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6 **RIPARIAN TREES RESPROUT REGARDLESS OF TIMING AND SEVERITY OF DISTURBANCE BY COPPING**

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13

14 **Abstract**

15 Human modification of waterways has reduced flooding in many river systems, leading to the decline of
16 riparian forests, which rely on flooding for their regeneration. Coppicing may help to promote the
17 persistence of riparian trees by triggering resprouting and vegetative regeneration. The vigour of
18 resprouting plants can vary with timing and height of coppicing and may depend on stored non-structural
19 carbohydrate reserves like starch, the availability of which can vary seasonally. However, starch storage
20 dynamics and the resprouting potential of broad-leaved evergreen riparian trees is not well understood.

21 We coppiced two riparian tree species, *Eucalyptus camphora* and *Melaleuca squarrosa*, at two different
22 times (autumn, spring) and at two different heights (0 cm and 90 cm). Over 52 weeks, we regularly

23 quantified shoot growth and changes in the starch storage pool size, compared to uncoppiced control
24 trees, in different tree organs (root and stem) and estimated the final shoot volume.

25 The final shoot volume did not differ significantly between coppice treatments. Trees coppiced in autumn
26 had a greater reliance on stored starch while they remained leafless (without shoots) over winter. Trees
27 cut at 90 cm had more starch reserves due to remaining stems but also had higher biomass maintenance
28 costs. Starch storage varied seasonally only in *E. camphora*, with starch concentrations in control trees
29 increasing over winter and decreasing over summer.

30 Although coppice timing and height affected use of stored starch, resprouting in our study species was
31 not limited by starch availability - both species regenerated vegetatively to recover from physical
32 disturbance. Thus, coppicing may be an efficient means to promote rejuvenation and persistence of tree
33 species where site and tree condition are degraded and no longer support recruitment.

34

35 **Key words:** forest restoration, non-structural carbohydrates, seasonality, shoot growth, tree felling,
36 vegetative regeneration

37

38 **Author declaration:**

39 All authors conceived the study and developed the methodology. SF and JG conducted the fieldwork. SF conducted
40 the lab work. SF, JG and CW analysed the data. SF wrote the main manuscript text; all other authors reviewed the
41 manuscript and provided editorial advice.

42 1. Introduction

43 Poor or absent natural recruitment from seeds threatens the integrity of many forests (Dey *et al.*, 2019),
44 including riparian forests. Forest restoration via planting can be slow and prone to failure due to high
45 vulnerability of seedlings to environmental stress (Greet *et al.*, 2020a; Laub *et al.*, 2020). Vegetative
46 regeneration (i.e. regeneration via resprouting) is an alternative means of regeneration, but many species
47 require disturbance to initiate resprouting (Meier *et al.*, 2012). However, under increasing anthropogenic
48 influence, disturbance regimes have changed substantially, and this is particularly true for riparian
49 ecosystems (Kingsford, 2000; Tonkin *et al.*, 2018). Most of the world's rivers have been modified (e.g.
50 through damming, water extraction or flow regulation) and many floodplains flood less frequently (Tonkin
51 *et al.*, 2018; Grill *et al.*, 2019). Flood disturbance acts as a trigger for vegetative regeneration in riparian
52 trees by causing stem leaning and tree injury which is typically followed by regrowth from resprouts,
53 enabling tree rejuvenation and longevity (Fischer *et al.*, 2021a). As a consequence of reduced or absent
54 flood disturbance riparian species may senesce and be gradually replaced by terrestrial vegetation
55 communities (Tockner & Stanford, 2002; Greet *et al.*, 2013; Foard *et al.*, 2016).

56 The initiation of vegetative regeneration via coppicing may help to promote the persistence of riparian
57 species and maintain species composition and forest structure (e.g. canopy closure). During the procedure
58 of coppicing, trees are, sometimes repeatedly, cut to stimulate sprout production from stumps or stems
59 (Del Tredici, 2001). Coppicing has a long tradition in forest management and wood production, is presently
60 of economic importance (e.g. in short-rotation plantations) and is also a relevant technique for
61 conservation and restoration (Sjölund & Jump, 2013; Müllerova *et al.*, 2014; Spinelli *et al.*, 2017; Schweier
62 *et al.*, 2019). Studies concerning tree resprouting potential are scarce for riparian ecosystems, especially
63 those composed of broad-leafed, evergreen species in temperate climates. Resprouting has primarily
64 been studied in response to fire but also in response to logging, hurricanes and landslides (Bellingham *et*
65 *al.*, 1996; Nzunda *et al.*, 2007; Clarke *et al.*, 2013; O'Hara *et al.*, 2017). Investigations into the resprouting

66 responses of trees from different ecosystem types are needed to help refine our general knowledge of
67 the resprouting trait, its diversity and the underlying mechanisms of resprouting. Given current and
68 projected changes to disturbance regimes resulting from human-driven environmental change (Dale *et*
69 *al.*, 2001; Sommerfeld *et al.*, 2018; O'Briain, 2019), increased understanding of resprouting is critically
70 important as it is central to understanding forest dynamics, predicting vegetation changes and informing
71 forest management (Pausas *et al.*, 2016; Stojanović *et al.*, 2017).

72 A primary requirement for species survival and recovery after physical disturbance, including coppicing,
73 is the ability to remobilize stored resources, mainly carbon in the form of non-structural carbohydrates
74 (NSC), like starch (Bond & Midgley, 2001; Wildy & Pate, 2002; Klimešová & Klimeš, 2007). Carbon is a
75 major building block of structural biomass required to form initial resprouts (Dietze *et al.*, 2014; Turnbull
76 *et al.*, 2014). In addition, NSC serve as respiratory substrate from which energy can be released and used
77 to maintain non-autotrophic tree components (e.g. roots and stems) while trees are leafless and thus, are
78 unable to assimilate carbon via photosynthesis (Kozłowski, 1992; Chen *et al.*, 2017).

79 The availability of stored NSC varies seasonally. The NSC pool is often depleted during sprouting, bud
80 break, periods of rapid growth, reproduction or dormancy and replenished when growth declines while
81 assimilation remains high (or when storage formation is prioritized over other functions) (Hoch *et al.*,
82 2003; Dietze *et al.*, 2014). Apart from phenological events, the occurrence of stress or disturbance causes
83 a reliance on stored NSC for survival (Miller *et al.*, 2019; Miranda *et al.*, 2020). Therefore, resprouting may
84 be driven by the interaction of seasonal dynamics of plant resource use and timing of disturbance
85 (Peguero & Espelta, 2011), which is why coppice timing can influence the resprouting response. Timing
86 will determine the environmental growth conditions (Wright & Clarke, 2007) and will regulate the time
87 until resprouting is initiated and thus has implications for the period for which coppiced trees need to
88 draw on stored NSC during the recovery process.

89 Plant NSC pool size and dynamics differ between biomes depending on the seasonality or disturbance
90 regime (Hoch *et al.*, 2003; Shibata *et al.*, 2016). Likewise, the NSC allocation among plant tissues depends
91 on the type of disturbance and the tissues' disturbance resistance (Clarke *et al.*, 2013). For example, where
92 disturbance is likely to kill above ground structures (e.g. severe fire), roots are often the primary NSC
93 storage organ (Bell & Ojeda, 1999; Knox & Clarke, 2005). Where aboveground structures survive (e.g. in
94 systems disturbed by wind or erosion) stems may be important storage organs to fuel regrowth (Myers &
95 Kitajima, 2007; Nzunda *et al.*, 2008; Franklin *et al.*, 2010). However, remaining stems may also consume
96 large proportions of stored NSC for their maintenance, especially while they are leafless (Smith *et al.*,
97 2018). Therefore, the disturbance severity or the coppicing height (i.e. the amount of remaining stem as a
98 storage organ) may be an important determinant of the resprouting response.

