% increase in poplar leaf nitrogen
420 concentrations, but poplar productivity was not significantly increased within two years. In our
421 study, soil mineral nitrogen (N-NO₃⁻) content was more than five times higher in agroforestry
422 than in the monocultures five years after planting. This is likely due to the symbiotic fixation of
423 atmospheric dinitrogen by the alfalfa and the clover but also due to increased nitrogen availability
424 through root deposition. Many studies have shown that alfalfa has very high N₂ fixation rates
425 (Burity et al., 1989; Russelle and Birr, 2004) and that legumes release nitrogen rhizodeposits with

426 a low C/N ratio that are assumed to represent a significant return of nitrogen to the soil (Mayer et
427 al., 2004). Excess soil nitrogen may therefore have benefited the trees, as evidenced by the
428 slightly higher leaf nitrogen content in the agroforestry poplars. This result could be evidence of a
429 facilitation process (Powell and Bork, 2004). Moreover, the different tree planting density in the
430 agroforestry treatment, where every second row of trees was replaced by the crop, probably
431 reduced the competition for light among the trees. Indeed, as the spacing between trees increases,
432 the competition for light decreases (Benomar et al., 2013). The predominant interaction in
433 agroforestry therefore seems to shift from competition, during the first years after planting, to a
434 combination of reduced competition and facilitation.

435 In agroforestry, poplar growth did not seem to be affected by the dry and warm summer in
436 2018. Indeed, height growth rates remained high during the summer months, compared to
437 monoculture where growth nearly stopped as of July. Overall, soil water content was the highest
438 in the agroforestry treatment and the lowest in the monoculture. In our study, at 10 cm in depth,
439 the SWC was between 7% and 12% higher in agroforestry than in forest treatments (both in
440 monoculture and mixed stands) for the dry period in 2018 (July-August). This is consistent with
441 Powell and Bork's (2004) findings; they showed that alfalfa can facilitate soil moisture retention.
442 A dense herbaceous cover (as alfalfa provides) limits evaporation from the top soil by reducing
443 the exposure of the soil to wind and sun (Powell and Bork, 2004). Moreover, poplar and the crop
444 (alfalfa – clover) may have different spatial distributions of their root system, thus reducing the
445 competition for soil water. This was shown by Thevathasan and Gordon (1995) for a poplar /
446 barley mixture (*Populus spp.* and *Hordeum vulgare*) where the barley roots were mostly confined
447 in the top 10 cm of the soil while the poplar roots were deeper. This could be another positive
448 effect of agroforestry on poplar growth, once the dominant effect of the crop on water
449 competition with tree roots in the first few years is passed.

450 *4.2.2. Forest mixture vs. monoculture*

451 At the end of the experiment, the poplars in the forest mixture were shorter and narrower
452 than the poplars in the monoculture. A recent meta-analysis has shown that mixed-tree
453 plantations including a N₂-fixing species like alder were globally more productive than the
454 corresponding monocultures of the non-fixing species (Marron and Epron, 2019), and that this
455 effect was more pronounced on poor soils (Binkley 1983). Despite this general trend, the meta-
456 analysis also inventoried studies where mixture plantations were less productive than
457 monocultures (e.g. Marron et al. 2018), as is the case in the present study. Indeed, the mean
458 diameter we recorded in our study was significantly lower for poplars in forest mixture than in
459 monoculture. The soil nitrogen content was slightly, but not significantly, higher in alder
460 monoculture and in forest mixture compared to poplar monoculture, suggesting that symbiotic
461 fixation by alders did occur but had no significant effect on the growth of the non-fixing species,
462 at least during the time span of our study. Teissier du Cros et al. (1984) also showed that, a few
463 years after planting, nitrogen fixation by alder (*Alnus glutinosa*) was not yet sufficient to benefit
464 poplar (*Populus trichocarpa* × *deltoides*) growth, at stand level.

465 We found no significant treatment effect on tree height or DBH for alders. According to
466 Piotto's meta-analysis (2008), forest mixtures have little or no effect on tree height growth rates
467 at stand level, but generally do have a positive effect on stem diameter increment. However, in
468 mixtures including N₂-fixing species, the diameter of the fixing species was negatively affected.
469 Sayyad et al. (2006) showed similar results in a poplar/alder mixture (*Populus deltoides* and
470 *Alnus subcordata*) where alder diameter was significantly higher in monocultures than in
471 association with poplars. In this association, poplar growth only benefited from the presence of
472 the other species. In our study, the absence of effect on alder may be due to the fact that, as alder
473 growth is slower than poplar growth, it was simply too soon to observe interaction effects.
474 Poplars were significantly taller than alders in forest mixture, i.e. slightly less than one and a half
475 times taller. Moreover, from 2015 to 2018, alders had an average height growth rate of 54 cm per

476 year while for poplars, the average rate was 75 cm per year. Our results are in agreement with
477 Côté and Camiré (1987), who showed that poplars (*Populus nigra* × *Populus trichocarpa*) were
478 between one and a half and two times taller than alders (*Alnus glutinosa*) in forest mixture. We
479 suppose that these size differences between species creates a stratification of their canopies in the
480 mixture, thus bringing about a reduction in competition for light. A study of competition indices
481 supports this theory. Based on the Hegyi index for poplars, it appeared that the intra-specific
482 competition in the monocultures was higher than the interspecific competition in the forest
483 mixture, in agreement with the trend observed for the *h/d* ratio. According to Vanclay (2006), a
484 high Hegyi index means that the subject tree has more and/or larger neighbors, resulting in a
485 decrease in the growth of the subject tree. In our study, with similar tree densities in all the forest
486 plots, a high Hegyi index therefore means that the subject tree has larger neighbors. In forest
487 mixture, the lower Hegyi index (reduced competition) for poplars compared to their monoculture
488 may indicate that canopy stratification reduced the competition for light (Ghorbani et al., 2018).
489 According to Forrester et al. (2004), canopy stratification is a factor to consider as long as there is
490 a significant difference in height between the species in the same treatment, which is what we
491 observed in our study. Furthermore, considering that the individuals of a given tree species have
492 similar ecological requirements and therefore more potential niche overlap than individuals from
493 different species (Yang et al., 2019), we assume that poplars probably competed for the same
494 resources, and this may explain why the Hegyi index of poplar was higher in the monoculture.
495 For alders, on the contrary, intra-specific competition was less strong than interspecific
496 competition. We assume that, because poplars were taller and the forest cover was gradually
497 starting to close, the alders suffered from poplar competition for light and allocated more carbon
498 to height than to diameter (Benomar et al., 2013). In other words, the alders sought light by
499 favoring growth in height in the forest mixture, whereas in alder monoculture, the canopy had not
500 yet started to close.

501 It is supposed that the stratification of the canopy and the root systems in mixed
502 plantations allows the trees to more efficiently capture light (Kelty, 1992), water (Bai et al., 2016;
503 Battipaglia et al., 2017) and nutrient resources (Binkley et al., 1992). However, at 30 cm in depth,
504 the soil water content was the lowest in the forest mixture, irrespective of the year. The roots of
505 the poplars and alders may have overlapped and been competing for water. Indeed, poplars in
506 general (*Populus spp.*) are highly competitive at this depth, compared to other species (e.g.
507 *Juglans nigra* and *Quercus rubra*), due to their high concentration of fine and coarse roots
508 (Borden et al., 2017). In our study, reduced competition could have occurred aboveground, thus
509 improving light capture in the mixture, at least for poplar, but belowground, competition for the
510 water resource could have remained strong, thus resulting in lower tree performances in terms of
511 growth in the forest mixture compared to the monocultures of the two species.

