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1 **Do trait responses to simulated browsing in *Quercus robur***
2 **saplings affect their attractiveness to *Capreolus capreolus***
3 **the following year?**

4
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20

21 **Abstract**

22 With the rise of large herbivore populations in most northern hemisphere forests, browsing is
23 becoming an increasingly important driver of forest regeneration dynamics. Among other
24 processes affecting the regeneration, the concept of plant-herbivore feedback loops holds that
25 browsed saplings are more subject to subsequent herbivory. This phenomenon is interpreted
26 as a consequence of compensatory growth following browsing since fast growth is generally
27 associated with higher digestibility and lower defense against herbivores. However, studies
28 linking browsing-induced trait variations to subsequent attractiveness to herbivores are still
29 lacking, especially in the forest context. In this study, we experimentally examine the
30 existence of a feedback loop between oak (*Quercus robur* L.) and roe deer (*Capreolus*
31 *capreolus*) and investigate its underlying morphological and chemical traits.

32 We simulated single and repeated roe deer browsing on nursery-grown oak saplings and
33 measured the changes in sapling height growth, lateral branching, leaf traits and winter shoot
34 traits over two years. We conducted winter feeding trials with tame roe deer one year after the
35 first treatment to test the effect of simulated browsing on sapling attractiveness.

36 Simulated browsing reduced sapling height growth but had no effect on branching. Simulated
37 browsing had no effect on leaf traits after half a year, but decreased the phenolic content and
38 increased the fiber content of winter shoots the following winter. Contrary to our predictions,
39 roe deer preferentially browsed control saplings over saplings previously browsed. After two
40 years, repeated browsing promoted fast carbon acquisition leaf traits (high chlorophyll, high
41 specific leaf area and low fiber content), reduced leaf phenolic content and increased leaf
42 digestibility.

43 We showed that a reduction in 1-year-old oak sapling height growth following browsing,
44 combined with increased structural defense at the expense of chemical defense in winter

45 shoots the following winter, was correlated with reduced browsing pressure, thereby
46 challenging the feedback loop hypothesis. However, we also demonstrated that repeated
47 browsing promoted fast carbon acquisition leaf traits in 2.5-year-old saplings, which tend to
48 support the existence of a feedback loop on older and more intensively browsed saplings. As
49 such, our study provides empirical evidence that morphological and physiological trait
50 responses to browsing influence oak sapling attractiveness, but that the direction and
51 magnitude of this effect depend on the ontogenic stage of the sapling and on the number of
52 browsing events.

53 **Keywords:** Simulated browsing, feeding trial, feedback loop, functional traits, plant-
54 herbivore interaction

55

1. Introduction

Over the last decades, most northern hemisphere forests have been facing an increasing herbivory pressure due to a globalized increase in wild ungulate populations (Beguin et al., 2016; Linnell and Zachos, 2011). Numerous studies show that the level of browsing damage observed on young saplings in these forests may compromise their ecological and economic value (Clasen et al., 2011; Côté et al., 2004). A better understanding of how young saplings respond to this increasing browsing pressure and of the influence of wild ungulates on forest regeneration dynamics is therefore critical to better manage these ecosystems. In temperate and boreal forests, several studies revealed that individual saplings browsed by ungulates tend to be more frequently browsed the following year (Craig, 2010; Cromsigt and Kuijper, 2011; Mathisen et al., 2017; Moore et al., 2000). This creates a positive “feedback loop” (Burkepile and Parker, 2017; Craig, 2010) between ungulates and saplings, which may decrease the number of saplings able to grow above the reach of ungulates (Bergqvist et al., 2003). In the context of feedback loops, a set of individual saplings undergo browsing almost every year and stay within the reach of cervids, whereas the remaining unbrowsed individuals should rapidly grow above browsing height. Conversely, in the absence of a feedback loop, a greater proportion of saplings are browsed at least once, which should result in a longer regeneration phase but with a higher number of individuals eventually able to grow above browsing height (Bergqvist et al., 2003). As such, feedback loops are likely to be critical for forest ecosystem dynamics, but the mechanisms governing this process remain highly understudied. In particular, it is unclear whether the variation in sapling trait in response to browsing could increase their attractiveness towards ungulates the following year.

80 Herbivory can induce various plant responses at the tree level, depending on the resistance
81 strategy of the tree species (Boege and Marquis, 2005; Züst and Agrawal, 2017). Tree species
82 that invest in defense strategies divert carbohydrate resource allocation toward structural
83 defense (e.g. high fiber content, spines, hairs) (Barrere et al., 2019; Takada et al., 2003) and/or
84 chemical defense (e.g. secondary metabolites like phenols) (Iason, 2005) following browsing,
85 thereby reducing the probability of future damage (Bee et al., 2011; Stolter et al., 2005). Tree
86 species that invest in rapid growth strategies allocate their carbohydrate resources toward fast
87 carbon acquisition following browsing in order to compensate for the loss of biomass
88 (Edenius et al., 1993; Palmer and Truscott, 2003). No study to date have investigated how
89 such trait response influences the probability of subsequent browsing, but an investment in
90 rapid growth strategies could in theory increase sapling attractiveness to ungulates via several
91 mechanisms. First, due to the well-documented trade-off between plant growth and defense
92 (Coley, 1988; Herms and Mattson, 1992; Züst and Agrawal, 2017), an investment in
93 compensatory growth implies fewer anti-herbivore defensive compounds in the leaves
94 (DuToit et al., 1990). Second, an investment in rapid growth following browsing also leads to
95 higher values of fast carbon acquisition traits such as higher specific leaf area (SLA hereafter)
96 (Baraza et al., 2010), or increased leaf chlorophyll content (Danell and Huss-Danell, 1985).
97 These traits are known to positively correlate with leaf nitrogen content (Wright et al., 2004)
98 and digestibility (Cornelissen et al., 2004), which are both important drivers of food selection
99 by ungulates (Bee et al., 2011; Felton et al., 2018; Lloyd et al., 2010). Finally, browsing may
100 increase attractiveness by modifying sapling stature and architecture (Hartley et al., 1997).
101 Common morphological adjustments following browsing include a reduction in height growth
102 and increased lateral branching (Danell et al., 1994; Drexhage and Colin, 2003), which
103 maintains a high number of shoots at the herbivore's optimal browsing height (Cromsigt and
104 Kuijper, 2011).

105

106 Chemical trait responses to browsing in deciduous saplings have been detected from 2 hours
107 (Ohse et al., 2017) to several months (Danell et al., 1994; Danell and Huss-Danell, 1985) after
108 the browsing event, but it is not known whether the trait variations related to compensatory
109 growth can persist after a growing season to influence subsequent attractiveness. Furthermore,
110 although the winter shoots of deciduous saplings are more frequently browsed than their
111 leaves (Petersson et al., 2020), studies on sapling physiological response to herbivory are
112 generally focused on leaf traits (Danell et al., 1994; Danell and Huss-Danell, 1985; Woolery
113 and Jacobs, 2014) and rarely on winter shoot traits (but see Ohse et al., 2017). The influence
114 of winter browsing on the chemical composition of shoots the following year is therefore
115 critical to understanding the mechanisms underlying feedback loops, but nevertheless remains
116 highly understudied. Our study aims at unraveling the mechanisms underlying feedback loops
117 by testing the effect of winter browsing on sapling morphology, leaf traits, the chemical
118 composition of shoots the following year and sapling attractiveness the following winter.
119 More precisely, we focused on the interaction between pedunculate oak (*Quercus robur* L.,
120 oak hereafter) and roe deer (*Capreolus capreolus*). Oak is a foundational species in European
121 temperate forests since it defines an entire ecological community or ecosystem by virtue of its
122 structural or functional attributes (Ellison et al., 2005). This species is of high value both for
123 economic reasons and for the high level of biodiversity provided by oak-dominated forests
124 (Mölder et al., 2019). Roe deer are widespread in European forests, and are known to
125 frequently browse on oak sapling shoots (Drexhage and Colin, 2003; Löff et al., 2021),
126 especially in winter (Petersson et al., 2020). We tested the following hypotheses:

127

128 **H1:** Winter browsing promotes leaf traits related to fast carbon acquisition at the expense of
129 defense, and lateral branching over height growth. We thus expect browsed saplings to have

130 higher SLA, chlorophyll content, nitrogen content, digestibility, and lower fiber and phenolic
131 content, but also lower height growth and higher lateral branching than unbrowsed saplings.