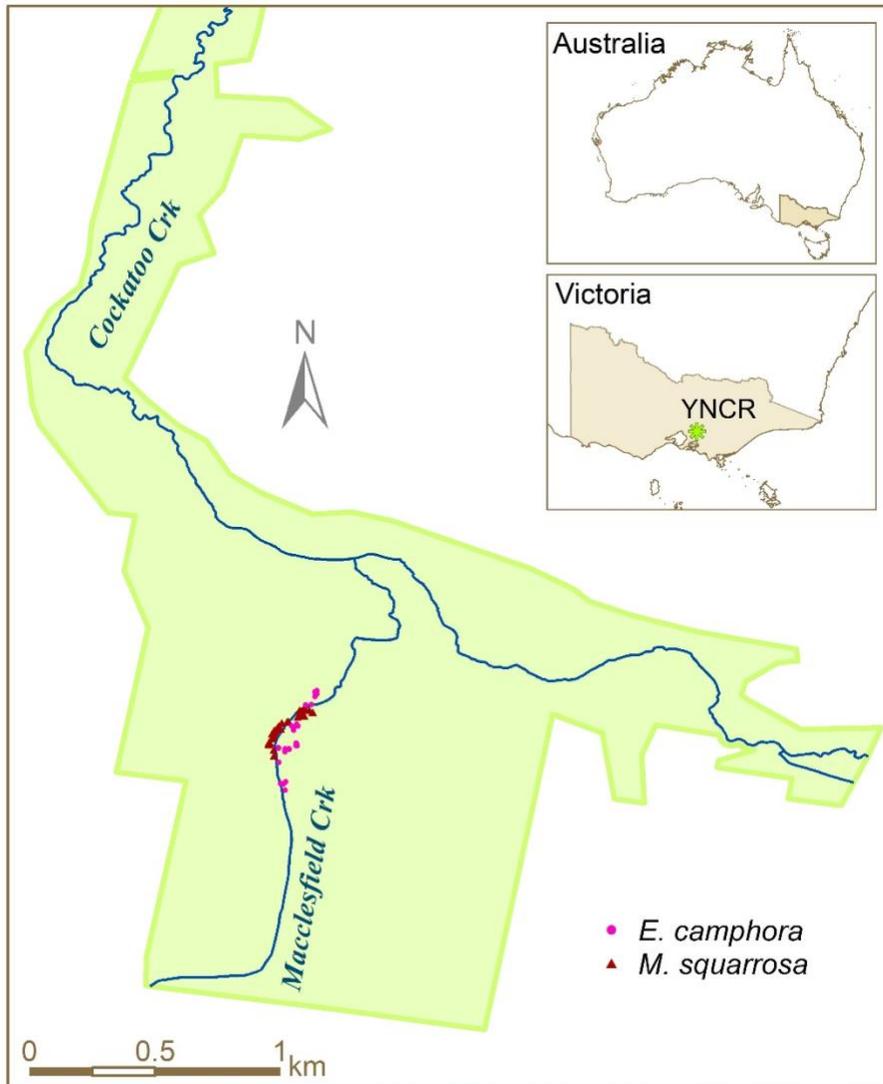
99 The seasonality of NSC storage pool size and the importance of different tree organs as storage pools for
100 riparian trees is unclear (i.e. the availability and requirement to draw on stored NSC from roots or stems
101 to recover from damage). Furthermore, individual tree characteristics (e.g. size or condition) or
102 environmental factors (e.g. light availability) have been documented to cause variation in resprouting
103 (Casals & Rios, 2018; Zhang *et al.*, 2021).

104 Here we investigate resprouting response of temperate broad-leafed, evergreen riparian trees after
105 artificial disturbance via coppicing (i.e. decapitation). We examine seasonal variability of resprouting and
106 its dependency on stored NSC resources in the form of starch in above and belowground plant organs.
107 Such knowledge will advance ecological understanding of resprouting and yield information on best
108 practice for coppicing (i.e. timing and height of cutting). Specifically, we ask: 1) does timing (cut season)
109 and severity (cut height) of coppicing influence recovery and resprouting (i.e. shoot production and
110 availability of stored starch in roots and shoots); 2) does resprouting depend on stored starch resources.

111

112 **2. Methods**

113 *Study site and study species*



114

115 *Figure 1 Map of the location of the coppiced trees within the Yellingbo Nature Conservation Reserve (YNCR, green polygon).*

116 *Inset maps show the location of the reserve (green star) in relation to Victoria, Australia.*

117

118 Our study was undertaken within the Yellingbo Nature Conservation Reserve located ~50 km east of

119 Melbourne, Australia (37°50' S 145°29' E, ~110 m above sea level, Figure 1). The area has a cool temperate

120 climate, experiences mean daily maximum temperatures of 13.6 °C in winter and 25.6 °C in summer and

121 receives ~1100 mm of rainfall annually. The reserve contains seasonally inundated riparian zones
122 populated by threatened 'Sedge-rich *Eucalyptus camphora* swamp forest'. The structure of this vegetation
123 community varies from open forest to woodland (canopy height 6–25 m) and features shrub thickets and
124 a dense understorey comprising sedges, rushes, grasses and forbs (Turner, 2003). Tree mortality,
125 deteriorating tree condition and an absence of natural regeneration has resulted in the local decline of
126 this globally unique vegetation community (Turner, 2003). This degradation is, at least in part, attributable
127 to reduced flooding as a result of past human modification of local watercourses, drainage and levee bank
128 construction (Greet, 2016; Harley, 2016). Forest restoration efforts are being undertaken within the
129 reserve as the last wild lowland population of the critically endangered Leadbeater's possum
130 (*Gymnobelideus leadbeateri*) is found within Yellingbo (Harley, 2016).



131

132 *Figure 2 E. camphora* (top row) and *M. squarrosa* (bottom row) stands in which coppicing was undertaken (A, D) and examples of
133 resprouting high coppice trees (B, E) and low coppice trees (C, F), photographed in late spring.

134

135 Our experiment was set up on the Macclesfield creek floodplain (Figure 1). Owing to poor condition and
136 growth form (i.e. small, upright, slender stems, Figure 2 A, D) the present vegetation structure consisting
137 of mostly even-aged trees does not support Leadbeater’s Possum foraging, moving and nesting (Greet *et*
138 *al.*, 2020b). Coppicing is a potential yet untested means to arrest further riparian swamp forest
139 degradation and promote its recovery. Our two study species are broad-leafed, evergreen, flood-tolerant,
140 woody species, pivotal to the overall physical structure of these swamp forests. *Eucalyptus camphora*
141 R.T.Baker is the sole canopy species in this vegetation community. *Melaleuca squarrosa* Donn. ex Sm.
142 (together with *Leptospermum lanigerum* (Aiton) Sm.) dominates the midstorey.

143

144 *Tree selection*

145 Trees selected for the experiment were scattered over the Macclesfield creek floodplain over an area of
146 ca. 2.4 ha so we could avoid clearing a larger forest patch (Figure 1). All trees were single-stemmed. *E.*
147 *camphora* had a mean diameter at breast height (DBH) of 11 cm (range 8–16 cm) and *M. squarrosa* had a
148 mean DBH of 9 cm (range 7–14 cm). Only subdominant trees were chosen for coppicing to prevent
149 substantial alteration of the canopy cover and therefore microclimate and light conditions at the tree
150 locations. Prior to the start of the experiment we assessed crown vigour, a proxy for tree condition, by
151 visually estimating the proportion of the potential crown supporting live foliage to the nearest 5%
152 (Cunningham *et al.*, 2007; Salter *et al.*, 2010). The mean crown vigor of the experimental trees was 50%
153 (range 30–70%) for both species.

154

155 *Experimental treatments*

156 We applied five treatments to 8 replicate trees per treatment of *E. camphora* and *M. squarrosa*: two
157 different cutting heights, two different cutting seasons [high autumn, low autumn, high spring, low spring]
158 and no cutting [control]. All coppice trees were randomly allocated to the four different coppice
159 treatments. Out of a total of 40 trees per species, 16 were cut at ground level (low) and 16 at height of
160 ~90 cm (high) using a chain saw (Figure 2 B, C, E, F). Half of these low and high coppiced trees were cut in
161 May 2018 (autumn) and the other half in October 2018 (spring). The remaining 8 trees per species were
162 left uncut as controls. To prevent browsing of emerging sprouts, all coppiced plants were guarded with
163 cylindrical guards ~90 cm in diameter and 1.8 m high made from chicken wire (5-cm mesh).