512 **5. Conclusion**

513 After six years of growth, positive interactions seem to be at play in the poplar / legume
514 association, in agreement with our main hypothesis. Our results show that intercrops with N₂-
515 fixing species can significantly improve poplar growth. However, careful weeding of tree rows
516 during the first years after planting is necessary in order to control the strong interspecific
517 competition between the trees and the herbaceous species. On the other hand, in the poplar / alder
518 association, poplar growth was negatively affected compared to its monoculture, despite a
519 stratification of the canopy suggesting aboveground niche sharing. This negative effect could be
520 due to a stronger competition for soil water between species than in the monoculture, and to the
521 fact that nitrogen fixation by the alder was not yet sufficient to benefit the poplars. Alder growth
522 did not appear to be affected by the different kinds of mixtures, suggesting that alder is not
523 limited by soil resources and/or the experiment ended too soon to observe interaction effects for
524 this species.

525

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803

804 **Figure captions**

805 **Fig. 1.** Experimental design of the La Bouzule site. Size of the plots and locations of humidity
806 probes and data loggers are indicated. Details of the forest mixture and agroforestry plots are also
807 presented, showing spacing between trees and crops.

808 **Fig. 2.** Cumulative monthly rainfall (histograms, mm) and mean temperatures (dots, °C) between
809 April 1st and August 31, from 2016 to 2019 at the experimental site. CAR = cumulative annual
810 rainfall (mm); MAT = mean annual temperature (°C).

811 **Fig. 3.** Inter-annual dynamics of stem heights (in cm) of poplars and alders in monocultures,
812 forest mixture and agroforestry between 2015 and 2019. The shaded areas show the 95%
813 confidence intervals. Different uppercase letters indicate significant differences between dates;
814 different lowercase letters indicate significant differences between treatments at the end of the
815 experiment. For each effect (D, date; S, species, T, treatment) and their interactions (S×T, T×D,
816 S×D, S×T×D), significant differences are indicated by asterisks: $P \leq 0.05^*$, $P \leq 0.01^{**}$,
817 $P \leq 0.001^{***}$, *ns* for non-significant.

818 **Fig. 4.** Annual-based height growth rates (HGR_{inter} , cm day⁻¹) for poplar (A) and alder (B) since
819 2015 in agroforestry, forest mixture and monocultures (n=60). Different letters indicate
820 significant differences between treatments for each growing season (April to August). For each
821 effect (D, date; S, species, T, treatment) and their interactions (S×T, T×D, S×D, S×T×D),
822 significant differences are indicated by asterisks: $P \leq 0.05^*$, $P \leq 0.01^{**}$, $P \leq 0.001^{***}$, *ns* for non-
823 significant. Each box represents the quartile below (Q1) and above (Q3) the median value. The
824 diamond in the box represents the mean of all trees. Vertical bars represent minimum and
825 maximum values. Grey dots are individual values.

826 **Fig. 5.** Intra-annual height growth rates (HGR_{intra} , cm day⁻¹) for poplar (A) and alder (B) in
827 monocultures, forest mixture and agroforestry between April and August 2018 (n=60). For each

828 effect (D, date; S, species, T, treatment) and their interactions (S×T, T×D, S×D, S×T×D),
829 significant differences are indicated by asterisks: $P \leq 0.05^*$, $P \leq 0.01^{**}$, $P \leq 0.001^{***}$, *ns* for non-
830 significant. Each box represents the quartile below (Q1) and above (Q3) the median value.
831 Vertical bars represent minimum and maximum values. Dots are outliers.

832 **Fig. 6.** Hegyi index for diameter for poplar and alder in monocultures and forest mixture in 2017,
833 2018 and 2019. Different uppercase letters indicate a significant difference between dates; for
834 each date, different lowercase letters indicate significant differences for the *S×T* interaction. For
835 each effect (D, date; S, species, T, treatment) and their interactions (S×T, T×D, S×D, S×T×D),
836 significant differences are indicated by asterisks: $P \leq 0.05^*$, $P \leq 0.01^{**}$, $P \leq 0.001^{***}$, *ns* for non-
837 significant.

838 **Fig. A1.** Time course of soil water content (SWC, %) at the experimental site between April and
839 August 2018 at 10 cm (A), 30 cm (B) and 80 cm (C) in depth, depending on the treatment and
840 species (P, poplar / A, alder). SWC values shown are the mean value for each month. Means \pm
841 standard errors.

842 **Fig. A2.** Time course of intra-annual height growth rates (HGR_{intra} , cm day^{-1}) for poplar (A) and
843 alder (B) in monocultures, forest mixture and agroforestry between April and August 2016
844 (n=60). The effects of date (D), treatment (T) and their interaction (D×T) are indicated for
845 $P \leq 0.05^*$, $P \leq 0.01^{**}$ and $P \leq 0.001^{***}$, *ns* for non-significant. Each box represents the quartile
846 below (Q1) and above (Q3) the median value. Vertical bars represent minimum and maximum
847 values. Dots are outliers.

848 **Fig. A3.** Time course of intra-annual height growth rates (HGR_{intra} , cm day^{-1}) for poplar (A) and
849 alder (B) in monocultures, forest mixture and agroforestry between April and August 2017
850 (n=60). The effects of date (D), treatment (T) and their interaction (D×T) are indicated for
851 $P \leq 0.05^*$, $P \leq 0.01^{**}$ and $P \leq 0.001^{***}$, *ns* for non-significant. Each box represents the quartile

852 below (Q1) and above (Q3) the median value. Vertical bars represent minimum and maximum
853 values. Dots are outliers.

854 **Fig. A4.** Time course of intra-annual height growth rates (HGR_{intra} , cm day^{-1}) for poplar (A) and
855 alder (B) in monocultures, forest mixture and agroforestry between April and August 2019
856 ($n=60$). The effects of date (D), treatment (T) and their interaction ($D \times T$) are indicated for
857 $P \leq 0.05^*$, $P \leq 0.01^{**}$, and $P \leq 0.001^{***}$, ns for non-significant. Each box represents the quartile
858 below (Q1) and above (Q3) the median value. Vertical bars represent minimum and maximum
859 values. Dots are outliers.

860 **Table captions**

861 **Table 1** Variations in volumetric soil water content (SWC %) depending on the treatment
862 between 2016 and 2019 at the experimental site. SWC values shown are the mean values during
863 the growing season (April to August). Within columns for each depth, significant differences
864 between species and treatment are indicated: $P \leq 0.05^*$, $P \leq 0.01^{**}$, $P \leq 0.001^{***}$, ns for non-
865 significant.

866 **Table 2** A) Soil organic nitrogen content (N-NO_3^-) in the upper 15 cm of the soil in the central
867 inter-row, depending on the modality (5 modalities: poplar/alder agroforestry, poplar/alder
868 monoculture, forest mixture) in 2018. Different letters indicate significant differences between
869 modalities. Means \pm standard errors; $n=9$. B) Leaf nitrogen content (N_{leaf}) for poplar and alder
870 depending on the treatment (3 treatments: agroforestry, forest mixture, monocultures) in 2018.
871 Different letters indicate significant differences between species and treatment. Means \pm standard
872 error; $n=30$.

873 **Table 3** Diameter at breast height (DBH in mm, means \pm standard errors) for poplar and alder
874 depending on the treatment at the end of each growing season (2017 to 2019). Different
875 uppercase letters indicate significant differences between dates; within each column, different

876 lowercase letters indicate significant differences between treatments. For each effect (D, date; S,
877 species, T, treatment) and their interactions (S×T, T×D, S×D, S×T×D), significant differences are
878 indicated by asterisks: $P \leq 0.05^*$, $P \leq 0.01^{**}$, $P \leq 0.001^{***}$, *ns* for non-significant.

879 **Table 4** Height to DBH ratio (h/d , m cm^{-1}) for poplar and alder in monocultures, forest mixture
880 and agroforestry at the end of each growing season (2017 to 2019) (means \pm standard errors).
881 Different uppercase letters indicate significant difference between dates; within each column,
882 different lowercase letters indicate significant differences between treatments. For each effect (D,
883 date; S, species, T, treatment) and their interactions (S×T, T×D, S×D, S×T×D), significant
884 differences are indicated by asterisks: $P \leq 0.05^*$, $P \leq 0.01^{**}$, $P \leq 0.001^{***}$, *ns* for non-significant.