132 **H2:** Browsing modifies the chemical composition of shoots the following winter, leading to
133 higher nitrogen content and digestibility, and lower phenolic and fiber content.

134 **H3:** Winter-browsed saplings are more attractive to roe deer the following winter than
135 unbrowsed saplings.

136

137 To test these hypotheses, we grew oak saplings from seed in a nursery and performed a
138 standardized simulation of roe deer browsing at the end of winter, keeping half of them as
139 controls. Six leaf traits (leaf chlorophyll, nitrogen, fiber and phenol content, SLA,
140 digestibility) were measured the following summer, and the plant architecture was monitored
141 before and after the growing season (H1). The next winter, four shoot traits (nitrogen, fibers
142 and phenol content, digestibility) were measured (H2), and feeding trials with tame roe deer
143 were performed to estimate the effect of previous browsing on oak attractiveness to roe deer
144 (H3).

145

146

147 **2. Material and methods**

148 *2.1. Plant material*

149 In March 2018 acorns collected in the Saône Valley (47°22' N, 5°29' E) in Autumn 2017
150 were sown in the experimental nursery of the French National Forest Office (ONF) in Saint-
151 Paul-lez-Durance (43°42' N, 5°44' E). Acorns were stored in a cold chamber at a temperature
152 ranging from 2°C to 4°C between collection and sowing. They were planted in 650 individual
153 pots (1120 cm³, 20-cm high x 56 cm² surface area) with a mix of blond peat (50%) and pine
154 bark (50%), and a single application of slow-release Osmocote fertilizer (2 kg/m³, NPK –

155 15:9:11) and of fast-release fertilizer (1 kg/m³, NPK – 12:12:17). This organic growing media
156 was selected to optimize water retention and aeration, following the study of Guehl et al.
157 (1989). The initial nutrient supply was complemented with a fertigation system in summer
158 2019 (12 applications from August 6 to September 24, NPK – 12:6:8, 2g/L, 5L/m³). Seedlings
159 were grown in a greenhouse the first year. They were watered on a daily basis to maintain the
160 growing media pF (log of the matric potential) between 1 and 1.5, which corresponded to a
161 spray volume ranging between 0.5 to 15 L/m²/day, depending on the season and the amount
162 of precipitation. As part of the experiment, 55 additional oak saplings were also grown in the
163 same conditions and used as a reference for the chemical analyses (see Section 2.3).

164

165 2.2. *Winter browsing treatment*

166 After one year of growth, the 650 saplings were moved outdoor and organized in two columns
167 of plastic crates (1500 cm², 30 cm x 50 cm) that contained 17 pot each, resulting in an average
168 density of 113 saplings.m⁻² (see Supplementary Material, Appendix B, Figure B.1.b). In
169 March 2019, the crates were assigning to the control or the “browsed” groups, so that crates
170 of the same group were not adjacent to each other (Supplementary Material, Appendix B).
171 The control group (C hereafter, n = 340, split in 20 crates of 17 saplings) did not undergo any
172 treatment, and the “browsed” group (Br hereafter, n = 310, split into 18 crates of 17 saplings
173 and 1 crate of 4 saplings) received a browsing treatment (Fig. 1.c). Browsing was simulated
174 by clipping a 5cm long piece of the apical shoot with scissors and applying 10 µL of roe deer
175 saliva on the clipped section with a pipette (Ohse et al., 2017) (Fig. 1.c; and see
176 Supplementary Material, Appendix A, for details on saliva collection).

177 After two year of growth, in March 2020, the simulated browsing treatment was repeated
178 according to the following design: 30 BrBr saplings underwent the browsing treatment in both
179 2019 and 2020, 30 CBr saplings underwent the treatment only in 2020, and 30 CC saplings

180 did not undergo any browsing treatment (Fig. 1.c). The 30 saplings of each treatment were
181 split into one crate of 17 saplings and one crate of 13 saplings (see Supplementary Material,
182 Appendix B, Figure B.1.b).

183

184 *2.2.Trait measurements*

185 Sapling architecture

186 To determine the influence of the browsing treatment on sapling height growth and lateral
187 branching (H1), we measured sapling height (distance between the collar and the highest
188 living bud), root-collar diameter (hereafter referred to as “diameter”) and the number of
189 ramifications before the beginning of (March, n=650) and after (December, n=590) the
190 growing season in 2019. All living shoots longer than 1 cm were considered to be
191 ramifications, regardless of whether they stemmed from the apical shoot or from other shoots
192 (Fig. 1.a).

193 Leaf traits

194 Six leaf traits were measured on 30 individual per treatment in August 2019 (treatments C and
195 Br), and in August 2020 (treatments CC, CBr and BrBr) to test the influence of the browsing
196 treatment on leaf traits the following summer over two years (H1) (Fig. 1.c).

197 Three large mature leaves exposed to direct solar radiation and located in the top fourth of the
198 plant were selected per sapling to measure their chlorophyll content (LChl hereafter) and
199 specific leaf area (SLA hereafter). LChl were obtained using a CCM-200 chlorophyll meter
200 (Opti-Sciences, Tyngsboro, MA, USA) and the equation presented in Bagard et al. (2008).
201 The sapling LChl value is the average of six points, made on the upper side of the three
202 leaves, one on each side of the midrib. The leaves were scanned to measure their projected
203 area (using ImageJ software version 1.52a (Rasband, 2012)) and oven-dried to measure their

204 dry mass. The saplings SLA value is the average the ratios between the leaf area and their dry
205 mass (mm^2/mg) (Pérez-Harguindeguy et al., 2013).

206 Leaf biochemical composition was estimated using near-infrared spectroscopy (NIRS). All
207 leaves from each individual sapling were harvested and pooled with the three leaves selected
208 for LChl and SLA measurements. They were then oven-dried (60°C for 24 h) and ground in a
209 cutting mill (Retsch SM100, Retsch GmbH, Hann, Germany) equipped with a 1-mm sieve. A
210 reflectance monochromator (FOSS NIRsystems 6500, Laurel, MD, USA) was used to scan
211 the samples placed in small circular cups (50 mm) with a quartz glass cover. Spectral data
212 were collected every 2 nm between 400 nm and 2500 nm. Each sample was scanned twice
213 (with different cup fillings) and the two values were averaged for each sapling. We predicted
214 the values of leaf fiber content (Neutral Detergent Fibers, LNDF hereafter), nitrogen content
215 (LNC hereafter), dry matter digestibility (LDMD hereafter) and total phenols (LPhenol
216 hereafter) (Singleton et al., 1999) from these NIRS spectra (table 1). We used an existing
217 calibration from CIRAD (Center for International Cooperation in Agronomic Research),
218 combined with direct measurements on 55 additional oak saplings grown in the nursery
219 (calibration R^2 ranging from 0.91 to 0.94 for the 4 traits measured). Calibration was
220 performed using modified partial least square regression with WINISI software (version 4,
221 Infracsoft International, Port Matilda, PA, USA). The oak leaf used for the calibration were
222 oven-dried (60°C for 24 h) and ground. We used a Kjeldahl procedure to measure nitrogen,
223 the Folin Ciocalteu colorimetric method (Singleton et al., 1999) for total phenols, the pepsin-
224 cellulase method (Aufrère et al., 2007) for dry matter digestibility, and sequential
225 fractionation (Van Soest et al., 1991) for fiber contents. Some studies reported that air-drying
226 underestimates some phenolic compounds (Eichenberg et al., 2014; Julkunen-Tiitto and
227 Sorsa, 2001), whereas other studies did not reveal any biases (Couture et al., 2016; Makkar

228 and Singh, 1991), but it has not been shown to affect the hierarchy between the different
229 individuals sampled in either cases.

230

231 Winter shoot traits

232 In March 2020, the shoots clipped after the second browsing treatment (applied on 30 C and
233 30 Br saplings, Fig. 1.c) were oven-dried and ground following the same methodology as that
234 was used for the leaves (H2). For methodological requirements of the NIRS methods, the
235 shoots of three saplings from the same treatment were pooled obtain ten samples of shoots per
236 treatment. Shoot fiber content (SNDF), nitrogen content (SNC), dry matter digestibility
237 (SDMD) and total phenolic content (SPhenol) were estimated using the same procedures as
238 described for the leaves, and with the same calibration spectra.