164

165 *Sampling protocol*

166 *Sprout measurements*

167 We regularly checked stumps for the onset of resprouting. Once the first shoots emerged (in week 19 of
168 the experiment in trees coppiced in autumn), the regrowth of shoots on all trees was monitored for one
169 growing season from October 2018 to June 2019. In weeks 19, 22, 26, 28, 32, 35, 49 and 52 of the
170 experiment we measured the length of the five longest resprouting shoots on each stump and calculated
171 the mean resprout length at each week (Spinelli *et al.*, 2017). At the conclusion of the experiment (52
172 weeks after first trees were coppiced in autumn) we also counted all living and dead shoots for each stump
173 and estimated shoot volume as a proxy of differences in shoot biomass between treatments. The
174 experimentally coppiced trees should improve the vegetation structure and habitat quality in the
175 Yellingbo Nature Conservation Reserve in the long term, thus, we were unable to perform a final,
176 destructive harvest for measuring shoot biomass. Hence, we measured the length and diameter at stem
177 base of the five longest shoots, which are a good indicator of coppice shoot biomass (Matula *et al.*, 2015).

178 Assuming a cone geometry for the shoots we used length and diameter measurements to calculate their
179 volume ($r^2 \times \pi \times \text{length}/3$).

180 Shoot growth can be influenced by light reaching the stump (Pelc *et al.*, 2011; Casals & Rios, 2018). To
181 account for different light availability during resprouting we estimated canopy openness for each stump
182 using hemispherical photography and image analysis. The photographs were taken on top of each stump
183 after trees had been cut and as such comprised shading by understory vegetation as well as the canopy.
184 The mean canopy openness was 27% (range 20–42%) for *E. camphora* and 26% (range 19–36%) for *M.*
185 *squarrosa*.

186

187 *Tissue sampling*

188 We sampled tissue from roots and stems (potential storage organs) to assess the carbon pool dynamics
189 following coppicing and during resprouting. Samples were taken four times: 1) in late autumn (early June
190 2018) prior to coppicing; 2) in spring (mid October 2018) when autumn coppice were still leafless and
191 prior to spring coppicing; 3) in early summer (mid December 2018) after shoots emerged from both
192 autumn and spring coppiced trees; and 4) in late autumn (early June 2019) at the end of the growing
193 season when shoots were expanded. This sampling schedule corresponds to week 0 (autumn and control
194 trees only), 19, 28 and 52 of the experiment. We assumed no differences in carbon pools between control
195 and spring coppice trees in week 0 and thus only sampled control and autumn coppice trees at that time.
196 Owing to the feasibility of the experiment and to reduce variability, we repeatedly sampled the same
197 individuals. Stem wood was sampled on high coppice and control trees after removing the bark by drilling
198 with a 4.5-mm drill 35 mm into the wood at a height of ~75 cm from two opposing sides (north and south)
199 and collecting the shavings. Root samples were taken on all trees by digging out a part of the root system
200 close to the stem and collecting tissue with the drill in the same manner. The drill was cleaned with a

201 sterilized cloth between samples. All tissues were immersed in liquid nitrogen directly after harvest and
202 subsequently kept at -80 °C until further processing to prevent enzymatic degradation of carbohydrates.
203 After being microwaved at 800 W for three minutes tissue samples were dried and ground to fine powder
204 using a bead mill (TissueLyser II, Qiagen, Hilden, Germany).

205

206 *Chemical analysis*

207 Starch is the main non-structural carbohydrate compound from which carbon is remobilized to enable
208 resprouting (Smith *et al.*, 2018). Thus, we focused on tissue starch concentration to relate resprouting
209 response to carbon storage. Starch was extracted and quantified following a modified version of Arndt *et*
210 *al.* (2008), described in Smith *et al.* (2018). Samples were washed with ethanol to remove soluble sugars
211 and then dried before being incubated with α -amylase (Sigma A4551, Castle Hill, Australia) and
212 amyloglucosidase (Sigma 10,115) to enzymatically convert starch into glucose molecules. Subsequently,
213 sample solution was incubated with hexokinase and glucose 6-phosphate dehydrogenase (Sigma G3293)
214 to convert glucose into glucose 6-phosphate and into 6-phosphogluconate. In the latter reaction oxidized
215 NAD (nicotinamide adenine dinucleotide) is reduced to NADH. The resulting change in absorbance at 340
216 nm is equivalent to the glucose concentration in the sample and was measured using a microplate
217 spectrophotometer (Multiskan GO, Thermo Fisher Scientific, Melbourne, Australia). We used a standard
218 curve (derived for each microplate) to calculate sample glucose concentration and expressed it as mg per
219 g dry weight. Each plate also included an internal lab starch standard to check for consistency of enzymatic
220 activity (Smith *et al.*, 2018).

221

222 *Statistical analysis*

223 We performed statistical analysis for each species separately.

224 Firstly, we evaluated if resprouting response (shoot growth, shoot number, shoot volume) differed
225 between treatments (Q1). Using the *lme4* package (Bates *et al.*, 2015), we fitted gaussian linear mixed
226 effect models to assess the difference in shoot length between treatments and over time (shoot growth).
227 The interaction between cut height, cut season and time (week of experiment) were modelled as fixed
228 factors and tree was included as random factor. Further, we fitted two simple linear models to test for
229 differences in the final shoot number and the final shoot volume, respectively, between cut-height and
230 cut-season treatments. Shoot volume (cm³) was $\ln(x + 1)$ transformed and shoot number was $\ln(x + 10)$
231 transformed to meet model assumptions of normality of residuals. Post-hoc contrasts between
232 treatments were performed with a Tukey correction for multiple comparisons using the *emmeans*
233 package (Lenth, 2021). Since there was no interaction between cut height and cut season (high autumn,
234 low autumn, high spring, low spring) in any model, we assessed the difference in shoot growth, shoot
235 number and shoot volume between cut height (low, high) and cut season (autumn, spring) separately.

236 We performed additional regression analysis to test the effect of coppicing treatment on starch
237 concentration in different tree organs (root and stem) (Q1). Using the *glmmTMB* package (Brooks *et al.*,
238 2017), we fitted generalized linear mixed models separately for roots and stems to assess differences in
239 starch concentration between treatments and over time. A single treatment effect with five levels (low-
240 autumn, low-spring, high-autumn, high-spring, and control) was used instead of separate height and
241 season effects because there was only a single control treatment that was not crossed with height and
242 season treatments. All starch concentrations were square-root transformed to meet model assumptions.
243 Treatment and its interaction with time (week of experiment) were modelled as fixed factors and tree was
244 included as random factor. Only weeks 19, 28 and 52 were included in the models where data was
245 available for all five treatments (starch concentrations in week 0 were only measured in autumn coppice
246 and control trees). Surprisingly, by visual assessment, starch concentrations in *E. camphora* stems differed

247 in week 0 between the control and high autumn coppice trees (Figure 3 C). Therefore, we fitted one
248 additional model including all experimental weeks (0, 19, 28, 52) and control and high autumn coppice
249 treatment to assess whether the initial differences between stem starch concentrations were significant,
250 but they were not. Post-hoc contrasts between treatments were performed using the *emmeans* package
251 (Lenth, 2021).

252 We tested if starch concentrations at the start of resprouting (week 19) and after resprouting (week 52)
253 were related to final shoot volume (Q2). Therefore, we fitted simple linear models (separately for each
254 tree organ) with starch concentration in week 19 and in week 52, respectively, as the predictor variable
255 and shoot volume as the response variable. Treatment was initially included as an interaction term but
256 was removed as the interaction between treatment and starch concentration was not significant. Shoot
257 volume (cm³) was $\ln(x + 1)$ transformed and starch concentrations were square root transformed to
258 reduce leverage of high values, and to be consistent with earlier analyses.

259 Finally, we tested if tree size, tree condition and light availability influenced coppice resprouting (Q2), as
260 tree factors and growth conditions may affect resprouting. To do this, we fitted general linear models with
261 crown extent, DBH and canopy openness as predictor variables and shoot volume ($\ln(x+1)$ transformed)
262 as the response variable.

263 All statistical analysis was performed in R version 3.5.0. (R Development Core Team, 2018). Differences
264 were inferred if $P < 0.05$.