885 **Table A1** Intra-annual height growth rates (HGR_{intra} , cm day^{-1}) for poplar and alder in
886 monocultures, forest mixture and agroforestry between April and August 2018 ($n=60$). Different
887 letters indicate significant differences between species and treatments for each month. The effects
888 of species (*S*), treatment (*T*) and their interaction (*S*×*T*) are indicated for $P \leq 0.05^*$, $P \leq 0.01^{**}$, and
889 $P \leq 0.001^{***}$, *ns* for non-significant. Means \pm standard error.

890

Figures and tables

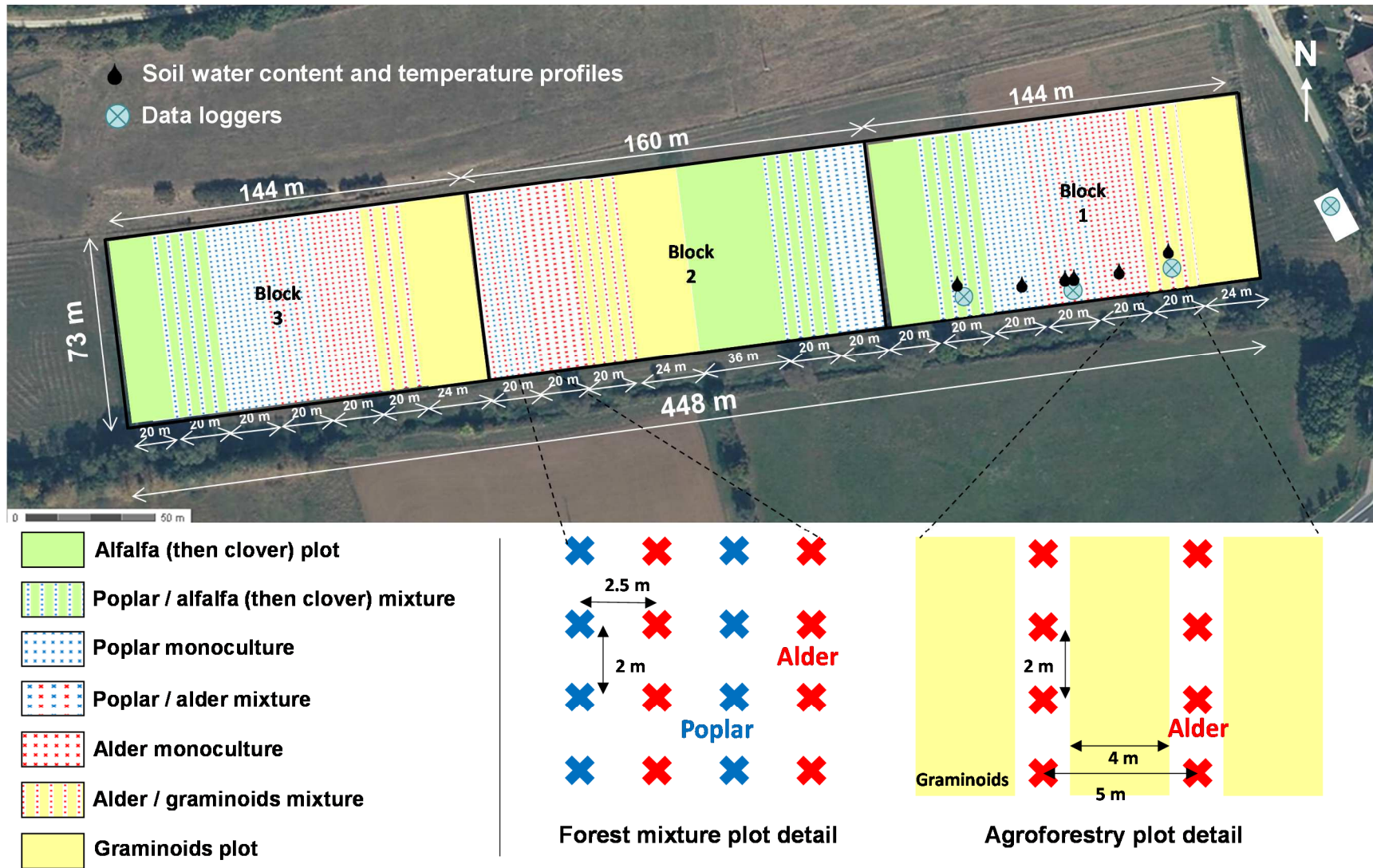


Fig. 1.

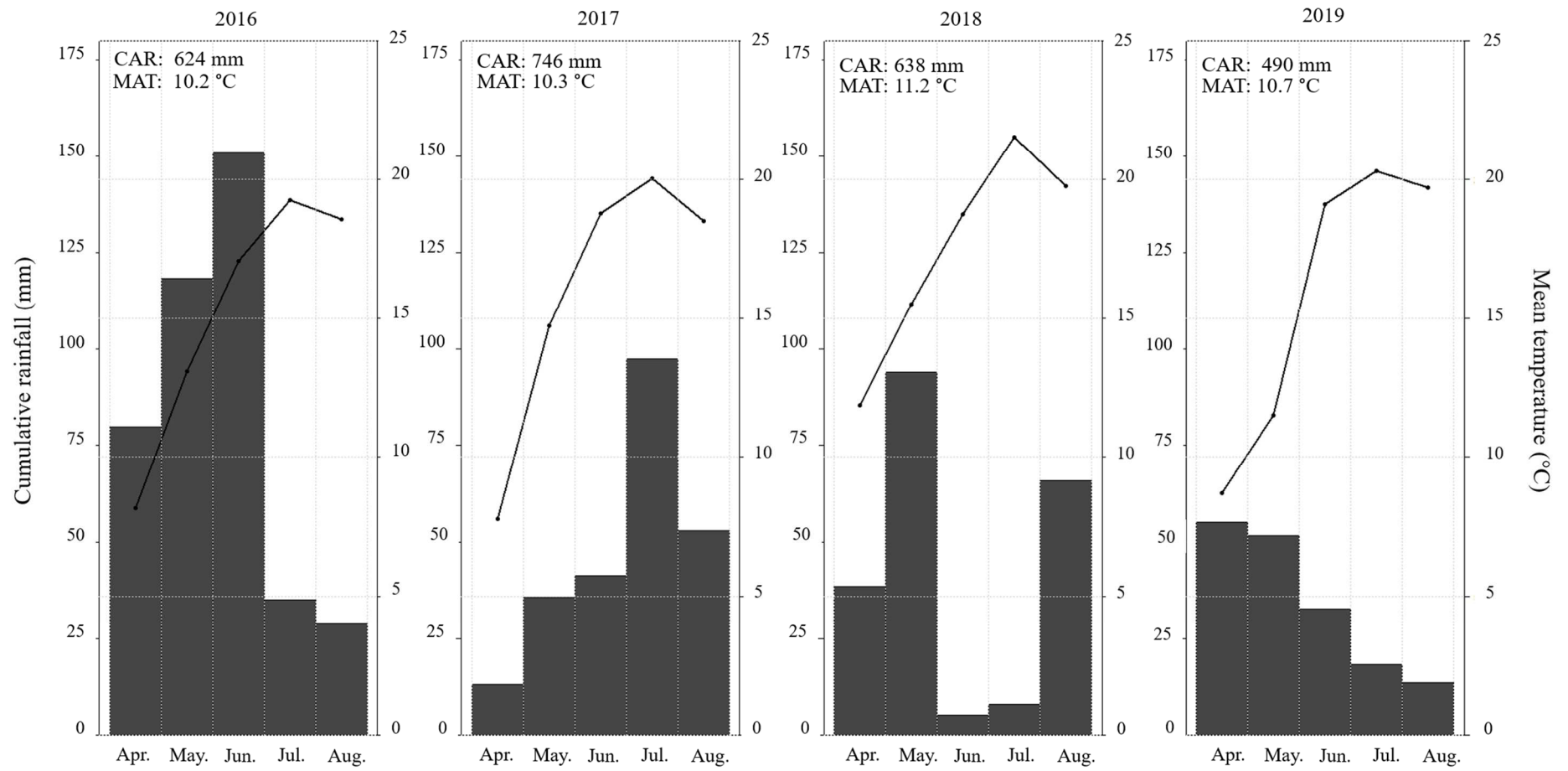


Fig. 2.