239

240 *2.3. Feeding trials*

241 In December 2019, 500 saplings (250 C and 250 Br) not used for any leaf and shoot trait
242 measurement were transferred to the experimental unit of the French National Institute for
243 Agricultural and Environment Research (INRAE) in Gardouch (43°22' N, 1°40' E) to test the
244 influence of the treatment on oak sapling attractiveness to tame roe deer (H3) (Fig. 1.c).
245 Feeding trials were conducted at the end of winter (February 2020), on leafless saplings
246 before budburst. The tests took place in three enclosures of approximately 0.5 ha that each
247 hosted a birth cohort of two or three adult female roe deer. The captive roe deer were fed with
248 pelleted food *ad libitum* and had access to the natural vegetation available in their enclosure
249 (mainly grasses and forbs). The deer were used to feeding on browse as they were regularly
250 given fresh branches of deciduous tree species to supplement their diet (i.e., *Prunus*
251 *domesticus*, *Quercus sp*, *Cornus sanguineus*, *Ulmus carpinifolia*, *Crataegus monogyna*, and
252 *Acer campestre*).

253 For each feeding trial, 24 saplings were placed in the center of the enclosure, in pre-dug holes
254 in the soil, to form two groups of 12 saplings per treatment (Br vs C) (Fig. 1b). The
255 aggregation of saplings of the same treatments helps the animal to detect differences between
256 the treatments (see Verheyden-Tixier and Duncan, 2000; Verheyden et al., 1998 or Rea et al.,
257 2017 for similar approaches). Saplings were spaced by 50 cm, which is sufficiently large to
258 enable the animal to move between saplings, but sufficiently small so that it can easily switch
259 from one group of saplings (i.e. treatment) to the other. (H. Verheyden, pers. obs.). The
260 position of the groups (C and Br) was systematically switched between two consecutive tests
261 to avoid any bias due to the positioning of the sapling groups. During the three weeks
262 preceding the feeding trials, the animals were acclimated to the experiment by placing 24 oak
263 saplings with morphological characteristics similar to the saplings in the experiment in each
264 enclosure one day per week. All the tests began between 8.45 and 9 a.m. A minimum period
265 of two days was left between two tests in the same enclosure. Two types of tests were
266 conducted over a period of four weeks from the 3rd to the 26th of February 2020.

267 (1) The immediate selection patterns were tested using ≤ 1 hour feeding trials (“1-h tests”
268 hereafter). Eight tests consisted in filming three roe deer (consuming the plant or not)
269 until half of the sapling were browsed at least once using a Canon SX60HS Power
270 Shot camera (Fig. 1.b). We used this method to avoid a bias due to resource depletion
271 (i.e., if all the saplings were browsed down, it might have altered the deer’s initial food
272 choice). The number of saplings browsed in each treatment was recorded. The shoot
273 length that has been consumed was also estimated as the difference between total
274 shoot lengths (including the plant height and all ramifications) measured before and
275 after the test. The video recordings were analyzed with version 6.3 of the Behavioral
276 Observation Research Interactive Software (Friard and Gamba, 2016). In the video

277 analysis, the total amount of time the roe deer spent sniffing and consuming the
278 saplings of each treatment was counted.

279 (2) Eleven longer feeding trials (“24-h tests” hereafter) were performed to assess
280 consumption preferences in two other enclosures containing two and three deer,
281 respectively. For each test, the saplings were left in place for 24 hours under the
282 surveillance of two camera traps, one facing the C saplings and the other facing the Br
283 saplings, to ensure that the animals consumed the saplings within the 24 h period.
284 Again, we counted the number of browsed saplings and the shoot length that has been
285 consumed after each test.

286

287

288 *2.4.Data analyses*

289

290 Effect of simulated browsing on sapling height growth, lateral branching and leaf traits (H1)

291 To compare height growth between treatments, we estimated a standardized measurement of
292 height increment between March and December 2019 that accounts for sapling root-collar
293 diameter. Indeed, both initial height and diameter accounted for a significant part of the
294 variability in final height (see Supplementary Material, Appendix C). Therefore, the
295 standardized height growth is the residuals of a linear model that predicted the final height
296 from initial height, initial diameter and their interaction. Differences between standardized
297 height growth were tested using Student’s t-test. Similarly, a standardized branching was
298 computed as the residuals of a generalized linear model with a Poisson error distribution that
299 predicted the number of ramifications in December 2019 as a function of the number of
300 ramifications and diameter in March 2019. These two models are presented in detail in the
301 Supplementary Material, Appendix C.

302 The effect of the treatment on leaf traits was tested using a redundancy analysis (RDA).
303 Although describing different leaf functions and properties, the selected traits are often found
304 to be correlated (see Coley 1988; Wright *et al.*, 2004; Sterck *et al.*, 2006; Díaz *et al.*, 2016)
305 (Fig. 3.b). This analysis shows the major axes of differentiation in leaf traits between
306 treatments in a multivariate space accounting for the correlation structure between traits. We
307 constructed a unique multivariate space using traits values from both years (2019 and 2020)
308 and the coordinates of individual saplings on the first RDA axis were compared between
309 treatments using an ANOVA, followed by Tukey's post-hoc test, for each year separately. All
310 traits were centered and scaled prior the analysis and LChl was log-transformed to fulfill
311 normality assumptions. Univariate analyses were also performed for each trait separately and
312 are presented in detail in the Supplementary Material, Appendix D.

313

314 Effect of simulated browsing on winter shoot traits (H2)

315 The effect of the simulated browsing was tested on all shoot traits simultaneously (SNC,
316 SDMD, SPhenol and SNDF) using a RDA. All shoot traits were centered and scaled prior to
317 the analysis. The coordinates on the first RDA axis of C and Br individuals were compared
318 using an ANOVA, followed by Tukey's post-hoc test. Univariate analyses were also
319 performed for shoot traits and are presented in detail in the Supplementary Material,
320 Appendix D.

321

322 Effect of simulated browsing on attractiveness for roe deer (H3)

323 For each test type separately (1 h or 24 h), paired Wilcoxon signed-rank tests were used to
324 analyze the effect of the simulated browsing on the number of saplings browsed and on the
325 shoot length consumed per treatment. In the 1-h tests, it was found that one individual roe
326 deer accounted for more than 90% of the total time spent both consuming and sniffing

327 saplings in all of the tests, the statistical analyses of these two variables was restricted to this
328 individual only. Paired Wilcoxon signed-rank tests were used to compare the time spent by
329 the animal consuming and sniffing C and Br saplings in each 1-h test.

330

331 All statistical analyses were conducted with R statistical software, version 3.6.3 (R Core
332 Team, 2019). Redundancy analyses were performed with the ‘vegan’ R package (Oksanen,
333 2017).

334

335

336 **3. Results**

337

338 *3.1. Effect of simulated browsing on sapling height growth, branching, and leaf traits (H1)*

339 The first year of the experiment, simulated browsing significantly reduced sapling
340 standardized height growth (Student’s t-test, $t_{582} = 3.06$, $p < 0.01$) (Fig. 2.a) – i.e., for a given
341 initial height and diameter, C saplings grew an average of 4 cm.year⁻¹ faster than Br saplings.
342 Simulated browsing did not influence lateral branching (Student’s t-test, $t_{576} = 0.95$, $p = 0.34$)
343 (Fig. 2.b).

344 The first axis (RDA1) of the RDA conducted on six leaf traits explained 15% of the
345 differences in trait values between groups, and mainly contrasted traits related to fast carbon
346 acquisition (i.e. LDMD and SLA) and to defense traits (i.e. LPhenol and LNDF), while LNC
347 and LChl had weak score values on RDA1 (Fig. 3.b, and Supplementary Material, Appendix
348 E). Simulated browsing had no effect on 1.5-year-old sapling leaf traits (ANOVA, $F_{1, 57} =$
349 1.91, $p = 0.17$). However, simulated browsing significantly influenced 2.5-year-old sapling
350 leaf traits (ANOVA, $F_{2, 80} = 3.91$, $p = 0.02$): BrBr saplings had higher values of fast carbon
351 acquisition traits, while CC saplings had higher values of defense traits (Fig. 3.a). The

352 univariate analysis showed that simulated browsing reduced 1.5-year-old sapling SLA and
353 increased 2.5-year-old sapling LNC and LChl (Supplementary Material, Appendix D).