265 **3. Results**

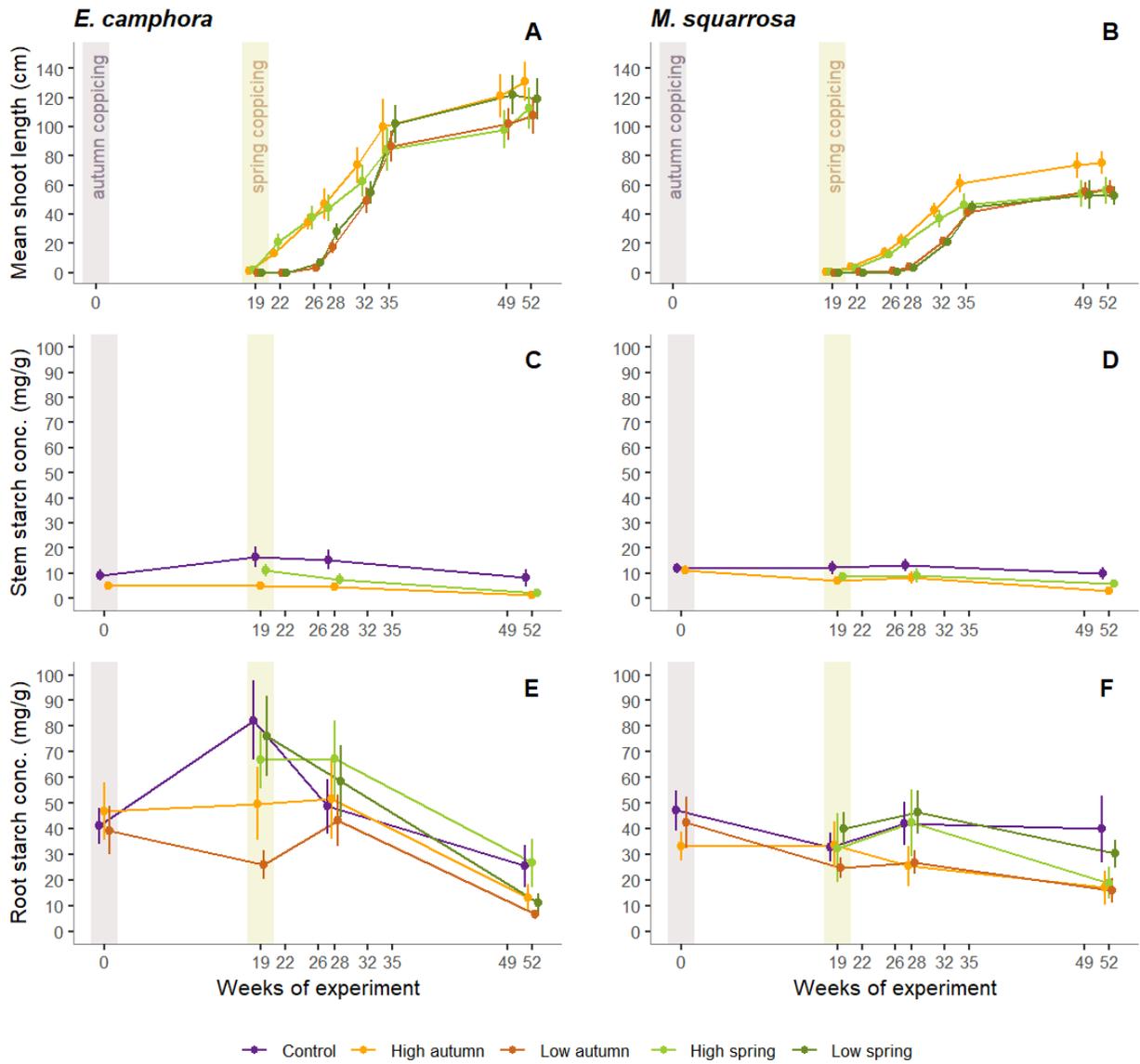
266 *Treatment effects on resprouting (Q1)*

267 *Shoot production*

268 All 64 coppiced trees except one *M. squarrosa* tree in the low autumn treatment resprouted. For both
269 species, autumn coppice remained leafless for ~19 weeks before resprouting and shoots became readily
270 apparent shortly after the spring coppice treatment was applied (Week 22). Spring coppice resprouted in
271 3–6 weeks (Week 26-28).

272 In *E. camphora* spring coppice shoots grew faster than those of trees coppiced in autumn. Shoot lengths
273 were significantly longer in autumn coppice trees than in spring coppice trees in weeks 26 (mean shoot
274 length \pm SE of 36 ± 5 cm versus 5 ± 1 cm) and week 28 (mean shoot length of 46 ± 7 cm versus 23 ± 4 cm),
275 but not thereafter (Figure 3 A, Appendix 1 Table A1). Shoot growth did not differ between high and low
276 coppice at any time in *E. camphora* (Appendix 1 Table A1).

277 In *M. squarrosa* autumn coppice trees had longer shoots than spring coppice trees from week 26 onward
278 (autumn shoots were 9–19 cm longer than spring shoots) (Figure 3 B, Appendix 1 Table A1). This difference
279 between autumn and spring coppice was significant in weeks 26, 28, 32, 35 and 52 but not in week 49
280 (Appendix 1 Table A1). *M. squarrosa* shoots of high coppice were significantly longer than those of low
281 coppice in the later weeks (mean shoot length of 65 ± 6 cm versus 54 ± 7 cm in week 49 and mean shoot
282 length of 66 ± 5 cm versus 54 ± 5 cm in week 52). In both species, resprout growth slowed in all treatments
283 after week 35.



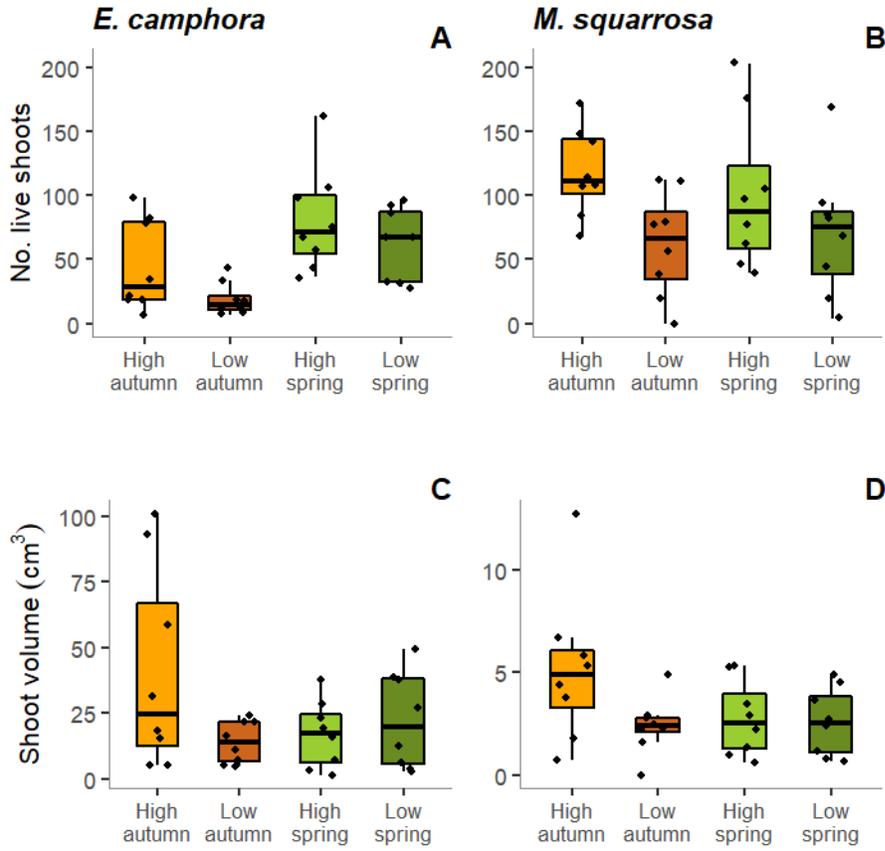
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286 *Figure 3 Mean length of the five longest shoots (means ± SE of raw data) (A, B) for trees of the four coppice treatments (n=8) and*
 287 *starch concentrations in stems (C,D) and roots (E,F) for both study species. Means ± SE of raw data presented for each of five*
 288 *different coppicing treatments (control, high autumn, low autumn, high spring, low spring). Note figures for mean resprout length*
 289 *(A, B) show raw data for crossed treatments whereas statistical analysis was performed with cut height and cut season as separate*
 290 *factors. Statistical analysis on starch concentrations (C, D, E, F) were performed on square root transformed data for crossed*
 291 *treatments. Note that low coppice treatments did not have stems and starch concentrations in week 0 were only measured on*