Table 1

SWC %		2016		2017		2018		2019	
		Poplar	Alder	Poplar	Alder	Poplar	Alder	Poplar	Alder
10 cm in depth	Agroforestry	37.6 ± 0.3	38.8 ± 0.4	30.5 ± 0.3 ^c	28.7 ± 0.4 ^{bc}	36.5 ± 0.5 ^{ab}	31.9 ± 0.6 ^{ab}	35.3 ± 0.6	24.8 ± 0.8
	Forest mixture	38.4 ± 0.7	43.6 ± 0.5	28.7 ± 0.4 ^{bc}	39.3 ± 0.3 ^d	31.3 ± 0.7 ^a	42.4 ± 0.5 ^b	32.7 ± 0.3	31.6 ± 0.5
	Monoculture	35.2 ± 0.6	38.9 ± 0.6	20.4 ± 0.3 ^a	36.2 ± 0.3 ^d	27.7 ± 0.8 ^a	39.9 ± 0.6 ^{ab}	28.2 ± 0.9	26.7 ± 0.8
		<i>ns, P = 0.06</i>				<i>ns, P = 0.39</i>			
30 cm in depth	Agroforestry	47.4 ± 0.3 ^{ab}	44.0 ± 0.1 ^{ab}	41.2 ± 0.2 ^b	38.9 ± 0.3 ^b	45.0 ± 0.3 ^b	34.5 ± 0.6 ^{ab}	37.1 ± 0.7	32.0 ± 0.7
	Forest mixture	36.0 ± 0.6 ^{ab}	36.1 ± 0.5 ^a	27.3 ± 0.4 ^a	25.7 ± 0.3 ^a	29.9 ± 0.4 ^a	29.2 ± 0.7 ^a	35.3 ± 0.4	28.3 ± 0.7
	Monoculture	45.1 ± 0.3 ^b	39.6 ± 0.5 ^{ab}	38.6 ± 0.3 ^b	24.6 ± 0.7 ^a	42.3 ± 0.4 ^{ab}	32.8 ± 0.7 ^{ab}	39.4 ± 0.5	28.8 ± 0.9
						<i>ns, P = 0.37</i>			
80 cm in depth	Agroforestry	48.4 ± 0.1 ^c	46.4 ± 0.0 ^{bc}	42.5 ± 0.1 ^b	42.8 ± 0.1 ^b	42.6 ± 0.2 ^b	44.9 ± 0.1 ^b	41.8 ± 0.3 ^{ab}	41.7 ± 0.2 ^{ab}
	Forest mixture	47.5 ± 0.1 ^c	45.0 ± 0.1 ^{bc}	42.6 ± 0.2 ^b	39.3 ± 0.2 ^b	45.0 ± 0.3 ^b	42.4 ± 0.3 ^b	42.9 ± 0.3 ^b	40.7 ± 0.3 ^{ab}
	Monoculture	40.7 ± 0.1 ^a	39.7 ± 0.1 ^a	35.5 ± 0.3 ^a	36.2 ± 0.2 ^a	37.4 ± 0.2 ^a	37.9 ± 0.2 ^a	36.0 ± 0.3 ^a	36.6 ± 0.5 ^{ab}

Table 2

A

Modality	N-NO ₃ ⁻ (mg kg ⁻¹ soil)	
Poplar agroforestry	28.7 ± 4.34	c
Poplar monoculture	3.91 ± 0.37	a
Forest mixture	5.53 ± 0.91	ab
Alder agroforestry	6.89 ± 0.80	b
Alder monoculture	4.94 ± 0.46	ab

B

Species	Treatment	N _{leaf} (mg g ⁻¹ leaf)	
Poplar	Agroforestry	19.3 ± 1.5	ab
	Forest mixture	16.5 ± 2.4	a
	Monoculture	17.4 ± 1.9	a
Alder	Agroforestry	26.7 ± 1.6	c
	Forest mixture	25.4 ± 1.5	bc
	Monoculture	25.8 ± 2.2	bc

Table 3

Trait	Species	Treatment	2017		2018		2019		
			Mean \pm SE	Variation	Mean \pm SE	Variation	Mean \pm SE	Variation	
DBH (mm)	Poplar	Agroforestry	15 \pm 0.6	b	27 \pm 0.9	c	46 \pm 1.4	d	
		Forest mixture	19 \pm 0.5	c	24 \pm 0.7	b	33 \pm 0.9	b	
		Monoculture	21 \pm 0.5	c	27 \pm 0.6	c	37 \pm 0.9	c	
	Alder	Agroforestry	11 \pm 0.3	a	19 \pm 0.4	a	24 \pm 0.5	a	<i>S</i> ***
		Forest mixture	11 \pm 0.3	a	17 \pm 0.4	a	22 \pm 0.5	a	<i>T</i> ***
		Monoculture	11 \pm 0.2	a	17 \pm 0.3	a	22 \pm 0.3	a	<i>D</i> ***
								<i>S</i> \times <i>T</i> *	
								<i>T</i> \times <i>D</i> ***	
								<i>S</i> \times <i>D</i> ***	
								<i>S</i> \times <i>T</i> \times <i>D</i> ***	