354

355 *3.2.Effect of simulated browsing on winter shoot traits (H2)*

356 The first axis of the RDA conducted on four shoot traits (SNC, SDMD, SPhenol and SNDF)
357 of 2-year-old saplings explained 14% of the differences in trait values between treatments,
358 and contrasted shoots with high phenolic content to shoots with high fiber content (Fig. 4.b,
359 and Supplementary Material, Appendix E). The simulated browsing treatment significantly
360 influenced shoot traits (ANOVA, $F_{1, 18} = 14.26$, $p < 0.01$): Br saplings had lower SPhenol and
361 higher SNDF compared to C saplings (Fig. 4.a). The univariate analysis also showed that
362 simulated browsing reduced SPhenol in 2-year-old oak saplings (Supplementary Material,
363 Appendix D).

364

365 *3.3.Effect of simulated browsing on attractiveness for roe deer (H3)*

366 During the 1-h tests, simulated browsing significantly reduced sapling attractiveness: roe deer
367 browsed an average of 7.88 C saplings compared to 4.38 Br saplings out of 12 saplings per
368 treatment, but the trend was not significant (Wilcoxon signed rank, $V_7 = 24$, $p = 0.12$). The
369 same trend was significant for the 24-h tests: 9.91 saplings browsed on average for C, vs. 6.27
370 for Br (Wilcoxon signed rank, $V_{10} = 45$, $p < 0.01$) (Fig. 5.a). Similarly, simulated browsing
371 reduced the shoot length browsed by roe deer (Fig. 5.b) both in the 1-h tests (Wilcoxon signed
372 rank, $V_7 = 31$, $p = 0.078$) and in the 24-h tests (Wilcoxon signed rank, $V_{10} = 24$, $p < 0.01$), but
373 the trend was only significant for the 24-h tests. During the 1-h tests, high inter-individual
374 variability was observed among the three female roe deer present in the enclosure: one
375 individual was responsible for 93% of the total time spent consuming. In six out of the eight
376 1-h tests, this individual spent more time consuming C than Br saplings, which resulted in a

377 significant negative effect of the simulated browsing treatment on the time spent consuming
378 (Wilcoxon signed rank, $V_7 = 34$, $p = 0.02$) (Fig. 5.c). However, the treatment did not
379 influence the time spent sniffing the saplings (Wilcoxon signed rank, $V_7 = 5$, $p = 0.42$) (Fig.
380 5.c).

381

382

383 **4. Discussion**

384

385 *4.1. Effect of simulated browsing on sapling height growth, lateral branching and leaf* 386 *traits (H1)*

387 Simulating apical bud browsing in winter was found to be sufficient to reduce oak sapling
388 height growth. While other species like beech (*Fagus sylvatica*) (Frank et al., 2019) or Scots
389 pine (*Pinus sylvestris*) (Edenius et al., 1993) have been found to compensate for the loss of
390 the apical bud by increasing their annual growth rate, our results indicate that one-year-old
391 oak saplings are not capable of such a response. A reduction in sapling height growth
392 following browsing of the apical shoot was found in similar studies conducted on sessile oak
393 (*Quercus petraea* (Matt.) Liebl.) saplings, but this decrease in height growth was
394 compensated for by an increase in the number of ramifications (Chaar et al., 1997; Drexhage
395 and Colin, 2003). This response is interpreted as a biomass allocation strategy to promote a
396 plurality of competitive growth axes, which could increase resilience in the eventuality of
397 future browsing events (Drexhage and Colin, 2003). In our study, simulated browsing did not
398 influence the production of new ramifications. The ability of saplings to develop more
399 ramifications following browsing has been shown to increase with the number of shoots
400 browsed (Bergström and Danell, 1987; Frank et al., 2019), and to increase with sapling age
401 (Hódar et al., 2008). Thus, the absence of response to browsing in our study is probably likely

402 due to the young age of the saplings (i.e., browsed at one year of age), and to the fact that only
403 one shoot was browsed. Alternatively, it cannot be excluded that the saplings in our study
404 responded to browsing by allocating their biomass to plant parts that we did not measure. For
405 instance, birch saplings (*Betula pubescens* and *B. pendula*) have been shown to increase the
406 growth of their existing lateral shoots following browsing (Bergström and Danell, 1987),
407 which tends to prevent large herbivores from accessing the internal parts of the sapling
408 (Archibald and Bond, 2003). Similarly, Hódar *et al.* (2008) found that Scots pine saplings
409 responded to browsing by allocating more biomass to roots, which protect carbon resources
410 from aboveground herbivores. Overall, our results indicate that young oak saplings do not
411 seem to show any morphological plasticity in response to browsing.

412 Browsed and unbrowsed 1.5-year-old saplings had similar values of leaf traits, whereas we
413 expected browsed saplings to have higher values of traits related to fast carbon acquisition
414 (LNC, SLA, LChl) and digestibility (LDMD), and lower values of defense traits (LPhenol and
415 LNDF). At this ontogenic stage, saplings have a very limited amount of stored reserves and
416 rely predominantly on carbon acquisition via photosynthesis to grow (Boege and Marquis,
417 2005). As a result, if saplings do not respond to herbivory by investing in traits related to fast
418 carbon acquisition, the removal of photosynthetic organs by herbivores will necessarily result
419 in lower carbon acquisition and, therefore, in reduced growth. Our observation that browsing
420 reduces height growth and does not influence branching tends to support this, although a
421 measurement of the plant biomass would be necessary to draw any conclusion on the effect of
422 browsing on primary productivity. A possible explanation for the absence of browsing-
423 induced leaf trait variation could be an insufficient intensity or frequency of the simulated
424 browsing. In this study, we only removed 5 cm of the apical shoot, whereas other studies
425 found that several winter browsing events within a year were necessary to induce changes in
426 leaf nutrient content of *Betula pubescens* saplings (Danell *et al.*, 1994). Nosko and Embury

427 (2018) even found a threshold of biomass removal in early summer that induced changes in
428 the phenolic content of balsam fir (*Abies balsamea*) sapling leaves.

429 Interestingly, 2.5-year-old oak saplings responded to the treatment: compared to unbrowsed
430 saplings, saplings browsed for two consecutive years had higher values of SLA and LDMD,
431 and lower values of LPhenol and LNDF, two traits related to chemical and structural defense,
432 respectively. Although LDMD is known to be an important driver of food selection by large
433 herbivores (Bee et al., 2011; Felton et al., 2018; Lloyd et al., 2010), studies on the influence
434 of browsing on this trait are surprisingly scarce (Danell and Huss-Danell, 1985). Digestibility
435 tends to be positively related to fast carbon acquisition traits such as SLA or chlorophyll
436 content (Cornelissen et al., 2004): an investment in fast carbon acquisition in response to
437 browsing should therefore also result in increased LDMD. Our study confirms this
438 hypothesis, thereby supporting the assumption that browsing can promote traits that increase
439 further attractiveness. While defense is often seen as the only mechanism used by woody
440 species to deal with herbivory, our study corroborates the less documented assumption that
441 woody species may also invest in growth rather than in defense to compensate for the loss of
442 tissues to herbivores (Haukioja and Koricheva, 2000). It is noteworthy that these changes only
443 occurred for 2.5-year-old saplings and not for 1.5-year-old saplings. This finding provides
444 strong empirical support for the theory that the ability of saplings to change their resource
445 allocation in response to herbivory depends on their ontogenic stage (Barton, 2013; Elger et
446 al., 2009). In particular, this theory predicts that the root:shoot ratio decreases throughout the
447 sapling stage, and that plants acquire an increasing amount of resources that can be either
448 stored, or allocated to resist herbivory via compensatory growth or defense (Boege and
449 Marquis, 2005).

450

451

452 *4.2. Influence of the simulated browsing treatment on winter shoot traits (H2)*

453 In our study, one year after the application of the simulated browsing treatment (at the end of
454 winter and before budburst), the shoots of the browsed saplings had a lower phenolic content
455 and a higher fiber content than the controls. To our knowledge, this is the first evidence that a
456 winter browsing event modifies shoot chemical composition the following winter. These
457 results suggest a trade-off between the investment in different types of defense, notably
458 chemical vs. physical defense. Palo et al., (1992) showed that as the thickness of birch winter
459 shoots increased, their phenolic content decreased and their fiber content increased, which is
460 interpreted as a positive correlation between the thickness of cell walls and shoot diameter.
461 Under this perspective, winter browsing would have induced an increase in shoot thickness at
462 the expense of their phenolic content, which would also be consistent with the findings of
463 Bergström and Danell (1987) who showed that simulated browsing enhanced the radial
464 growth of birch sapling lateral shoots.