292 *autumn coppice and control trees. Points for each treatment have been slightly shifted horizontally to avoid overlapping of*
293 *confidence interval lines. Gray and beige shading indicate time of autumn and spring coppice treatment application, respectively.*

294

295 Generally, coppiced *M. squarrosa* tended to produce more shoots than coppiced *E. camphora* but *E.*
296 *camphora* shoot volume was on average ~5 times greater than that of *M. squarrosa* (Figure 4). In both
297 species high coppice trees had significantly more alive shoots than low coppice trees (mean of 63 versus
298 41 shoots in *E. camphora* and mean of 109 versus 66 shoots in *M. squarrosa* high and low coppice,
299 respectively) at the end of the experiment (week 52) and in *E. camphora* spring coppice trees had
300 significantly more alive shoots than autumn coppice trees (mean of 72 versus 32 shots) (Figure 4 A, B;
301 Appendix 2 Table A2). Shoot volume at the end of the experiment did not differ between high and low or
302 between spring and autumn coppice in either species (Figure 4 C, D; Appendix 2 Table A2). However, on
303 average, high autumn coppice trees produced the highest shoot volume (Figure 4 C, D).



304

305 *Figure 4* Boxplots of number of live shoots (A, B) and shoot volume (C, D) for trees in four different coppice treatments (n=8) for
 306 the two study species. Points indicate raw data. No. = number. Note figures show raw data for crossed treatments whereas
 307 statistical analysis was performed on log transformed data with cut height and cut season as separate factors. Note the
 308 different scales on the y-axis in C and D.

309

310 *Starch concentrations*

311 In both species starch concentrations were higher in roots (~4 times) than in stems (Fig. 3C vs 3E, 3D vs
 312 3F). Starch dynamics within a year, as observed in control trees across the 52 weeks of the experiment,
 313 differed between the study species. In control trees of *E. camphora* starch concentrations of both stems
 314 and roots increased during winter between week 0 and week 19 of the experiment and subsequently

315 decreased over spring and summer between week 19 and week 52 of the experiment (Figure 3 C, E).
316 Starch concentration dynamics in all treatments of *M. squarrosa* were less pronounced and remained
317 relatively stable throughout the year (Figure 3 D, F).

318 Coppicing treatment affected the starch concentrations in autumn coppice trees in *E. camphora*. Stem
319 starch concentrations in trees coppiced in autumn (high autumn treatment) were significantly lower than
320 control trees: at week 19 prior to the onset of resprouting; at week 28 during resprouting; and at week 52
321 after resprouting (Figure 3 C; Appendix 3 Table A3). Likewise, the starch concentrations in roots of low
322 autumn coppice trees were significantly lower than those in uncoppiced trees (control and low spring but
323 not high spring and high autumn) at week 19 at the time of spring coppice implementation, prior to the
324 onset of resprouting (Figure 3 E; Appendix 3 Table A3).

325 In *M. squarrosa*, stem starch concentrations of autumn coppice trees were significantly lower than those
326 of control trees at the end of the experiment in week 52 (Figure 3 D; Appendix 3 Table A3). There were
327 no significant differences in starch concentrations between treatments at any other time in *M. squarrosa*
328 (Appendix 3 Table A3).

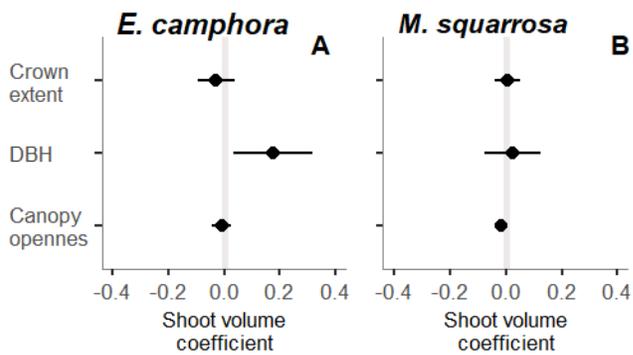
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330 *Importance of storage, tree factors and growth conditions for resprouting (Q2)*

331 The variability in final shoot volume was not explained by the starch concentrations in roots or stems in
332 week 19 (prior to resprouting) or week 52 (after resprouting) in either species (Appendix 4 Figure A1 A, B,
333 C, D; Appendix 5 Table A4).

334

335 Pre-coppice tree DBH had a significant positive effect on shoot volume in *E. camphora* but not *M.*
336 *squarrosa* (Figure 5 A, B). Pre-coppice tree crown extent or canopy openness did not affect final shoot
337 volume in either species.



338
339 *Figure 5 Coefficient estimates (±95% confidence intervals) of fixed effects (pre-coppice crown extent, pre-coppice DBH, canopy*
340 *openness) for shoot volume in week 52 of the experiment for both study species. DBH = diameter at breast height.*

341

342 **4. Discussion**

343 Both riparian tree species resprouted successfully after coppicing, regardless of coppice timing or severity.
344 Although coppice timing and height affected the availability and use of stored starch in some coppiced
345 trees, these treatments did not affect the shoot volume produced over the course of a year (Q1),
346 indicating that resprouting is not limited by resource storage (Q2). Our findings indicate that *E. camphora*
347 and *M. squarrosa* can regenerate vegetatively following physical disturbance such that coppicing may
348 provide a practical means to promote riparian forest regeneration.

349 As observed in other temperate, evergreen trees, resprouting coincided with seasonal growth flushes
350 rather than subsequent to disturbance via coppicing (Smith *et al.*, 2018). Although evergreen trees have
351 the potential to grow all year (Griebel *et al.*, 2017), bud burst in temperate climates typically requires
352 seasonal environmental stimuli, for example increases in temperature or solar radiation (Klimešová &
353 Klimeš, 2007; Masaka *et al.*, 2015). Therefore, the autumn coppice trees were dormant and remained
354 leafless for ~19 weeks. Spring conditions (i.e. warmer temperatures and moist, but well aerated, soils after
355 flood recession) were favorable for resprout emergence and growth. As such, spring coppice trees
356 resprouted relatively quickly after cutting (within ~3 weeks) and resprouted more vigorously (i.e. shoots
357 grew faster) than trees coppiced in autumn.

358 Coppice timing did not affect the shoot volume of resprouts which was produced by our study species at
359 week 52. In contrast, resprout biomass has been shown to vary with coppice timing in other species,
360 which can be attributed to the extent of seasonal fluctuation of resources stored within stumps and roots,
361 which can be crucial for resprouting success (Wildy & Pate, 2002; Pelc *et al.*, 2011; Hmielowski *et al.*,
362 2014). Only one of our study species, *E. camphora*, displayed substantial seasonal variation of starch
363 concentrations between the two coppice times in autumn and spring. Starch concentrations increased
364 considerably in roots and stems of control *E. camphora* trees over winter. Typically, winter flooding occurs

365 in our study area and *E. camphora* ceases shoot expansion when flooded (Fischer *et al.*, 2021b). Since *E.*
366 *camphora* is flood tolerant, and photosynthesis likely did not cease in the evergreen tree, the slow growth
367 in winter might have allowed plants to accumulate starch in storage pools. *M. squarrosa*, in contrast,
368 maintains growth during flooding in winter and thus may not prioritize starch storage formation, which
369 might explain why starch concentrations remained relatively stable.

370 Coppicing altered storage use as the starch dynamics in coppiced trees differed from those of control
371 trees during the leafless period. Unlike in uncoppiced *E. camphora* trees, starch decreased in roots of low
372 coppiced trees and starch did not accumulate in stems of high-coppiced trees. Starch was also depleted
373 in stems of autumn-coppiced *M. squarrosa* over winter, however not to significantly lower levels than in
374 control trees. Stored starch was likely consumed for tissue maintenance respiration in coppiced trees
375 while carbon assimilation remained absent (Smith *et al.*, 2018).