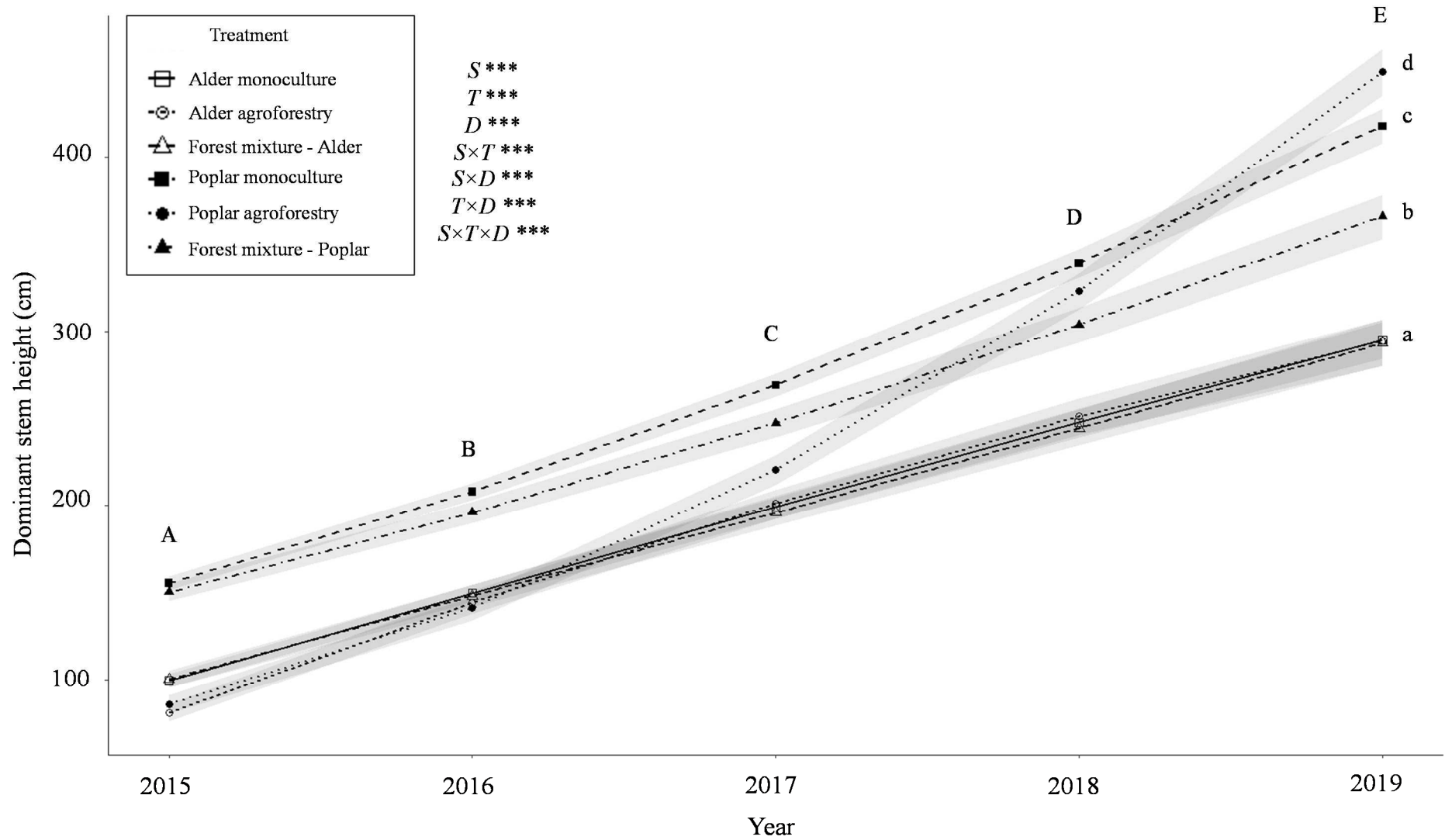


Fig. 3.

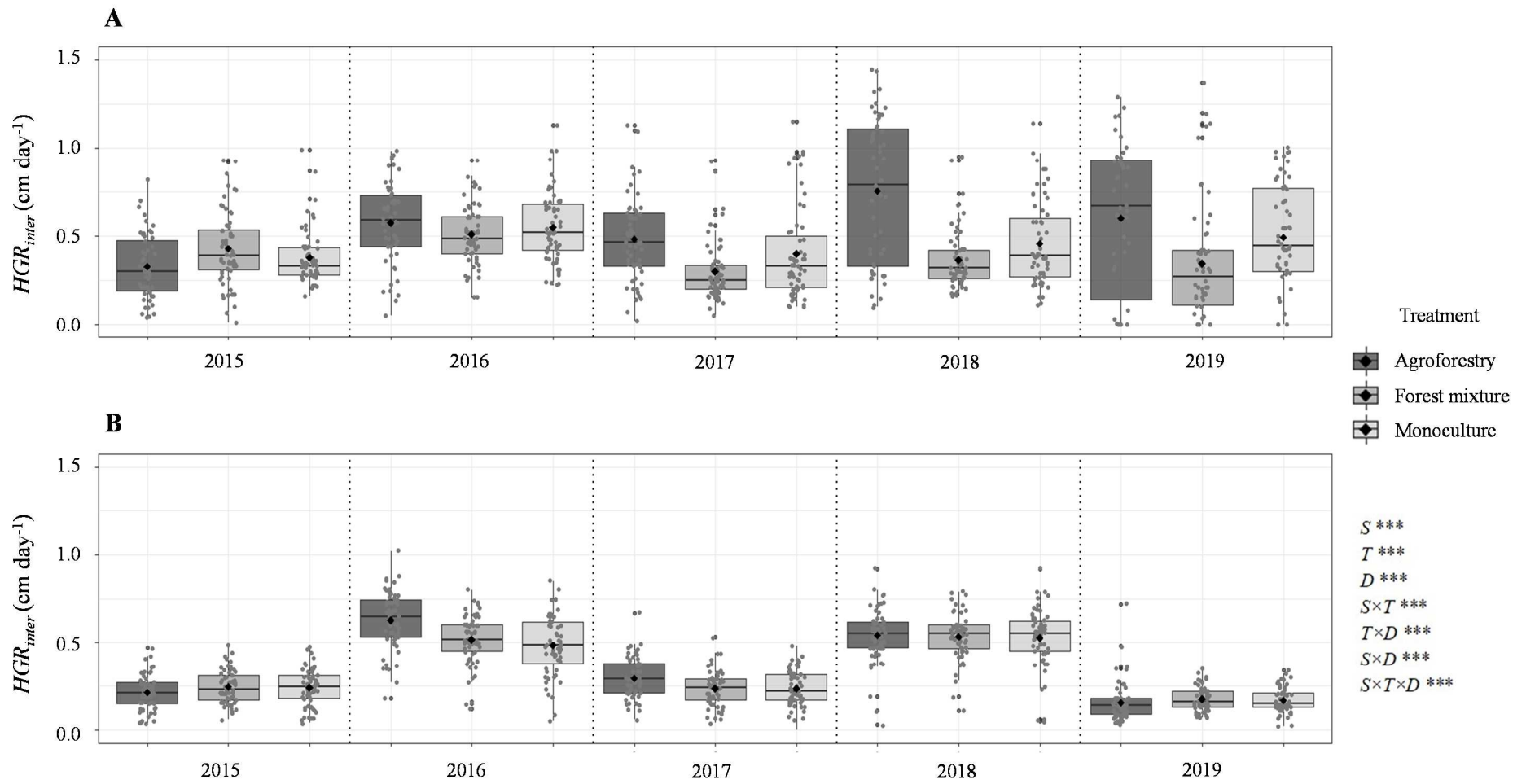


Fig. 4.