465 Although both phenolic and fiber content tend to decrease attractiveness by reducing the
466 nutritional value of plant tissues (Iason, 2005), their relative efficiency depends on the
467 herbivore species. In the case of cervids, high fiber content is known to deter herbivory (Bee
468 et al., 2011), but a few species, including roe deer, digest tannins relatively well since some of
469 the proteins contained in their saliva are able to bind with tannins. Roe deer are even known
470 to select for a certain level of hydrolysable tannin in their diet (Verheyden-Tixier and Duncan,
471 2000). Although hydrolysable tannins are not the only component of total phenols, it could be
472 expected that phenol-rich shoots of unbrowsed seedlings are more palatable for roe deer than
473 fiber-rich shoots of previously browsed saplings.

474 In this study, leaves and winter shoots did not respond similarly to browsing, which is
475 consistent with the recent findings of Ohse et al., (2017) who reported that simulated
476 browsing decreased phenolic acid content in beech sapling buds but not in their leaves. These

477 differential responses could be due to different constrains in the functioning of these organs.
478 In leaves, investment in defense trade-offs with the capacity of carbon acquisition (Herms and
479 Mattson, 1992; Züst and Agrawal, 2017), and different browsing-induced chemical changes
480 are found across species, ranging from low defense associated with high carbon acquisition
481 traits (e.g., oak in this study, birch in Danell and Huss-Danell, 1985) to high chemical defense
482 but low carbon acquisition rate (e.g., *Acer pseudoplatanus* in Ohse et al., 2017 and *Pinus*
483 *strobus* in Champagne et al., 2021). Conversely, no function clearly trade-offs with defense in
484 winter shoots, which likely explains the consistent response to browsing across tree species
485 (see Ohse et al., 2017 for beech, Danell and Huss-Danell, 1985 for birch or Keefover-Ring et
486 al., 2016 for *Populus tremuloides*).

487

488

489 *4.3. Influence of the simulated browsing treatment on roe deer feeding preference (H3)*

490 In the feeding trials conducted on 2-year-old saplings, a consistent trend in roe deer
491 preference appeared in both type of tests, although the results of the 1h-test must be
492 cautiously interpreted since they rely on the decision of only one individual. While it was
493 expected that roe deer would prefer saplings browsed the previous winter, the animals
494 preferentially fed on unbrowsed oak saplings. Whereas similar findings have been found in
495 other feeding trials conducted with red deer (*Cervus elaphus*) (A. J. Duncan et al., 1998) and
496 moose (Edenius, 1993), most studies conducted in field conditions found the opposite: cervids
497 tend to prefer previously browsed saplings (Bergqvist et al., 2003; Makhabu and Skarpe,
498 2006; Mathisen et al., 2017; Moore et al., 2000). The preferences for unbrowsed individuals
499 in our study could be the consequence of the lower fiber content in their winter shoots, which
500 would be consistent with previous observations that roe deer tend to select plants with low

501 fiber content despite high levels of hydrolysable tannins (Verheyden-Tixier and Duncan,
502 2000).

503 The preference of roe deer for unbrowsed saplings could also be linked to differences in
504 architecture since these saplings were generally higher and more ramified compared to
505 previously browsed saplings (Supplementary Material, Appendix F). Several studies have
506 shown that sapling morphology, particularly the distribution of biomass in 3D space,
507 influences attractiveness to deer (Hartley et al., 1997; Renaud et al., 2003). According to the
508 optimal foraging theory, deer make their foraging decisions to maximize their net energy gain
509 (Stephens and Krebs, 1986). The animal's energy gain depends on its feeding rate – which is
510 the product of bite size (biomass available at each bite) and bite rate – and on plant chemical
511 composition (Charles-Dominique et al., 2020). It has been shown that the production of a high
512 number of ramifications leads to the formation of a 'cage-like' structure that decreases the
513 feeding rate (Charles-Dominique et al., 2020), and, consequently, saplings attractiveness to
514 large herbivores (Archibald and Bond, 2003). Despite the fact that sapling height has a rather
515 weak influence on feeding rate (Renaud et al., 2003), studies show that deer preferentially
516 browse near their shoulder height (P. Duncan et al., 1998; Nichols et al., 2015). As a
517 consequence, deer browsing often prevents saplings from growing above their maximum
518 browsing height, thus maintaining a high density of saplings at their optimal browsing height
519 – around 75 cm for roe deer (P. Duncan et al., 1998). Cromsigt & Kuijper (2011) showed that
520 palatable trees were maintained at a constant height of 80 cm, which corresponds to the
521 optimal browsing height for red deer (Nichols et al., 2015). In that regard, our findings
522 support the assumption that height, rather than the number of ramifications, is the main
523 morphological factor undermining roe deer preferences.

524

525 *4.4. Is there any evidence of feedback loops between oak and roe deer?*

526 The theory of feedback loops presumes that the trait response of saplings to browsing
527 increases their subsequent attractiveness to herbivores, thereby trapping them within the reach
528 of large herbivores through repeated browsing (Craig, 2010; Cromsigt and Kuijper, 2011;
529 Mathisen et al., 2017). At first glance, the fact that roe deer in our study preferred unbrowsed
530 saplings conflicts with the existence of any feedback loops between oak and roe deer. On the
531 other hand, several results in our study also tend to support this theory. Indeed, roe deer
532 preferred the tallest saplings, and browsing reduced sapling height growth, which support the
533 idea that through feedback loops, roe deer actively prevent taller plants from growing beyond
534 their reach and therefore maintain the saplings at their optimal browsing height (Cromsigt and
535 Kuijper, 2011). In addition, we showed that repeated browsing over two years increased leaf
536 digestibility at the expense of fiber content. Although not tested in our study, higher leaf
537 digestibility has been shown to positively influence deer preferences (Felton et al., 2018;
538 Lloyd et al., 2010), while leaf fiber content tends to deter herbivory by cervids (Bee et al.,
539 2011). Finally, browsing increased the fiber content and decreased the phenolic content of
540 winter shoots. Our results therefore show that the trait response of oak saplings to browsing
541 modifies their subsequent attractiveness to roe deer, but that the magnitude and direction of
542 this effect is likely to depend on the sapling phenological and ontogenic stage, but also on the
543 browsing intensity. Our findings thus shed light on the factors driving feedback loops by
544 showing that trait plasticity at the plant level (i.e., height growth) but also organ levels (leaf
545 and winter shoots chemical composition) affected sapling attractiveness.

546

547 Whereas this trait plasticity in response to browsing seems consistent across species in winter
548 shoots, as confirmed by our study, there is a high interspecific variability in leaf responses.
549 Interestingly, the species known to exhibit a tolerance response to browsing in their leaf traits
550 (higher digestibility, lower defense) – i.e., oak in this study, birch (Danell and Huss-Danell,

551 1985) or aspen (Keefover-Ring et al., 2016) – share the common feature of being relatively
552 palatable for large herbivores (Boulanger et al., 2009; Hjältén et al., 1993). Conversely,
553 unpalatable species such as spruce or beech tend to show limited leaf trait plasticity following
554 browsing (Barrere et al., 2019; A. J. Duncan et al., 1998; Ohse et al., 2017), which suggest
555 that the tree species inherent palatability could determine the strength of its plasticity in
556 response to browsing. Testing this hypothesis with an experiment comparing the traits of
557 browsed and unbrowsed saplings for tree species of contrasted palatability would constitute a
558 first step towards a more general and multi-specific understanding of the relationship between
559 browsing and subsequent attractiveness for herbivores.

560

561 **5. Conclusions**

562 We showed that (i) winter browsing reduced sapling height growth and modified the chemical
563 composition of shoots the following winter, resulting in an increase in fiber content and a
564 decrease in phenol content, and that (ii) these changes decreased the probability of subsequent
565 herbivory by roe deer. This study is, to our knowledge, the first to connect browsing-induced
566 sapling trait variations to subsequent browsing. We also showed that older and more
567 intensively browsed saplings were able to respond to browsing by investing in fast carbon
568 acquisition traits at the expense of defense traits, thereby supporting the assumption that
569 browsing can promote leaf traits known to increase attractiveness (i.e., high digestibility and
570 low phenolic content). These changes in leaf traits, along with the browsing-induced
571 reduction in height growth and roe deer preference for higher saplings tend to support the
572 theory that large herbivores can maintain trees at their optimal browsing height by repeated
573 browsing. However, we suggest that further studies verify the existence of these possible
574 feedback loops between oak and deer in field conditions, and investigate their consequences
575 on oak dynamics at the population level to assess how they may influence forest management.