376 There was no relationship between stem/root starch concentrations and the shoot volume in our study
377 species. In contrast, trees in other ecosystems have been shown to either not survive or resprout poorly
378 when coppiced or disturbed at a time of low carbon storage levels (e.g. after drought or at the end of the
379 growing season) (Von Fircks & Sennerby-Forsse, 1998; Hmielowski *et al.*, 2014). Among all treatments
380 high autumn coppice would have had the highest starch demands since these trees had a larger biomass
381 to maintain than low coppice and for an extended period without photosynthetic input, unlike spring
382 coppice. The fact that the high-autumn treatment also produced the highest shoot volume in both species
383 provides further evidence that starch reserves are not limiting for resprouting, potentially because starch
384 is stored in excess (Cruz *et al.*, 2003; Moreira *et al.*, 2012; Wiley *et al.*, 2019). Stored reserves in riparian
385 trees may satisfy the demands for both maintaining biomass after disturbance and for restoring biomass.

386 The high site productivity (i.e. nutrient richness, moisture availability) of riparian zones (Naiman and &
387 Decamps, 1997) might have been conducive for resprout growth (Clarke *et al.*, 2005) and thus alleviated

388 coppiced trees' dependency on stored resources for resprouting. Unlike temperate *Eucalyptus* growing in
389 upland areas, riparian species seem not to experience drought stress during dry summer months which
390 induces a storage depletion (Smith *et al.*, 2018). Root groundwater access might have allowed for
391 continued photosynthesis throughout the resprouting period. Being photosynthetically active, newly
392 formed shoots likely self-supported their own growth with freshly assimilated carbon (Landhäusser, 2011;
393 Wiley *et al.*, 2019). Light conditions, a key determinant for photosynthesis, can be highly influential on
394 resprouting responses in trees (Pelc *et al.*, 2011; Casals & Rios, 2018). In our study canopy openness was
395 not related to the shoot volume of resprouting trees, which suggests similar light availability across our
396 experimental trees. This is not surprising given all experimental trees were subdominant.

397 Stem diameter can influence resprouting response (Matula *et al.*, 2019; Zhang *et al.*, 2021) and accordingly
398 we found larger diameter *E. camphora* stumps to produce a higher shoot volume. Given the absence of a
399 correlation between resource availability and resprouting in this study, higher shoot volume in larger trees
400 or stumps might have been due to better moisture and nutrient access because of larger root systems,
401 rather than due to a greater amount of stored reserves.

402 Where stems remained, below and above ground starch reserves were reduced following coppicing in our
403 study trees. Storage and remobilization of stem resources is common in trees which resprout
404 epicormically after disturbance which leaves stems intact (Clarke *et al.*, 2013). The fact that root starch
405 depletion and shoot volume did not differ between high and low coppice implies that the presence of
406 stems and the availability of stored starch therein does not translate into better resprouting. The overall
407 higher starch depletion (in roots and stems combined) of high coppice trees indicates that their higher
408 biomass entails higher maintenance cost which in turn requires more starch remobilization (Salomón *et*
409 *al.*, 2018; Smith *et al.*, 2018).

410 The ability to resprout from stems and to remobilize stored stem resources mirrors allocation patterns
411 from other disturbance prone ecosystems where stems are retained (Nzunda *et al.*, 2008; Franklin *et al.*,
412 2010; Smith *et al.*, 2018). Where disturbance types and severities vary the diversification of storage across
413 above and belowground organs may allow for flexible response to disturbance (Nzunda *et al.*, 2008;
414 Franklin *et al.*, 2010). Coppicing poses a more severe disturbance than damage from seasonal flooding.
415 The ability to resprout both epicormically and from stumps indicates that resprouting is not purely an
416 adaptation to regular flooding, but rather that these riparian trees are well equipped to survive more
417 destructive disturbance such as fire, which also occurs at our study site (Pearce, 2000).

418 Physical disturbance has the potential to promote tree longevity by inducing rejuvenation and reversing
419 senescence. Since human impacts often reduce or eliminate flooding in riparian ecosystems (Kingsford,
420 2000; Grill *et al.*, 2019), coppicing may help to preserve native tree species at degraded sites which no
421 longer support recruitment (i.e. natural regeneration from seed). Altered flooding regimes can preclude
422 germination and establishment of riparian trees due to altered dispersal vectors, increased understory
423 competition and lack of soil moisture (Fischer *et al.*, 2021b; Greet *et al.*, 2022). Besides, deteriorated
424 health of adult trees, caused by inadequate flooding regimes, can reduce the production and release of
425 seeds (Jensen *et al.*, 2008; Greet *et al.*, 2022). Our study suggests that reduced tree condition does not,
426 however, impair the ability of trees to regenerate vegetatively following disturbance by coppicing.
427 Coppiced trees are likely also less vulnerable to environmental stresses (e.g. water limitation) than tree
428 seedlings and thus require less specific site conditions, which highlights the advantage of coppice
429 management (Pietras *et al.*, 2016). However, the long-term development of coppiced riparian trees
430 (including potential consequences for genetic diversity of forest stands) requires further investigation.

431

432 5. Conclusion

433 Given the good ability of *E. camphora* and *M. squarrosa* to resprout regardless of coppice timing and
434 severity, it is more likely that their mortality will occur sooner due to the absence rather than the
435 occurrence of physical disturbance. Coppicing alters tree architecture, changes tree physiology and
436 increases tree growth rates (Drake *et al.*, 2009; Nolan *et al.*, 2014). Therefore, trees may be better suited
437 for persisting at a site which has undergone degradation if they are coppiced rather than left untreated.
438 Nonetheless, stress and disturbance history as well as tree phenology should be considered when
439 undertaking coppicing. Based on our observations, coppicing of temperate evergreen riparian trees may
440 be undertaken in autumn or spring. Coppicing immediately before the seasonal growth flush may be
441 favorable as trees are less likely to deplete their carbon storage, which will increase resilience to potential
442 subsequent disturbances or stress such as browsing, drought or waterlogging. Cut height can be chosen
443 to optimize vegetation structure outcomes. For example, coppicing at greater height will potentially
444 reduce browsing of new shoots which often emerge on the upper parts of the remaining stem (Pyttel *et*
445 *al.*, 2013; Smith *et al.*, 2018) and thus potentially out of reach of browsers. Coppicing at ground level, in
446 contrast, leads to basal resprouting which more likely results in multi-stemmed trees. Regardless of cut
447 height, coppiced trees within existing, even-aged forest stands may then form an additional forest storey
448 and increase structural complexity and vegetation density.