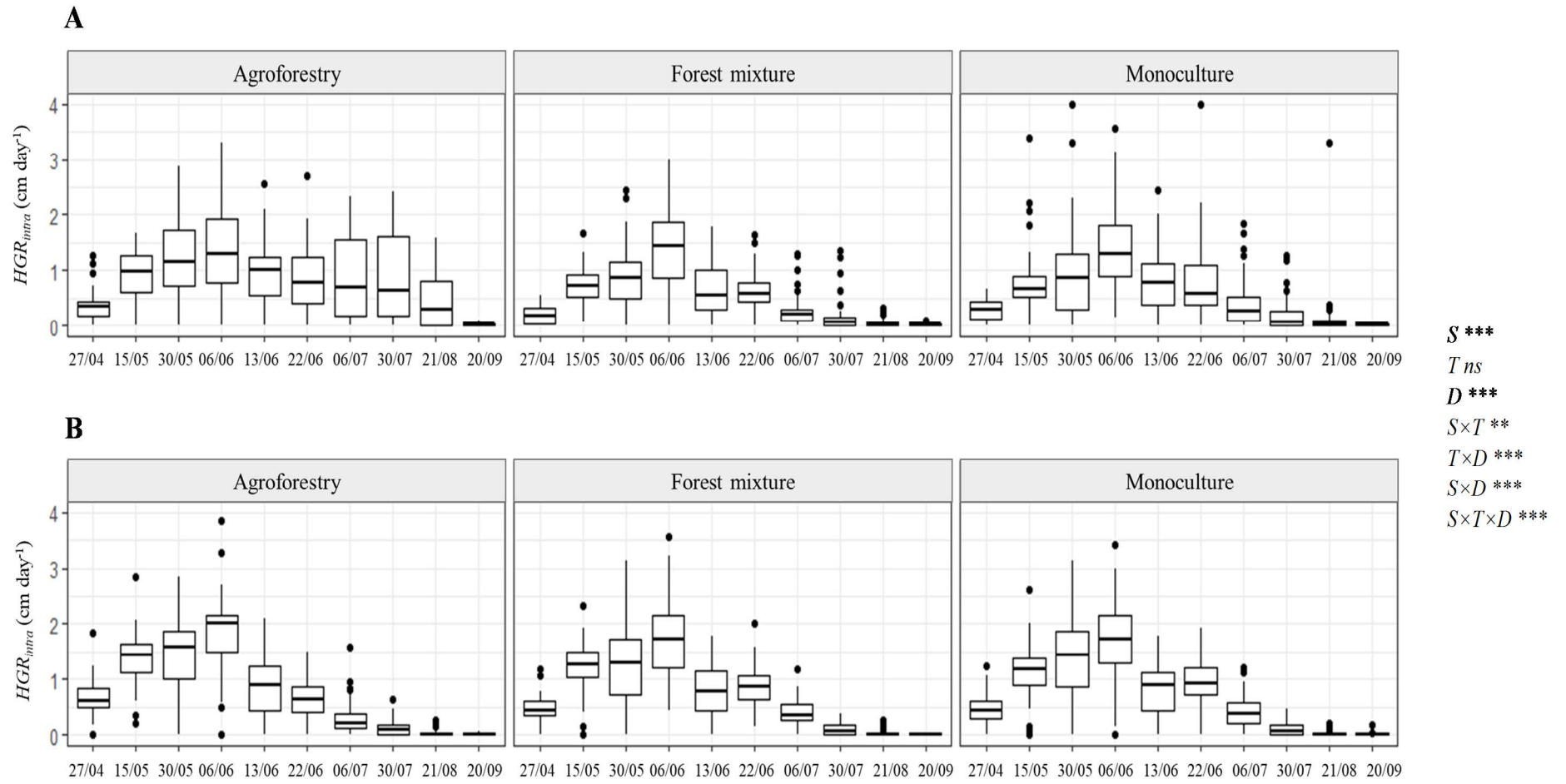


Fig. 5.

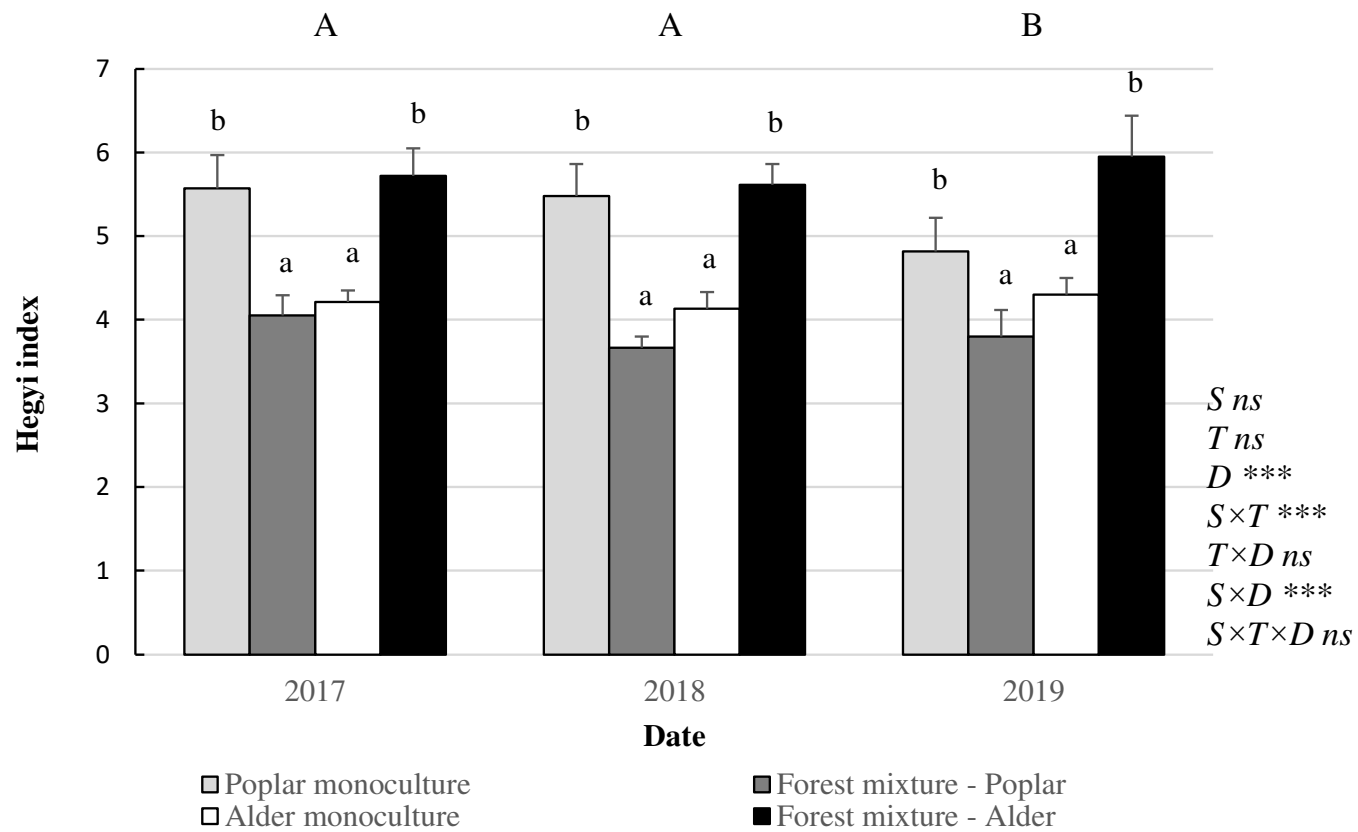


Fig. 6.

Table 4

Trait	Species	Treatment	2017 A		2018 B		2019 C		
			Mean \pm SE	Variation	Mean \pm SE	Variation	Mean \pm SE	Variation	
<i>h/d</i> (m cm ⁻¹)	Poplar	Agroforestry	2.09 \pm 0.05	b	1.66 \pm 0.04	a	1.25 \pm 0.03	ab	<hr/> <i>S</i> *** <i>T ns</i> <i>D</i> *** <i>S</i> \times <i>T</i> * <i>T</i> \times <i>D</i> *** <i>S</i> \times <i>D</i> *** <i>S</i> \times <i>T</i> \times <i>D</i> ***
		Forest mixture	1.83 \pm 0.04	a	1.68 \pm 0.04	a	1.41 \pm 0.03	bc	
		Monoculture	1.75 \pm 0.03	a	1.67 \pm 0.03	a	1.53 \pm 0.04	cd	
	Alder	Agroforestry	2.16 \pm 0.05	b	1.61 \pm 0.03	a	1.36 \pm 0.03	ab	
		Forest mixture	2.20 \pm 0.06	b	1.89 \pm 0.05	b	1.58 \pm 0.03	d	
		Monoculture	2.19 \pm 0.04	b	1.79 \pm 0.03	ab	1.49 \pm 0.02	bd	