576 This is all the more necessary given that the regeneration of oak populations in the presence
577 of high deer densities is an increasingly critical issue for forest management and conservation
578 (Barrere et al., 2021; Petersson et al., 2019).

579

580 **Supplementary data**

581 Supplementary data are available online at xxx and consist of the following.

582 Appendix A – Protocol for roe deer saliva collection.

583 Appendix B – Spatial organization of the saplings at the nursery.

584 Appendix C – Standardization of height growth and branching.

585 Appendix D – Analysis of the effect of the simulated browsing treatment on each trait
586 separately.

587 Appendix E –Redundancy analysis scores for leaf and shoot traits.

588 Appendix F – Morphology of the saplings included in the feeding trials.

589

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597

598 **Authorship**

599 JB, CC, SS, HV and VB designed the study. JB and VB monitored sapling morphology and
600 collected leaf and shoot samples at the nursery. DB supervised the chemical analyses. JB, HV,

601 HC and AB conducted the feeding trials. JB and SS collected roe deer saliva. JB and JS
602 conducted the statistical analyses. JB led the writing of the manuscript. All authors critically
603 contributed to the draft and approved the final version of the manuscript.

604

605 **Declaration of competing interests**

606 The authors declare that they have no conflict of interest that could have influenced the work
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608

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FIGURE CAPTIONS

879

880 **Figure 1:** Overview of the experimental approach: (a) morphological measurements; (b)
881 simplified representation of a feeding trial; and (c) chronology of the experiment.

882

883 **Figure 2:** (a) Standardized height growth, and (b) branching (mean \pm standard deviation)
884 during the 2019 growing season for the different treatments of simulated browsing. The
885 symbol “*” indicates that the two treatments are significantly different from each other ($\alpha =$
886 0.05).

887

888 **Figure 3:** (a) Coordinates of the individual saplings per treatment on the first component
889 (RDA1) of the redundancy analysis conducted on six leaf traits (i.e., LPhenol, LNDF, SLA,
890 LChl, LDMD and LNC). Treatments with no letters in common are statistically significantly
891 different from each other ($\alpha = 0.05$). (b) Value of the correlation between each trait and
892 RDA1.

893

894 **Figure 4:** (a) Coordinates of the individual saplings per treatment on the first component
895 (RDA1) of the redundancy analysis conducted on six shoot traits (i.e., SPhenol, SNDF,
896 SDMD and SNC). Treatments with no letters in common are significantly different from each
897 other ($\alpha = 0.05$). (b) Value of the correlation between each trait and RDA1.

898

899 **Figure 5:** (a) Number of saplings browsed per test and per treatment, (b) shoot length
900 consumed, and (c) time spent by roe deer consuming and sniffing the saplings (bottom) for
901 treatments C and Br. “*” indicates a statistically significant difference between treatments C
902 and Br at $\alpha = 0.05$.

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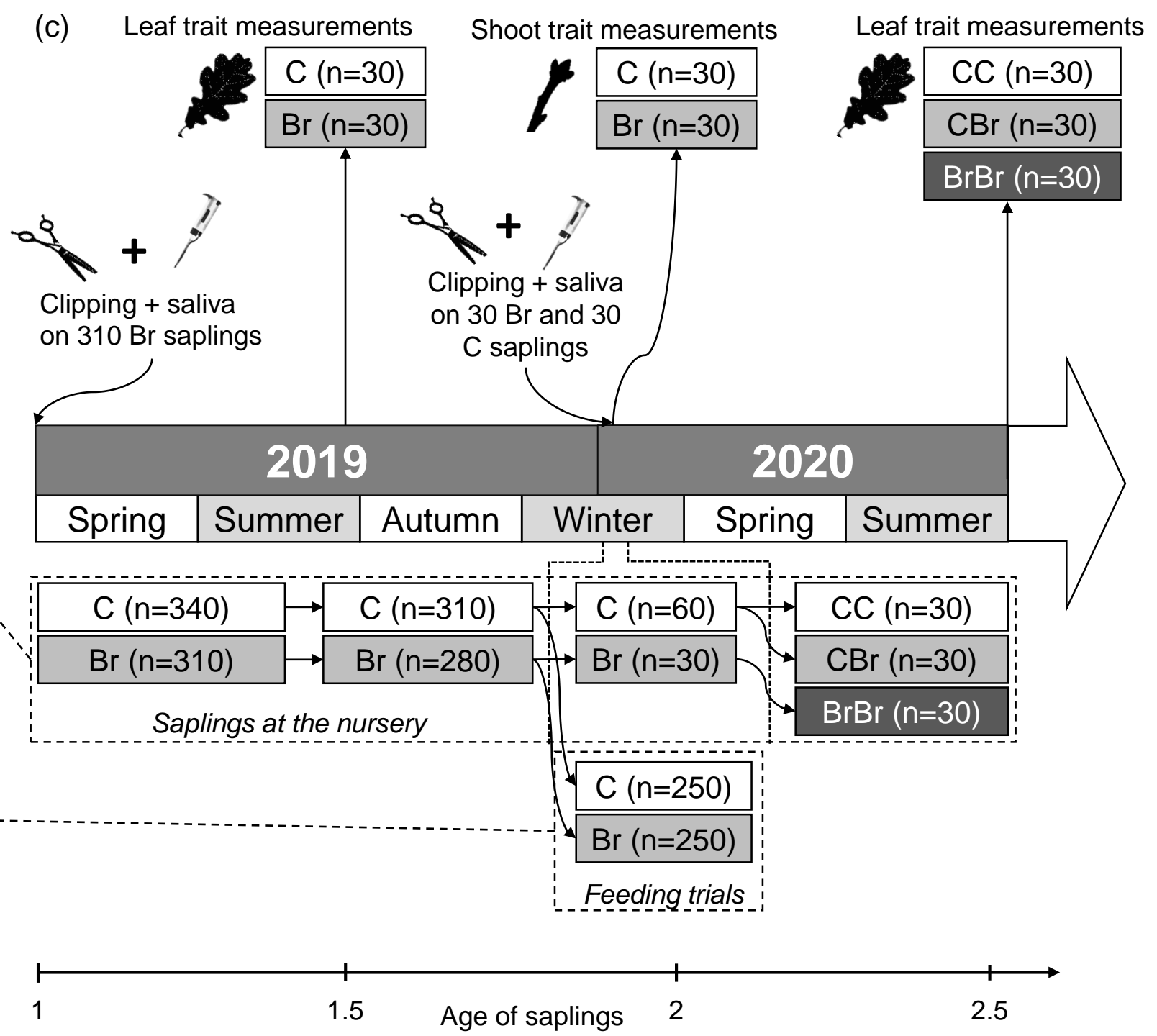
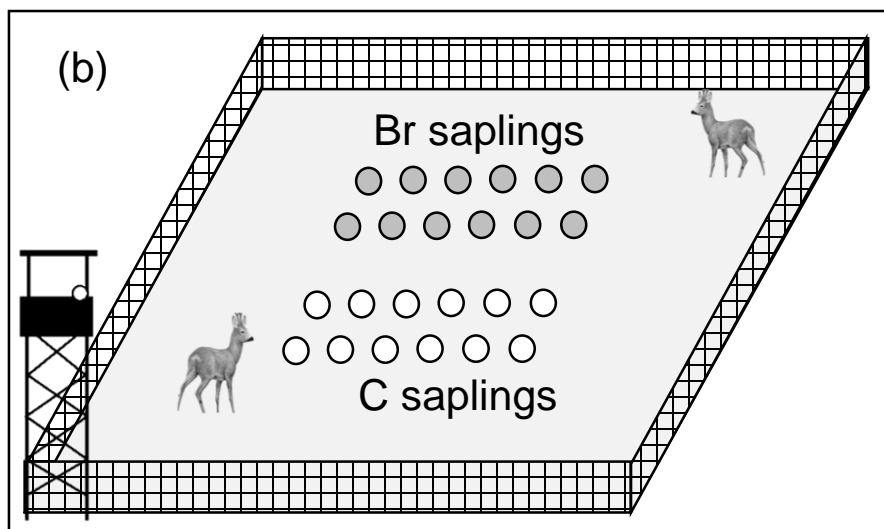
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TABLES

Table 1: Abbreviation, full name, organizational level, methodology used and unit of the different leaf and shoot traits measured on oak saplings.