449

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461 **References**

- 462 **Arndt SK, Livesley SJ, Merchant A, Bleby TM, Grierson PF. 2008.** Quercitol and osmotic adaptation of
 463 field-grown Eucalyptus under seasonal drought stress. *Plant, cell & environment* **31**(7): 915-924.
- 464 **Bates D, Mächler M, Bolker B, Walker S. 2015.** Fitting Linear Mixed-Effects Models Using lme4. *Journal*
 465 *of Statistical Software* **67**(1): 1-48.
- 466 **Bell TL, Ojeda F. 1999.** Underground starch storage in *Erica* species of the Cape Floristic Region–
 467 differences between seeders and resprouters. *The New Phytologist* **144**(1): 143-152.
- 468 **Bond WJ, Midgley JJ. 2001.** Ecology of sprouting in woody plants: the persistence niche. *Trends in*
 469 *ecology & evolution* **16**(1): 45-51.
- 470 **Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Machler M,**
 471 **Bolker BM. 2017.** glmmTMB balances speed and flexibility among packages for zero-inflated
 472 generalized linear mixed modeling. *The R journal* **9**(2): 378-400.
- 473 **Casals P, Rios A. 2018.** Burning intensity and low light availability reduce resprouting ability and vigor of
 474 *Buxus sempervirens* L. after clearing. *Science of the Total Environment* **627**: 403-416.
- 475 **Chen Z, Wang L, Dai Y, Wan X, Liu S. 2017.** Phenology-dependent variation in the non-structural
 476 carbohydrates of broadleaf evergreen species plays an important role in determining tolerance
 477 to defoliation (or herbivory). *Scientific Reports* **7**(1): 10125.
- 478 **Clarke PJ, Knox KJ, Wills KE, Campbell M. 2005.** Landscape patterns of woody plant response to crown
 479 fire: disturbance and productivity influence sprouting ability. *Journal of Ecology* **93**(3): 544-555.
- 480 **Clarke PJ, Lawes M, Midgley J, Lamont B, Ojeda F, Burrows G, Enright N, Knox K. 2013.** Resprouting as
 481 a key functional trait: how buds, protection and resources drive persistence after fire. *New*
 482 *Phytologist* **197**(1): 19-35.
- 483 **Cruz A, Pérez B, Moreno JM. 2003.** Plant stored reserves do not drive resprouting of the lignotuberous
 484 shrub *Erica australis*. *New Phytologist* **157**(2): 251-261.
- 485 **Cunningham SC, Read J, Baker PJ, Mac Nally R. 2007.** Quantitative assessment of stand condition and
 486 its relationship to physiological stress in stands of *Eucalyptus camaldulensis* (Myrtaceae).
 487 *Australian Journal of Botany* **55**(7): 692-699.
- 488 **Dale VH, Joyce LA, McNulty S, Neilson RP, Ayres MP, Flannigan MD, Hanson PJ, Irland LC, Lugo AE,**
 489 **Peterson CJ, et al. 2001.** Climate Change and Forest Disturbances: Climate change can affect
 490 forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced
 491 species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides.
 492 *BioScience* **51**(9): 723-734.
- 493 **Del Tredici P. 2001.** Sprouting in temperate trees: a morphological and ecological review. *The botanical*
 494 *review* **67**(2): 121-140.
- 495 **Dey DC, Knapp BO, Battaglia MA, Deal RL, Hart JL, O'Hara KL, Schweitzer CJ, Schuler TM. 2019.** Barriers
 496 to natural regeneration in temperate forests across the USA. *New Forests* **50**(1): 11-40.
- 497 **Dietze MC, Sala A, Carbone MS, Czimczik CI, Mantooth JA, Richardson AD, Vargas R. 2014.**
 498 Nonstructural carbon in woody plants. *Annual review of plant biology* **65**: 667-687.
- 499 **Drake PL, Mendham DS, White DA, Ogden GN. 2009.** A comparison of growth, photosynthetic capacity
 500 and water stress in *Eucalyptus globulus* coppice regrowth and seedlings during early
 501 development. *Tree Physiology* **29**(5): 663-674.
- 502 **Fischer S, Greet J, Walsh CJ, Catford JA. 2021a.** Flood disturbance affects morphology and reproduction
 503 of woody riparian plants. *Scientific Reports* **11**(1): 16477.
- 504 **Fischer S, Greet J, Walsh CJ, Catford JA. 2021b.** Restored river-floodplain connectivity promotes woody
 505 plant establishment. *Forest Ecology and Management* **493**: 119264.

506 **Foard M, Burnette DJ, Burge DR, Marsico TD. 2016.** Influence of river channelization and the invasive
507 shrub, *Ligustrum sinense*, on oak (*Quercus* spp.) growth rates in bottomland hardwood forests.
508 *Applied Vegetation Science* **19**(3): 401-412.

509 **Franklin DC, Gunton RM, Schatz J, Lawes MJ. 2010.** Resprouting responses of trees in a fire-prone
510 tropical savanna following severe tornado damage. *Austral Ecology* **35**(6): 685-694.

511 **Greet J. 2016.** The potential of soil seed banks of a eucalypt wetland forest to aid restoration. *Wetlands*
512 *Ecology and Management* **24**(5): 565-577.

513 **Greet J, Cousens RD, Webb J. 2013.** More exotic and fewer native plant species: riverine vegetation
514 patterns associated with altered seasonal flow patterns. *River Research and Applications* **29**(6):
515 686-706.

516 **Greet J, Ede F, Robertson D, McKendrick S. 2020a.** Should I plant or should I sow? Restoration outcomes
517 compared across seven riparian revegetation projects. *Ecological Management & Restoration*
518 **21**(1): 58-65.

519 **Greet J, Fischer S, Walsh CJ, Sammonds MJ, Catford JA. 2022.** Restored river-floodplain connectivity
520 promotes riparian tree maintenance and recruitment. *Forest Ecology and Management* **506**:
521 119952.

522 **Greet J, Harley D, Ashman K, Watchorn D, Duncan D. 2020b.** The vegetation structure and condition of
523 contracting lowland habitat for Leadbeater's possum (*Gymnobelideus leadbeateri*). *Australian*
524 *Mammalogy* **43**(3): 344-353.

525 **Griebel A, Bennett LT, Arndt SK. 2017.** Evergreen and ever growing—Stem and canopy growth dynamics
526 of a temperate eucalypt forest. *Forest Ecology and Management* **389**: 417-426.

527 **Grill G, Lehner B, Thieme M, Geenen B, Tickner D, Antonelli F, Babu S, Borrelli P, Cheng L, Crochetiere**
528 **H, et al. 2019.** Mapping the world's free-flowing rivers. *Nature* **569**(7755): 215-221.

529 **Harley D. 2016.** An overview of actions to conserve Leadbeater's Possum *Gymnobelideus leadbeateri*.
530 *The Victorian Naturalist* **133**(3): 85.

531 **Hmielowski TL, Robertson KM, Platt WJ. 2014.** Influence of season and method of topkill on resprouting
532 characteristics and biomass of *Quercus nigra* saplings from a southeastern US pine-grassland
533 ecosystem. *Plant Ecology* **215**(10): 1221-1231.

534 **Hoch G, Richter A, Körner C. 2003.** Non-structural carbon compounds in temperate forest trees. *Plant,*
535 *cell & environment* **26**(7): 1067-1081.

536 **Jensen AE, Walker KF, Paton DC. 2008.** The role of seedbanks in restoration of floodplain woodlands.
537 *River Research and Applications* **24**(5): 632-649.

538 **Kingsford RT. 2000.** Ecological impacts of dams, water diversions and river management on floodplain
539 wetlands in Australia. *Austral Ecology* **25**(2): 109-127.

540 **Klimešová J, Klimeš L. 2007.** Bud banks and their role in vegetative regeneration – A literature review
541 and proposal for simple classification and assessment. *Perspectives in Plant Ecology, Evolution*
542 *and Systematics* **8**(3): 115-129.

543 **Knox K, Clarke P. 2005.** Nutrient availability induces contrasting allocation and starch formation in
544 resprouting and obligate seeding shrubs. *Functional Ecology* **19**(4): 690-698.

545 **Kozlowski T. 1992.** Carbohydrate sources and sinks in woody plants. *The botanical review* **58**(2): 107-
546 222.

547 **Landhäuser SM. 2011.** Aspen shoots are carbon autonomous during bud break. *Trees* **25**(3): 531-536.

548 **Laub BG, Detlor J, Keller DL. 2020.** Determining factors of cottonwood planting survival in a desert river
549 restoration project. *Restoration ecology* **28**: A24-A34.

550 **Lenth RV 2021.** emmeans: Estimated marginal means, aka leastsquares means (R package version 1.6.0).
551 <https://CRAN.R-project.org/package=emmeans>

552 **Masaka K, Torita H, Kon H, Fukuchi M. 2015.** Seasonality of sprouting in the exotic tree *Robinia*
553 *pseudoacacia* L. in Hokkaido, northern Japan. *Journal of Forest Research* **20**(4): 386-395.

554 **Matula R, Damborská L, Nečasová M, Geršl M, Šrámek M. 2015.** Measuring biomass and carbon stock
555 in resprouting woody plants. *PloS one* **10**(2): e0118388-e0118388.

556 **Matula R, Šrámek M, Kvasnica J, Uherková B, Slepíčka J, Matoušková M, Kutchartt E, Svátek M. 2019.**
557 Pre-disturbance tree size, sprouting vigour and competition drive the survival and growth of
558 resprouting trees. *Forest Ecology and Management* **446**: 71-79.

559 **Meier AR, Saunders MR, Michler CH. 2012.** Epicormic buds in trees: a review of bud establishment,
560 development and dormancy release. *Tree Physiology* **32**(5): 565-584.