Appendix

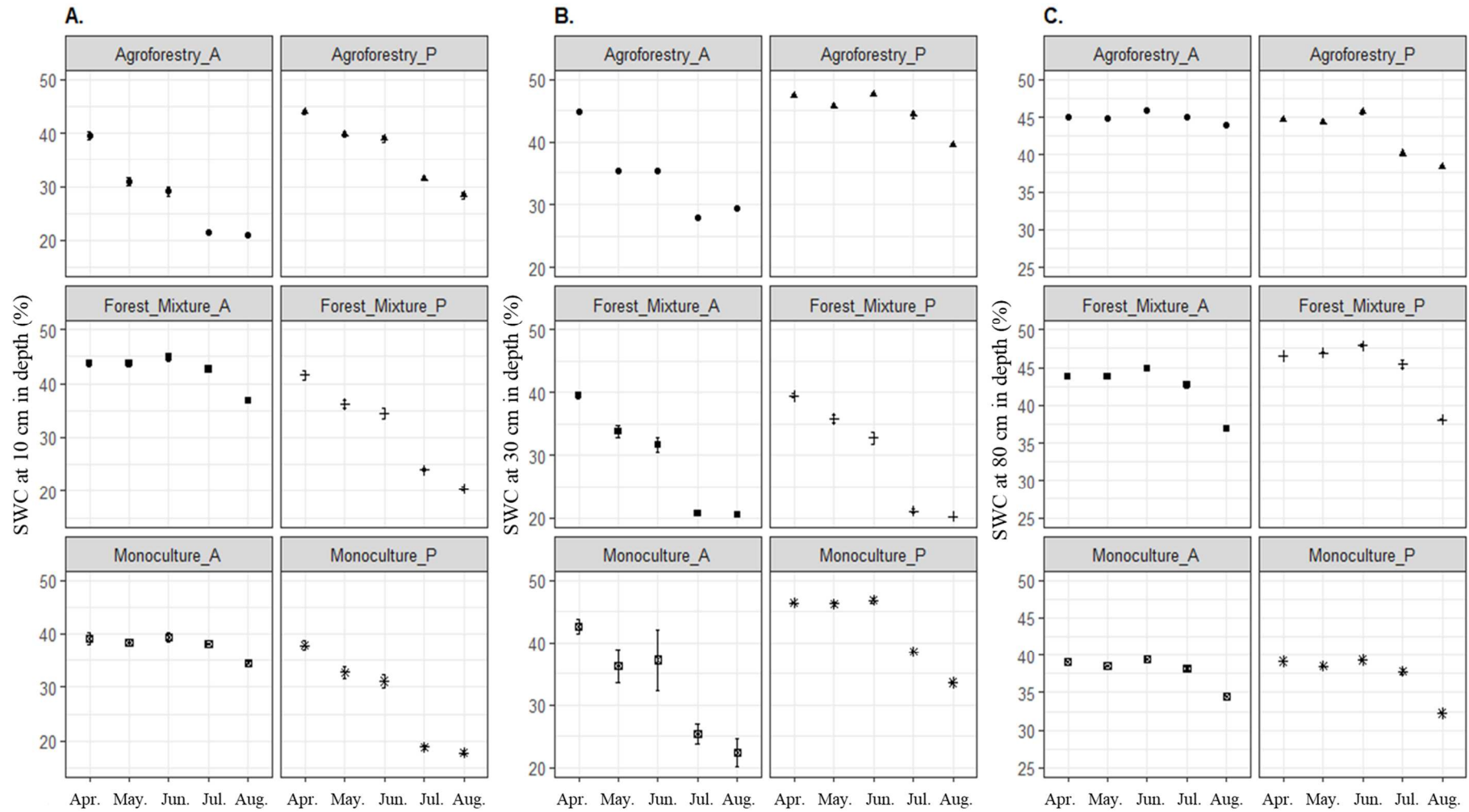


Fig. A1.

Table A1

HGR_{intra} (cm day ⁻¹)		2018				
		Apr.	May	Jun.	Jul.	Aug.
Poplar	Agroforestry	0.31 ± 0.03 ^a	1.01 ± 0.15 ^a	1.09 ± 0.09 ^{ab}	0.86 ± 0.10 ^b	0.43 ± 0.06 ^b
	Forest mixture	0.18 ± 0.04 ^a	1.10 ± 0.46 ^a	0.70 ± 0.42 ^a	0.18 ± 0.04 ^a	0.02 ± 0.01 ^a
	Monoculture	0.27 ± 0.03 ^a	0.86 ± 0.22 ^a	0.99 ± 0.10 ^{ab}	0.24 ± 0.08 ^a	0.08 ± 0.06 ^a
Alder	Agroforestry	0.62 ± 0.05 ^c	1.37 ± 0.10 ^a	1.14 ± 0.13 ^{ab}	0.18 ± 0.03 ^a	0.00 ± 0.01 ^a
	Forest mixture	0.47 ± 0.03 ^b	0.97 ± 0.41 ^a	1.32 ± 0.32 ^b	0.27 ± 0.06 ^a	0.00 ± 0.06 ^a
	Monoculture	0.46 ± 0.03 ^b	1.31 ± 0.21 ^a	1.12 ± 0.09 ^{ab}	0.24 ± 0.03 ^a	0.00 ± 0.10 ^a
		<i>S</i> ***	<i>S</i> <i>ns</i>	<i>S</i> <i>ns</i>	<i>S</i> ***	<i>S</i> ***
		<i>T</i> ***	<i>T</i> <i>ns</i>	<i>T</i> *	<i>T</i> ***	<i>T</i> ***
		<i>S</i> × <i>T</i> <i>ns</i>	<i>S</i> × <i>T</i> <i>ns</i>	<i>S</i> × <i>T</i> <i>ns</i>	<i>S</i> × <i>T</i> ***	<i>S</i> × <i>T</i> ***