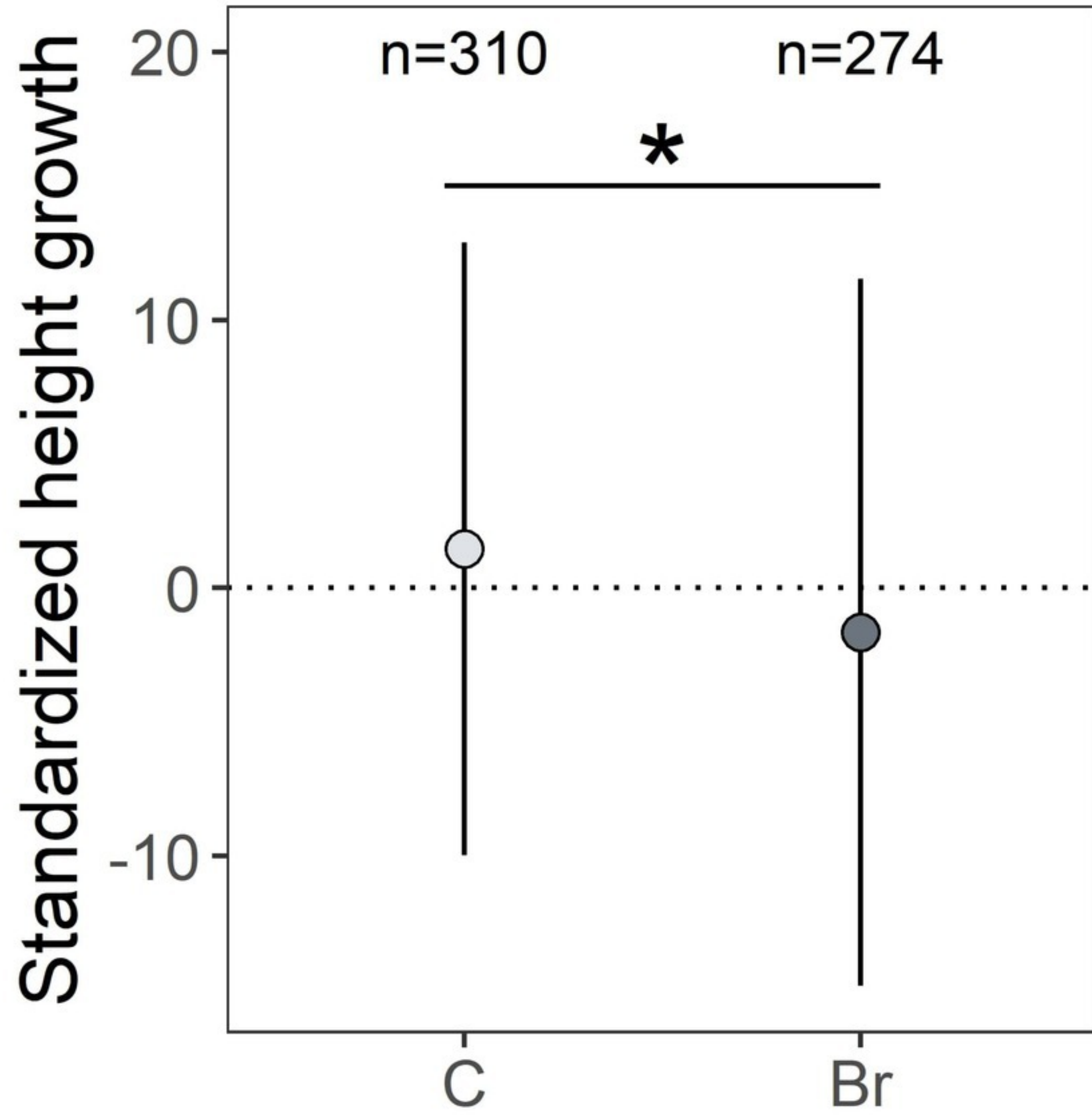
Trait	Full name	Organizational level	Method	Unit
<i>Leaf traits</i>				
LChl	Leaf chlorophyll content	Individual (average of three leaves per individual)	CCM-200 chlorophyll meter	mm ² .mg ⁻¹
LNC	Leaf nitrogen content	Individual (all leaves pooled together)	NIRS	% of dry matter
LNDF	Leaf neutral detergent fiber	Individual (all leaves pooled together)	NIRS	% of dry matter
LPhenol	Leaf phenolic content	Individual (all leaves pooled together)	NIRS	% of dry matter
SLA	Specific leaf area	Individual (average of three leaves per individual)		g.m ⁻²
LDMD	Leaf dry matter digestibility	Individual (all leaves pooled together)	NIRS	% of dry matter
<i>Winter shoot traits</i>				
SNC	Shoot nitrogen content	Browsing treatment (Shoots of three individuals pooled)	NIRS	% of dry matter
SNDF	Shoot neutral detergent fiber	Browsing treatment (Shoots of three individuals pooled)	NIRS	% of dry matter
SPhenol	Shoot phenolic content	Browsing treatment (Shoots of three individuals pooled)	NIRS	% of dry matter
SDMD	Shoot dry matter digestibility	Browsing treatment (Shoots of three individuals pooled)	NIRS	% of dry matter

909



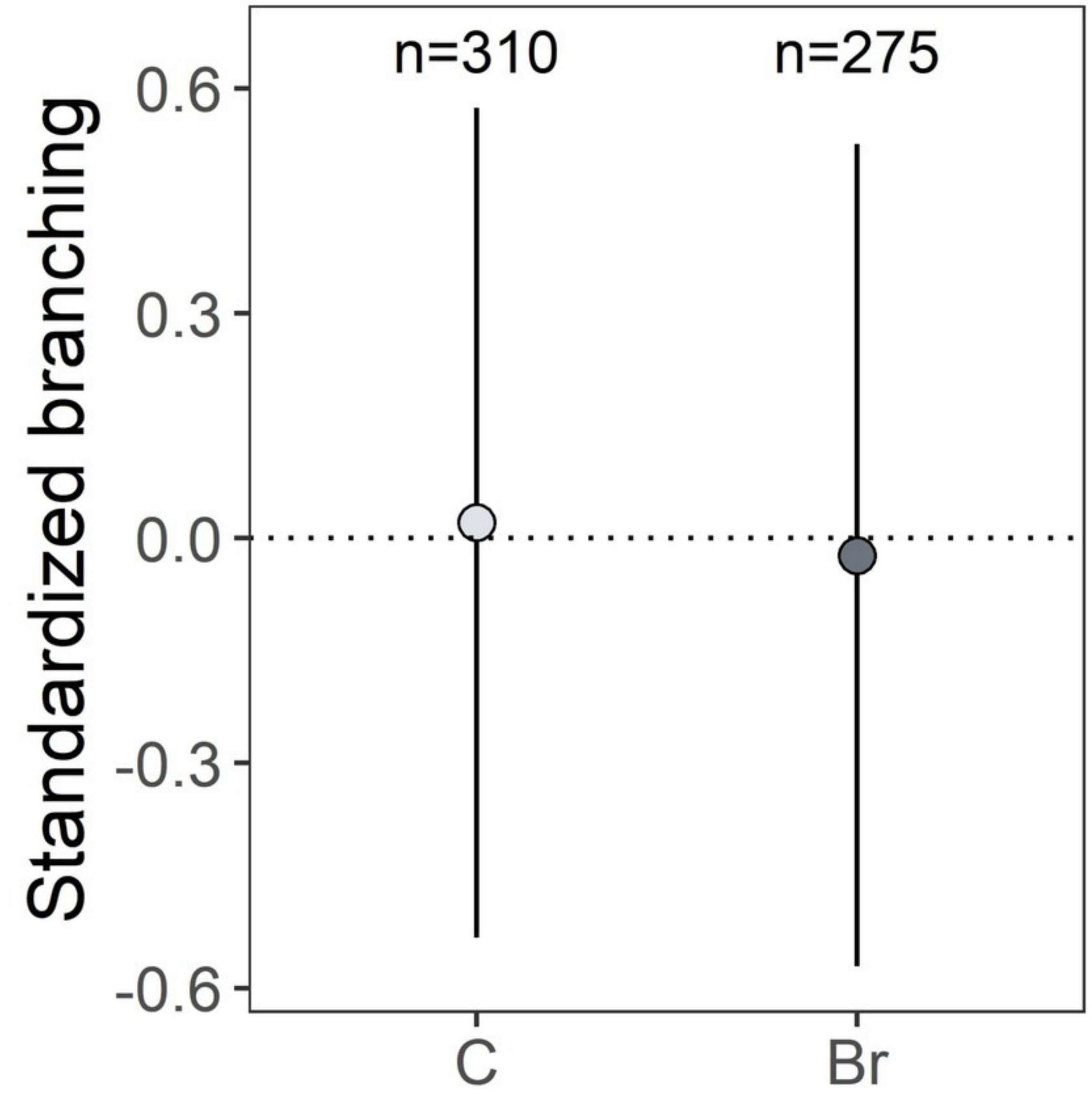
(a)