561 **Miller RG, Tangney R, Enright NJ, Fontaine JB, Merritt DJ, Ooi MK, Ruthrof KX, Miller BP. 2019.**
562 Mechanisms of fire seasonality effects on plant populations. *Trends in ecology & evolution*
563 **34**(12): 1104-1117.

564 **Miranda JC, Rodríguez-Calcerrada J, Pita P, Saurer M, Oleksyn J, Gil L. 2020.** Carbohydrate dynamics in
565 a resprouting species after severe aboveground perturbations. *European Journal of Forest*
566 *Research* **139**: 841-852.

567 **Moreira B, Tormo J, Pausas JG. 2012.** To resprout or not to resprout: factors driving intraspecific
568 variability in resprouting. *Oikos* **121**(10): 1577-1584.

569 **Müllerova J, Szabo P, Hedl R. 2014.** The rise and fall of traditional forest management in southern
570 Moravia: a history of the past 700 years. *Forest Ecology and Management* **331**: 104-115.

571 **Myers JA, Kitajima K. 2007.** Carbohydrate storage enhances seedling shade and stress tolerance in a
572 neotropical forest. *Journal of Ecology* **95**(2): 383-395.

573 **Naiman and RJ, Decamps H. 1997.** The ecology of interfaces: riparian zones. *Annual review of Ecology*
574 *and Systematics* **28**(1): 621-658.

575 **Nolan RH, Mitchell PJ, Bradstock RA, Lane PN. 2014.** Structural adjustments in resprouting trees drive
576 differences in post-fire transpiration. *Tree Physiology* **34**(2): 123-136.

577 **Nzunda E, Griffiths M, Lawes M. 2008.** Sprouting by remobilization of above-ground resources ensures
578 persistence after disturbance of coastal dune forest trees. *Functional Ecology* **22**(4): 577-582.

579 **O'Briain R. 2019.** Climate change and European rivers: An eco-hydromorphological perspective.
580 *Ecohydrology* **12**(5): e2099.

581 **Pausas JG, Pratt RB, Keeley JE, Jacobsen AL, Ramirez AR, Vilagrosa A, Paula S, Kaneakua-Pia IN, Davis**
582 **SD. 2016.** Towards understanding resprouting at the global scale. *New Phytologist* **209**(3): 945-
583 954.

584 **Pearce J. 2000.** Mountain Swamp Gum *Eucalyptus camphora* at Yellingbo State Nature Reserve: Habitat
585 use by the endangered Helmeted Honeyeater *Lichenostomus melanops cassidix* and implications
586 for management. *Victorian Naturalist* **117**(3): 84-92.

587 **Peguero G, Espelta JM. 2011.** Disturbance intensity and seasonality affect the resprouting ability of the
588 neotropical dry-forest tree *Acacia pennatula*: do resources stored below-ground matter? *Journal*
589 *of tropical ecology* **27**(5): 539-546.

590 **Pelc BD, Montgomery RA, Reich PB. 2011.** Frequency and timing of stem removal influence *Corylus*
591 *americana* resprout vigor in oak savanna. *Forest Ecology and Management* **261**(1): 136-142.

592 **Pietras J, Stojanović M, Knott R, Pokorný R. 2016.** Oak sprouts grow better than seedlings under
593 drought stress. *iForest-Biogeosciences Forestry* **9**(4): 529.

594 **Pyttel PL, Fischer UF, Suchomel C, Gärtner SM, Bauhus J. 2013.** The effect of harvesting on stump
595 mortality and re-sprouting in aged oak coppice forests. *Forest Ecology and Management* **289**:
596 18-27.

597 **R Development Core Team 2018.** R: A language and environment for statistical computing. R
598 Foundation for Statistical Computing. Vienna, Austria.

599 **Salomón RL, Rodríguez-Calcerrada J, Gil L, Valbuena-Carabana M. 2018.** Respiratory costs of woody
600 tissues in a *Quercus pyrenaica* coppice. *iForest-Biogeosciences Forestry* **11**(3): 437.

601 **Salter J, Morris K, Read J, Boon PI. 2010.** Understanding the potential effects of water regime and
602 salinity on recruitment of *Melaleuca ericifolia* Sm. *Aquatic Botany* **92**(3): 200-206.

603 **Schweier J, Arranz C, Nock CA, Jaeger D, Scherer-Lorenzen M. 2019.** Impact of increased genotype or
604 species diversity in Short Rotation Coppice on biomass production and wood characteristics.
605 *BioEnergy Research* **12**(3): 497-508.

606 **Shibata R, Kurokawa H, Shibata M, Tanaka H, Iida S, Masaki T, Nakashizuka T. 2016.** Relationships
607 between resprouting ability, species traits and resource allocation patterns in woody species in a
608 temperate forest. *Functional Ecology* **30**(7): 1205-1215.

609 **Sjölund MJ, Jump AS. 2013.** The benefits and hazards of exploiting vegetative regeneration for forest
610 conservation management in a warming world. *Forestry* **86**(5): 503-513.

611 **Smith MG, Arndt SK, Miller RE, Kasel S, Bennett L. 2018.** Trees use more non-structural carbohydrate
612 reserves during epicormic than basal resprouting. *Tree Physiology* **38**(12): 1779-1791.

613 **Sommerfeld A, Senf C, Buma B, D'Amato AW, Després T, Díaz-Hormazábal I, Fraver S, Frelich LE,
614 Gutiérrez ÁG, Hart SJ, et al. 2018.** Patterns and drivers of recent disturbances across the
615 temperate forest biome. *Nature Communications* **9**(1): 4355.

616 **Spinelli R, Pari L, Aminti G, Magagnotti N, Giovannelli A. 2017.** Mortality, re-sprouting vigor and
617 physiology of coppice stumps after mechanized cutting. *Annals of Forest Science* **74**(1): 5.

618 **Stojanović M, Sánchez-Salguero R, Levanič T, Szatniewska J, Pokorný R, Linares JC. 2017.** Forecasting
619 tree growth in coppiced and high forests in the Czech Republic. The legacy of management
620 drives the coming *Quercus petraea* climate responses. *Forest Ecology and Management* **405**: 56-
621 68.

622 **Tockner K, Stanford JA. 2002.** Riverine flood plains: present state and future trends. *Environmental
623 conservation* **29**(3): 308-330.

624 **Tonkin JD, Merritt DM, Olden JD, Reynolds LV, Lytle DA. 2018.** Flow regime alteration degrades
625 ecological networks in riparian ecosystems. *Nature ecology & evolution* **2**(1): 86-93.

626 **Turnbull TL, Buckley TN, Barlow AM, Adams MA. 2014.** Anatomical and physiological regulation of post-
627 fire carbon and water exchange in canopies of two resprouting *Eucalyptus* species. *Oecologia*
628 **176**(2): 333-343.

629 **Turner V. 2003.** Action statement: Sedge-rich *Eucalyptis camphora* Swamp. *Report to the Department of
630 Sustainability and Environment, Aurthur Rylah Institute, Melbourne.*

631 **Von Fircks Y, Sennerby-Forsse L. 1998.** Seasonal fluctuations of starch in root and stem tissues of
632 coppiced *Salix viminalis* plants grown under two nitrogen regimes. *Tree Physiology* **18**(4): 243-
633 249.

634 **Wildy DT, Pate JS. 2002.** Quantifying above-and below-ground growth responses of the western
635 Australian oil mallee, *Eucalyptus kochii* subsp. *plenissima*, to contrasting decapitation regimes.
636 *Annals of Botany* **90**(2): 185-197.

637 **Wiley E, King CM, Landhäusser SM. 2019.** Identifying the relevant carbohydrate storage pools available
638 for remobilization in aspen roots. *Tree Physiology* **39**(7): 1109-1120.

639 **Wright BR, Clarke PJ. 2007.** Resprouting responses of *Acacia* shrubs in the Western Desert of Australia—
640 fire severity, interval and season influence survival. *International Journal of Wildland Fire* **16**(3):
641 317-323.

642 **Zhang T, Yan Q, Wang GG, Zhu J. 2021.** The effects of stump size and within-gap position on sprout non-
643 structural carbohydrates concentrations and regeneration in forest gaps vary among species
644 with different shade tolerances. *Ecological Processes* **10**(1): 1-14.

645