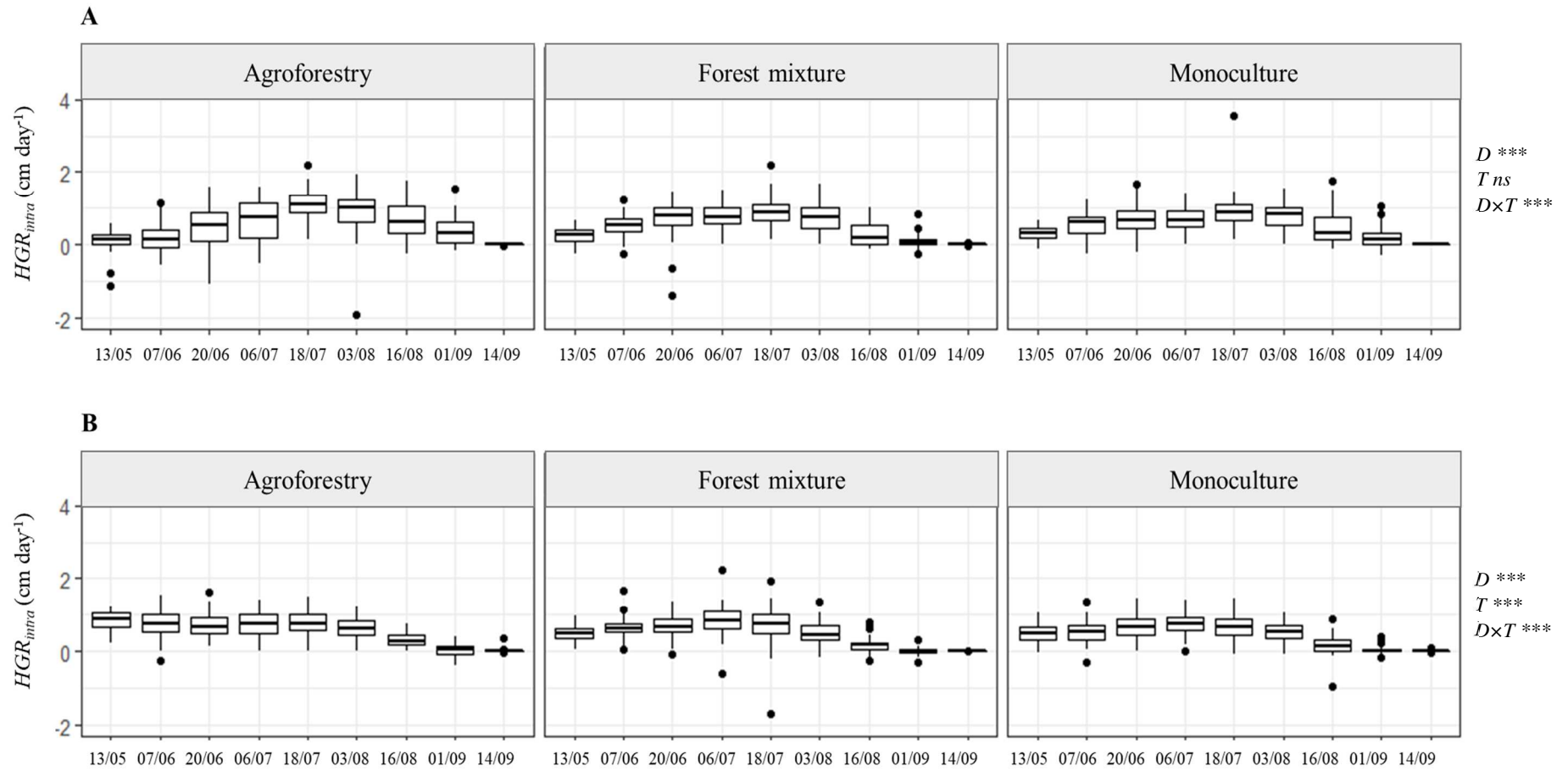
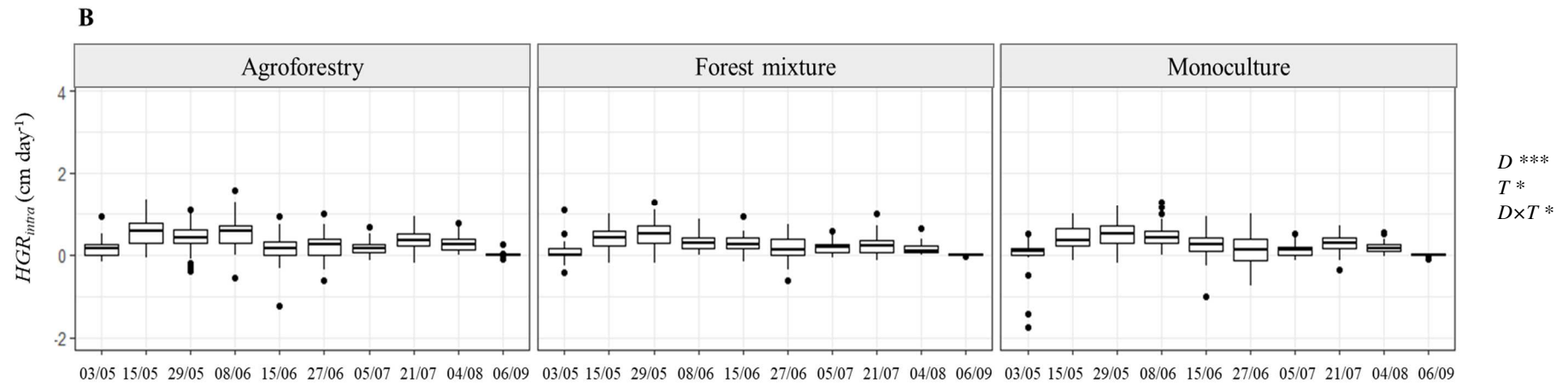
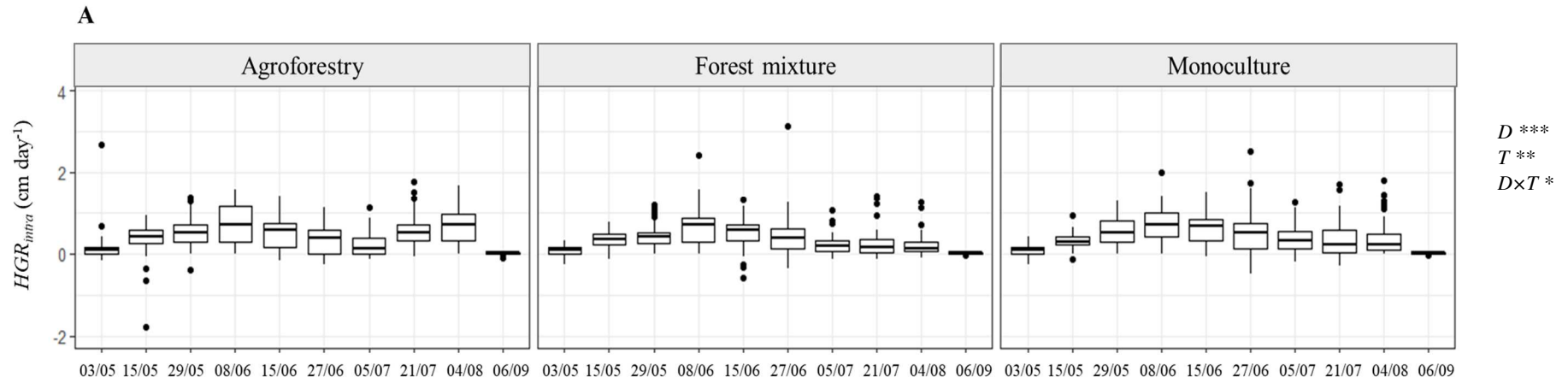


Fig. A2.



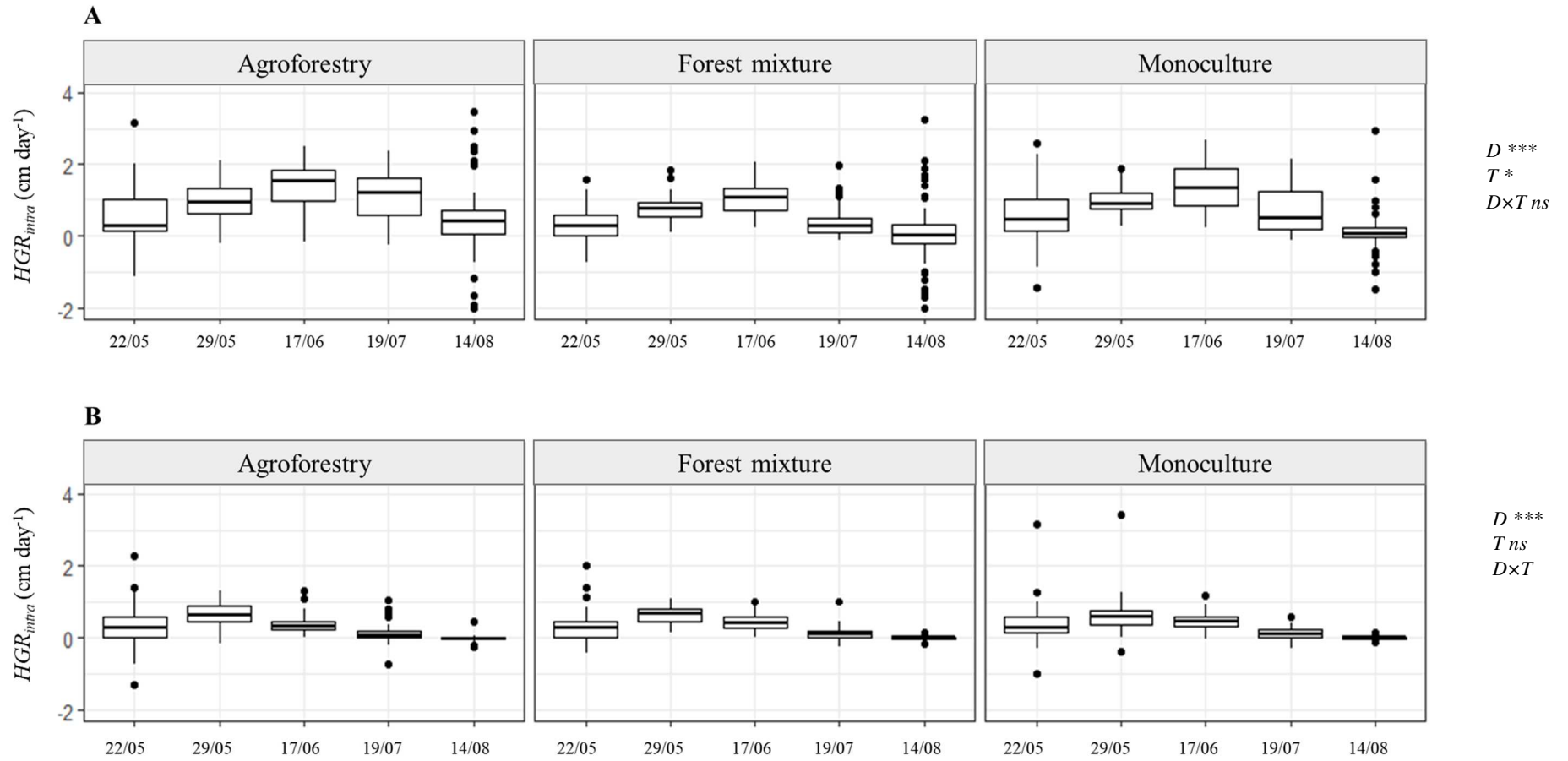


Fig. A4.