2-year-old
saplings



(b)

2-year-old
saplings



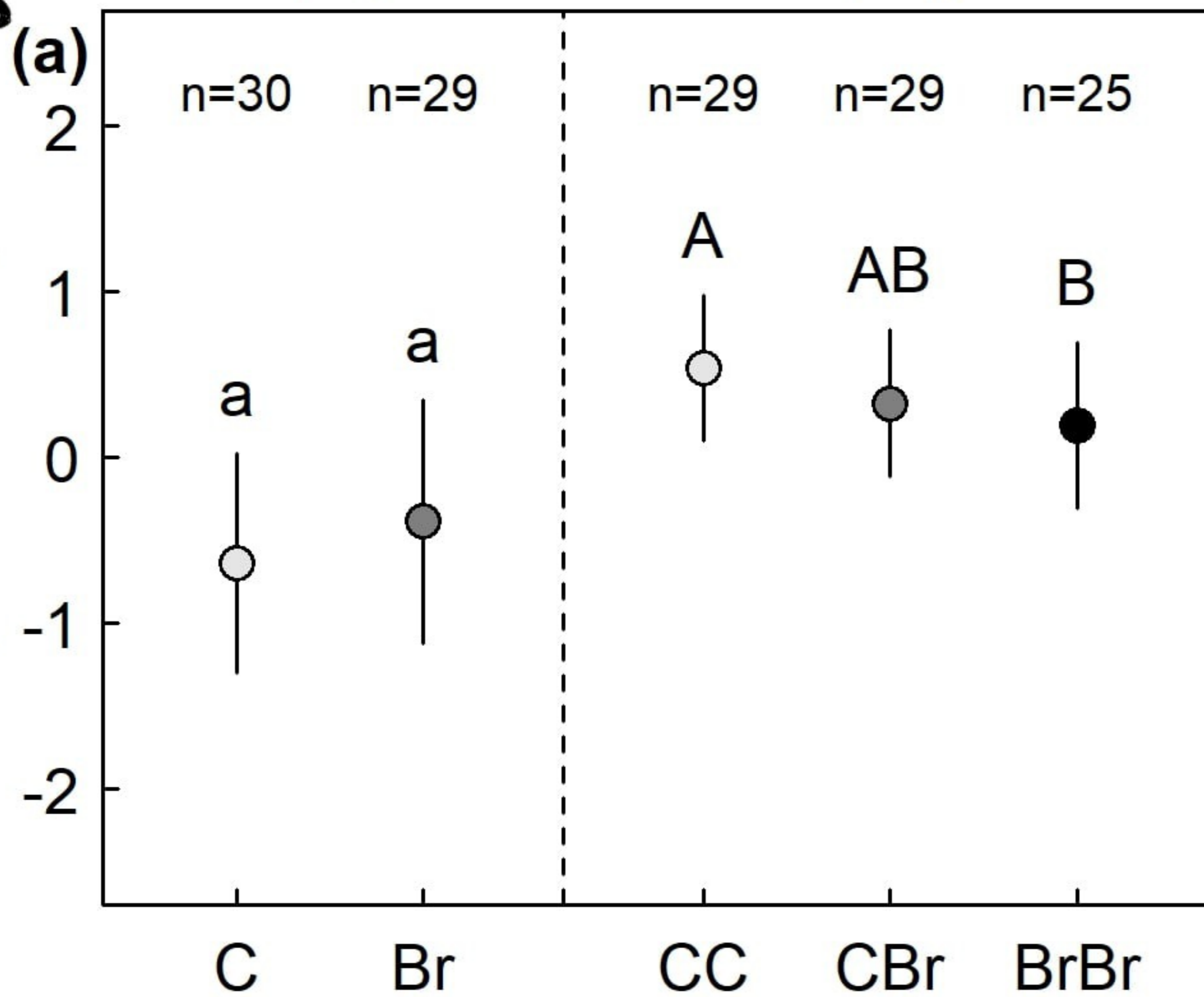


Leaf traits
(RDA1 = 15%)

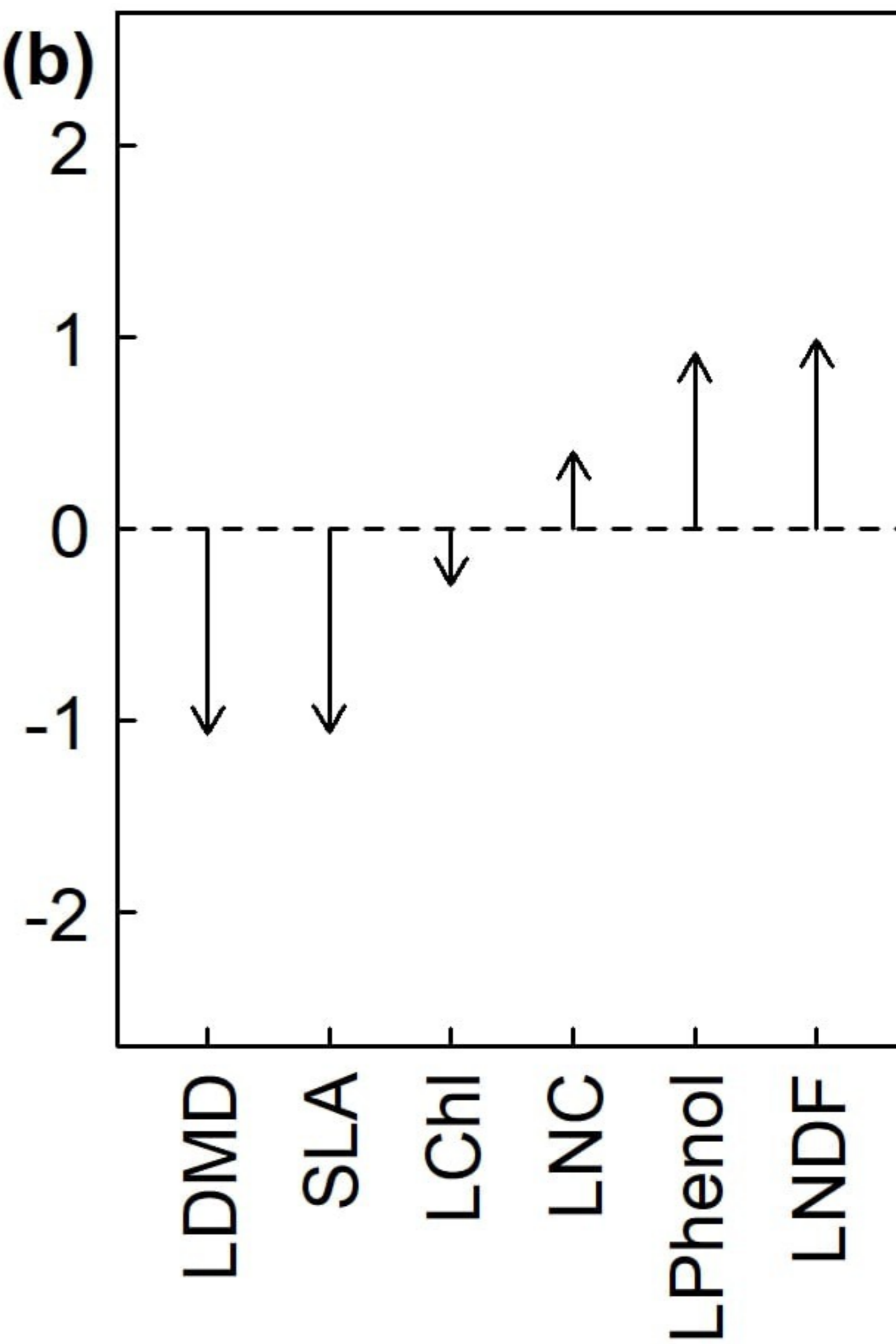
1.5-year-old
saplings

2.5-year-old
saplings

(a)



(b)



Winter shoot traits
(RDA1 = 14%)



2-year-old
saplings

